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Spatial ecology of the European adder (*Vipera berus*) in commercial forestry plantations

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James Thomas Stroud, BSc (Hons)

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Scarborough Campus

Spatial ecology of the European adder (*Vipera berus*) in commercial forestry plantations

James T. Stroud

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Supervisor: Dr Philip M. Wheeler

Abstract

Although the European adder (*Vipera berus*) is arguably the most studied terrestrial snake species in the world, little is known about the factors that influence its distribution across a landscape. One of the difficulties in assessing the pattern of a species distribution in a patchy landscape is that surveying is often limited to presence-absence data, and these raw data do not easily explain the processes behind the observed patterns. I employed patch occupancy methods to investigate the spatial ecology of adders in the highly spatially structured, dynamic landscape of commercial forestry plantations. Habitat factors hypothesised to influence adder presence were assessed at multiple spatial scales, while a multi-component analysis of habitat quality was carried out by investigating basking site availability, small mammal prey abundance, and potential predation pressure. Adders were observed to exhibit specific basking site microhabitat selection, however patch occupancy analysis suggested that detection probabilities vary with habitat, but occupancy did not, emphasising the importance of accounting for detection probability in distribution surveys of this species. Optimum adder habitat is increasingly being limited due to development, land use change and agricultural intensification. This research suggests that current plantation systems provide a suitable habitat matrix for adders, but that landscape-level management could increase population dispersal, and site-specific management would increase habitat suitability in occupied sites. Future reviews (e.g. Baker *et al*. 2006) and regional to national scale conservation plans should include plantation forests as important habitat for adders in the UK, and their viability as a potential conservation refuge for this species recognised.

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1.1 Introduction

The European adder (*Vipera berus*) is the most widely distributed, and arguably the most intensively-studied, terrestrial snake species in the world (Shine and Madsen 1994, Phelps 2004). While the ecology of the species is well studied, comparatively little is known about the factors that influence adder distribution across a landscape and key questions relevant to species management remain poorly investigated. Assessing the status of elusive species, such as adders, is often difficult because they may frequently be present at sites but remain undetected (Mackenzie 2005).

The current status of adders in Britain is unclear as there is no established monitoring method at either a local or national scale (e.g. see Reading and Davies 1996, Reading 1997 or Wilkinson and Arnell 2011). There have been suggestions that the species may be declining due to a loss of habitat, mainly from land use change and agricultural intensification (UK BAP 2009), although conservation habitat management could also be a factor (Wilkinson and Arnell 2011).

Habitat change, such as fragmentation, is widely acknowledged as the primary cause of the loss of global biodiversity (Sala et al. 2000). Although the effects are being widely researched in vertebrates, one group that is known to be particularly affected but has been relatively understudied is herpetofauna (Gardner et al. 2007). Herpetofauna, comprising of amphibians and reptiles, are currently classified as having the highest threat status of all terrestrial vertebrates (IUCN 2007) and are known to be

experiencing a global decline (Gibbons et al. 2000, Beebee and Griffiths 2005, Wake and Vredenburg 2008).

Habitat change is known to be particularly detrimental to herpetofauna populations (Alford and Richards 1999, Gibbons et al. 2000, Collins and Storfer 2003, Hazell 2003, Cushman 2006), with species acting as good indicators of terrestrial habitat quality due to their relatively low tolerance of ecological change (Wyman 1990, Thompson et al. 2008). Although studies on herpetofauna are becoming more common, detailed monitoring studies of single species are still rare. Exploring the spatial ecology of a single species allows more specific questions to be investigated about the factors that affect their distribution across different spatial scales.

The UK has only 12 native species of herpetofauna (Arnold 1995). Although local population studies are relatively common, little is known about the species' ability to adapt to habitat change at a large spatial scale. There is increasing evidence that many of these species are showing national declines (Baker et al. 2006, UK BAP 2009). The monitoring of herpetofaunal populations in human-influenced landscapes provides valuable information that can be used to model the effects of future habitat change.

Assessing the factors that affect the spatial distribution of herpetofauna in the UK provides key information for future management and conservation, as well as allowing recommendations to be formulated for similar ecological research.

*1.2 The European adder (*Vipera berus*)*

1.2.1 Introduction

The European adder (*Vipera berus*) is the most widespread terrestrial snake in the world, largely owing to its ability to surpass altitudinal, climatic and habitat restrictions of similar sympatric species (Nilson 1980, Gasc *et al*. 1997, Carlsson and Tegelström 2002, Carlsson 2003, Ursenbacher *et al*. 2006, Herczeg *et al*. 2007).

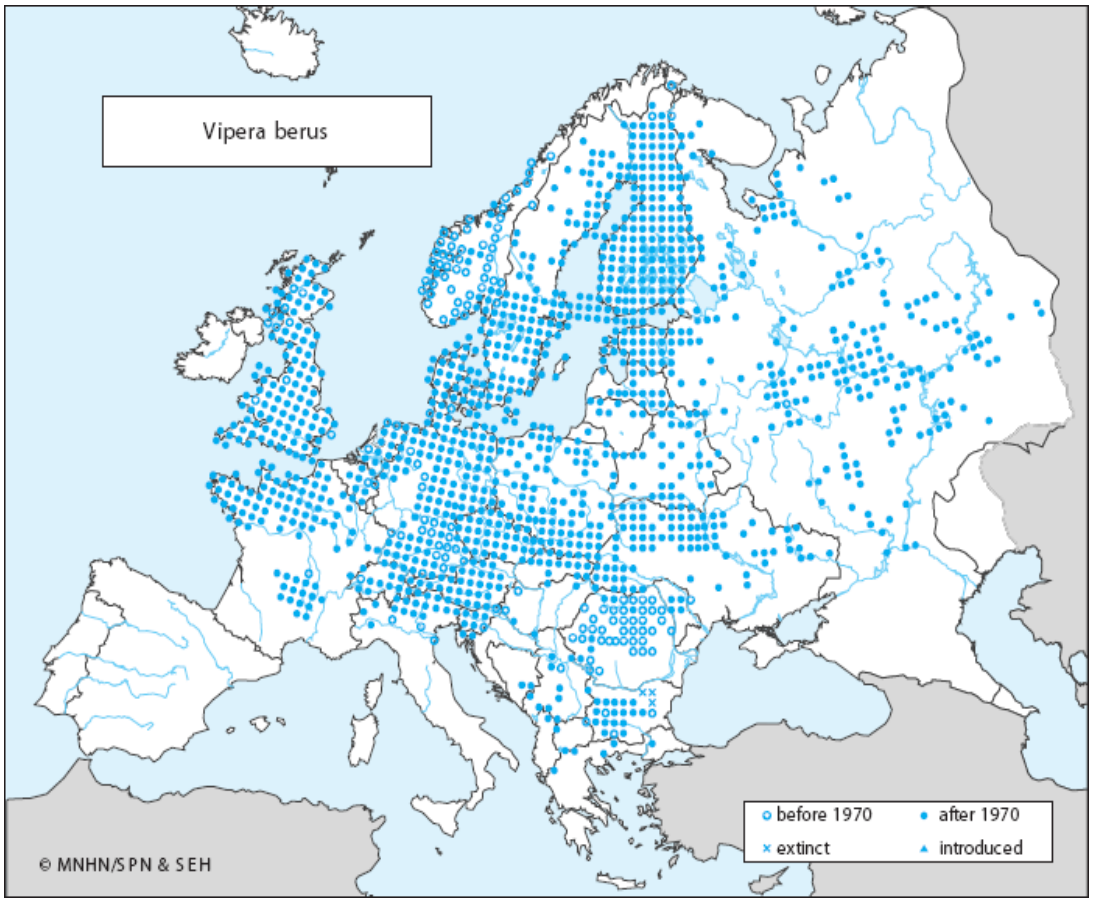
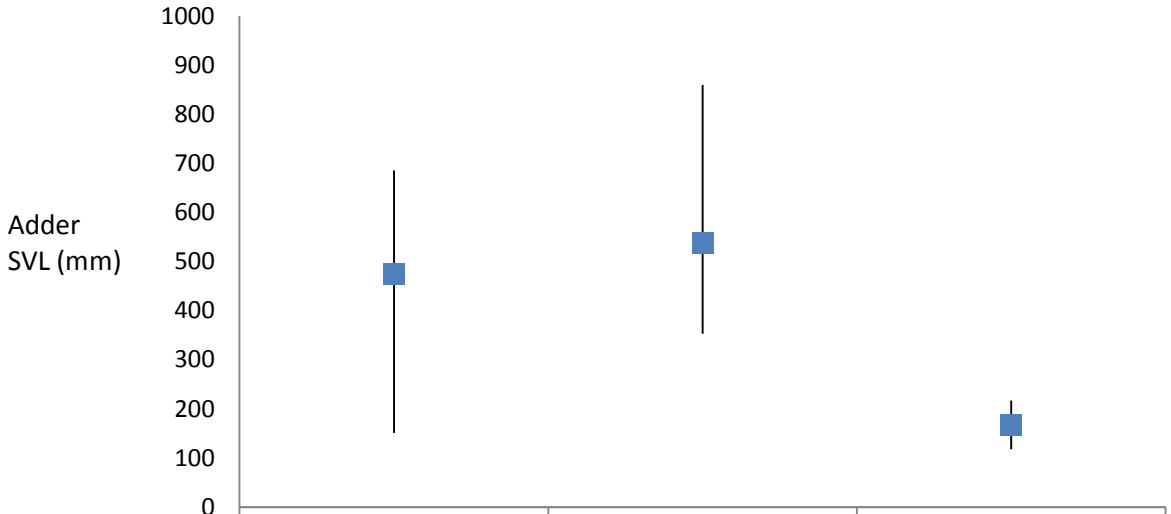


Figure 1.1. European distribution of *Vipera berus* from *The Atlas of Amphibians and Reptiles in Europe* (Gasc *et al*. 1997 (http://www.seh-herpetology.org). Each dot represents a 50 x 50 km UTM grid square. Copyright © Muséum National d'Histoire Naturelle & Service du Petrimone Naturel and Societas Europaea Herpetologica. Used with permission.

Adders have a wide but patchy range in the UK (Wilkinson and Arnell 2011). It has recently been added as a Priority Species to the UK BAP and is currently experiencing declines at both national and local levels (UK BAP 2009). Its range extends longitudinally from the Atlantic coasts of Western Europe (6° W)to the Pacific island of Sakhalin in eastern Siberia (143° E), latitudinally from the Arctic Circle in northern Scandinavia (69° N) to northern Albania (42° N), and up to 3000 metres in altitude in the Swiss Alps (Gasc *et al*. 1997, Carlsson 2003) (Figure 1.1).

1.2.2 Morphology and taxonomic status

The adder is a small-medium sized, ovoviviparous viper (Carlsson 2003, Figure 1.2). The family Viperidae, is classically subdivided into the 'pitvipers' (Crotalinae) and the 'true' old world vipers (Viperinae), of which the latter includes the nominate genus *Vipera* (Wüster *et al*. 2008). Average life span of adders is commonly accepted to be between 8-9 years (Madsen 1988, Capula and Luiselli 1994), although some studies have suggested this to be a very conservative estimate (Phelps 2004).



	Male	Female	Juveniles
Min	153	355	120
Max	684	858	215
Mean	475	538	167

Figure 1.2. Bars represent the minimum-maximum range of adder snout to vent lengths (SVL) gathered from a review of the literature (Appendices A-C), with averages indicated by blue squares

The adder is sexually dimorphic both in size and colour, with females being larger than males (Andren 1985, Shine and Madsen 1994). Males have a grey to black base colour, with a dark dorsal stripe; females have a tan to brown base colour, with a brown dorsal stripe (Forsman 1995). This form of sexual identification is extremely reliable for experienced surveyors. Juveniles have a typically brown-copper colour; however they are easily distinguishable from mature females by size (Figure 1.2). External morphology is relatively homogenous throughout much of the northern and eastern parts of their range, with morphological variations being highest in Central Europe and the Balkans (Carlsson 2003, Zinenko 2006). In Europe it occurs sympatrically with *Vipera aspis* (Ursenbacher *et al*. 2006), *V. nikolskii* (Zinenko 2006), *V. ammodytes* (Lapini 1983 cited in Luiselli 2006 mini review), *V. seoanei* (Kalyabina-Hauf *et al*. 2004) and *V. barani* (Joger *et al*. 1997).

The taxonomic status of the *V. berus* complex is well studied with three currently recognised subspecies; *V. b. berus* (Linnaeus 1758), *V. b. sachaliensis* (Zarevsky 1917) and *V. b. bosniensis* (Boettger 1880) (Franzen and Heckes 2000, in Kalyabina-Hauf *et al*. 2004). The nominate form is most widespread, with *V. b. bosniensis* occurring only on the Balkan peninsula and *V. b. sachaliensis* restricted to Sakhalin island and the extreme east of Russia (Joger *et al*. 1997).

1.2.3 UK reptiles and habitat associations

The adder is one of only three native snake species in the British Isles. Although it has the broadest distribution of all British reptiles, it remains patchy and highest densities are often associated with southern heathlands (Prestt 1971, Spellerberg 1975, Wilkinson and Arnell 2011). Of the other two species of snake only the smooth snake (*Coronella austriaca*) commonly overlaps habitat with the adder, however this species is restricted to dry lowland heath in southern England (Spellerberg and Phelps 1977, Phelps 1978, Table 1.1). The grass snake (*Natrix natrix*), although wide ranging, is commonly associated with marshland, deciduous woodland and hedgerows (Madsen 1984) where it's primary prey, amphibians, are common (Drobenkov 1995, Reading and Davies 1996).

Adders, a more philopatric species, require a sufficient habitat variability at a local scale to provide hibernating, basking and foraging sites as daily movement rates are low (Bruno 1985). Although adders are most closely associated with heathland, they are found in a variety of habitats throughout their range and could be considered a

true habitat generalist (Andren 1982, Andren and Nilson 1983, Forsman and Lindell 1991, Carlsson 2003, Thomas 2004, Kowalewski and Profus 2007), particularly in the UK (Prestt 1971, Reading *et al*. 1996, Reading 1997, Baker *et al*. 2006) (Table 1.1). Suitable protection from both predators and human harassment is needed within any potential habitat patch (Bruno 1985).

Habitat	No. adders
Other	1
Allotment	4
Bog/mire	10
Garden	12
Quarry	18
Dune/Coastal	18
Moor	20
Agriculatural	25
Coniferous woodland	34
Development	34
Deciduous woodland	57
Rough Grassland	59
Scrub	61
Heathland	88

Table 1.1 Number of adders reported to English Nature per habitat type during a questionnaire survey conducted in 2002 (data from Baker *et al*. 2006)

Woodland, both deciduous (Reading *et al.* 1996, Baker *et al*. 2006, Zinenko 2006, Kowalewski and Profus 2007) and coniferous (Forsman and Lindell 1991, Luiselli and Anibaldi 1991, Luiselli *et al.* 1995, Reading *et al.* 1996, Thomas 2004, Baker *et al*. 2006, Kowalewski and Profus 2007) can be suitable adder habitat. However, within these habitats adders have previously been observed to be restricted to margins, clearings and areas of low tree density (Thomas 2004).

1.2.4 The annual cycle

1.2.4.1 Spring – Emergence, basking and mating

Adders demonstrate seasonal behavior, classified into 3 active phases and an over-wintering hibernation period (Prestt 1971). Emergence from hibernation in spring is asynchronous, with males appearing earlier to begin pre-mating spermiogenesis (Nilson 1980, Herczeg *et al*. 2007). Emergence is triggered by ambient air temperature, usually upon reaching 3-5°C, although it can be altitude-dependent (Neumeyer 1987, Kowalewski and Profus 2007). Males remain close to hibernacula within this period and no feeding occurs (Prestt 1971). A synchronised male ecdysis triggered by female emergence up to 3 weeks later prompts an explosive period of mating activity in April-May (Viitanen 1967, Prestt 1971). Mating usually occurs close to the hibernation sites (Prestt 1971, Phelps 2004), although males will disperse to find females (Andren 1986, Madsen 1988, Forsman 1997).

Females remain relatively sedentary throughout this process (Prestt 1971). As a result of the high reproductive costs females operate on a biennial, or even triennial, breeding cycle (Prestt 1971, Carlsson 2003). Reproductive males mate annually, with sex ratios accordingly skewed towards them as they engage in combat bouts to determine the right to mate with individual females (Madsen 1988, Lindell *et al*. 1993, Olsson *et al*. 1997, Phelps 2004).

1.2.4.2 Summer – Dispersal and feeding

Dispersal from hibernation sites to separate summer feeding grounds is well documented and defines the second stage of the annual cycle (Viitanen 1967, Prestt 1971, Phelps 1978, 2004). In the UK, post-breeding dispersal occurs most commonly in late April-May. Feeding grounds are often bordering or within short dispersal distances of hibernation sites and frequently represent a shift in habitat type (Prestt 1971, Thomas 2004). Longer dispersal distances of up to 2km have been recorded rarely (Viitnanen 1967). Adders are generalist vertebrate predators, and often change diet according to resource availability (see Chapter 3 for a review). An ontogenetic shift from ecothermic to endothermic prey is recorded in other *Vipera* and is likely to also occur in *V. berus* (Luiselli and Agrimi 1991, Monney 1993, Luiselli *et al*. 1995).

1.2.4.3 Late Summer-Autumn – Birth of young and return to hibernacula

Females produce an average clutch size of 7 offspring (Prestt 1971, Madsen and Shine 1992, 1993, 1994), and litters with mixed paternity have been recorded (Stille *et al*. 1986, Höggren and Tegelström 1995). In the UK males are the first to return to hibernation sites as early as August. Breeding females do not begin to return until September to prolong the feeding period in an attempt to recoup energy lost during breeding (Prestt 1971). Hibernation for both sexes begins in September-October and can last for as long as 8 months (Carlsson 2003).

1.2.5 Current status

In Britain, the adder is currently only protected under the Wildlife and Countryside Act (1981), which outlawed killing, injuring, harming or selling of the species. Similar levels of protection are also given in Europe (e.g. Poland, Kowalewski and Profus 2007). The status of *V. berus* in Britain is unclear as no established protocol for monitoring at either a local or national scale currently exists. Due to its size and cryptic morphology, there has been no one reliable method of monitoring accepted by ecologists to reliably assess their distribution, though there are ongoing efforts to collect data on the distribution of this species (Wilkinson and Arnell 2011). The effect of habitat loss on adder populations, mainly from land use change and agricultural intensification, also remains unclear and could present a major obstacle in formulating an effective conservation plan.

1.3 Monitoring of snake populations: an introduction and a review of current methods

There are many reasons, relevant to modern society, why we need to monitor wildlife populations; ranging from management to business to ecological research (Witmer 2005). For example, there may be a particular interest in monitoring the status of an endangered or threatened species, or the progress of its recovery program (e.g. Campbell *et al.* 2002). Similarly if the species has already become locally extinct, assessment of the potential reintroduction of that species, or the introduction of another to the area, may be needed (e.g. Hirzel *et al.* 2004). The population could be an extant or potential pest species, posing a risk to agriculture, property, natural

resources or the transmission of human or livestock disease (e.g. Arbogast *et al.* 2000). From a commercial perspective, the population may be a valued game species, with monitoring essential for sustainable management (e.g. Williams *et al.* 2003). At a larger scale, there may be a need to record the biological diversity, or assess the 'ecological health', of an area, with long-term monitoring particularly valuable (e.g. Noss 1990). Most importantly, the reasons could be more practical; assessing how land-use management or human activities have an effect on the population of one or more species (e.g. White *et al.* 1997, Liu *et al.* 1999, Gardner *et al.* 2008).

Snake population monitoring projects employ a wide range of sampling methods dependent upon the aims of the research. Studies of the spatial ecology of single snake species are rare, with much monitoring research choosing to assess broader parameters (e.g. species richness – Soares and Brito 2007, species abundance – Herrera-Montas and Brokaw 2010, community composition – Wanger *et al.* 2010). When attempting to identify relationships between a species distribution and habitat characteristics the sampling method of choice will be an important factor. Surveying methods that can rapidly evaluate species distributions at a large spatial scale are particularly important to studies of spatial ecology, however many studies on snakes have relied on the time-costly method of radio telemetry (Whiting *et al.* 1997, Roth 2005, Kapfer *et al.* 2008).

A review of the literature highlighted the wide range of sampling techniques currently employed in snake research (Table 1.2), which range from the novel (e.g. tracking and

monitoring the warning calls of Sooty Mangabeys *Cercocebus torquatus atys* as an indication of *Bitis rhinoceros* presence – Penner *et al*. 2008) to better established methods (e.g. observational studies of known populations).

	All species	Viperidae	*Vipera berus*
Glue traps	1	0	0
Monkey tracking	1	1	0
Plots	1	0	0
Spotlight searches	2	0	0
Flap traps	4	0	0
Opportunistic	4	0	0
Time-constrained	4	0	0
Pitfall traps	10	0	0
Visual surveys	6	3	1
Funnel traps	12	1	1
Questionnaire	2	2	2
Roads	13	4	2
Coverboards	4	3	3
Transects	9	6	5
Capture-mark-recapture	31	30	25
Known population	39	36	28

Table 1.2. A review of the snake studies identifying the type of surveying method used to collect distribution data. The full table including references can be found in Appendix D

Although widely used in herpetofauna surveys, techniques that rely on species movements such as pitfall trapping, road surveys and funnel traps, are particularly unreliable for sedentary species such as the Viperidae. Due to their philopatric nature, the vast majority of ecological studies on adders have been conducted on known populations, which have been intensively studied, often through mark-recapture studies (Prestt 1971, Andren 1982, Forsman and As 1987, Neumeyer 1987, Madsen

1988, Madsen and Stille 1988, Sheldon and Bradley 1989, Forsman 1991, Forsman and Lindell 1991, Madsen and Shine 1992, Forsman 1993a, 1993b, Lindell *et al*. 1993, Luiselli 1993, Madsen and Shine 1993, Forsman *et al*. 1994, Madsen and Shine 1994, Luiselli *et al*. 1995, Lindell and Forsman 1996, Forsman and Lindell 1997, Olsson *et al*. 1997, Benson 1999, Madsen *et al*. 2004, Phelps 2004, Thomas 2004, Ursenbacher *et al*. 2008). Very few studies have identified reliable methods for monitoring a single species over a large spatial scale.

1.4 The development of patch occupancy modelling

A relatively new tool gaining popularity in wildlife population monitoring is patch occupancy analysis (POA). The value of occupancy data (i.e. recording of species presence or absence) was not widely acknowledged until the late 1990s, with research instead focussed more on the complex problems associated with estimating abundance, birth rates, survival probabilities and related demographic parameters using mark-recapture data (MacKenzie *et al*. 2006). POA was developed during research by the U.S. Geological Survey's Amphibian Research and Monitoring Initiative (ARMI), where difficulties soon became apparent in trying to estimate changes in abundance at a large spatial scale over time (MacKenzie *et al*. 2006). Instead the development of presence-absence surveys in a range of habitat patches, in this case ponds and wetlands for amphibians, was suggested. When asked if it was reasonable to assume that target species were always detectable within occupied habitat, statisticians were answered by field biologists with a resounding "No!", leading to an

increase in research focus on the formation of analytical methods to account for imperfect detection (MacKenzie *et al*. 2006).

The team behind ARMI first published their results in 2002, coining the term 'probability of area occupied' as the key population parameter to be estimated (MacKenzie *et al*. 2002). This led to a flurry of research by contributors within ARMI investigating analytical techniques attempting to reliably estimate occupancy, or changes in occupancy, with species that were often imperfectly detected (e.g. MacKenzie *et al*. 2003, 2004, Dorazio *et al*. 2005, MacKenzie and Royle 2005, Royle *et al*. 2005). However, it became apparent that the problems identified by the ARMI team were general ones in many species surveys as also highlighted by other research groups (e.g. Tyre *et al*. 2003, Stauffer *et al*. 2004).

There are several advantages to conducting research using patch occupancy methods. Primarily, as previous mentioned, it allows occupancy to be estimated while accounting for imperfect detection, but more practically, it also allows monitoring to occur at a large spatial scale with an associated low cost in time. The method of POA is particularly applicable to species that have multiple presence indicators, e.g. birds (visual and auditory – Castellon and Sieving 2006) or mammals (visual – individuals, tracks, droppings, and auditory – Lawes *et al.* 2000). Patch occupancy modelling continued to be widely employed in amphibian studies (e.g. see Pellet and Schmidt 2005, Schmidt and Pellet 2005, Weir *et al.* 2005), and is increasingly used in wider

herpetofaunal studies (e.g. Fischer *et* al. 2004), although it has not been widely employed in studies solely focussing on snake species (e.g. Luiselli 2006c).

1.5 Commercial plantations; history, extent and conservation value

The first records of production plantations in the UK stem from Elizabeth I's concern over the sustainability of naval timber, leading to the establishment of harvestable stands of *Quercus* (Savill *et al*. 1997). The establishment of native species on patches of historical woodland such as this dominated the extent of early plantations. However, towards the mid-19th century afforestation of bare land began to see the introduction of non-native trees, with a selection of original *Larix* and *Pinus* stands still existing in Scotland today. The increased employment of this plantation type has meant that many of the non-native conifer species used in British forestry today (e.g. *Picea abies* and *P. sitchensis*, *Pinus contorta*, and *Larix kaempferi*) were first established over 150 years ago (Savill *et al*. 1997).

In Britain, forests now cover 2.85 million hectares of land, accounting for 12% of total land use (Forestry Commission 2010). However, this also represents the smallest proportion of forested area per nation within the EU, where the average stands at 37% (Forestry Commission 2010). Globally, the conservation of forest biodiversity is considered a priority (Lindenmayer *et al*. 2006), and has become an integral part of both national (e.g. Montreal Process Liaison Office 2000) and international (e.g. Food and Agriculture Organisation of the United Nations 2001) forest management plans. Ferris *et al*. (2000) highlighted the commitment shown by the UK government to

conserving and enhancing biodiversity in all types of British woodland, with a clear initial proposal submitted to provide guidelines for biodiversity management and conservation in the UK Forestry Standard (Forestry Commission 2004).

Of particular interest is the 57.1% majority of British woodland (6.8% of total land use) that is represented by coniferous production forests (Forestry Commission 2010), which has only received secondary attention in comparison to native woodland (Ferris *et al*. 2000). Commercial forestry plantations are specifically managed for timber production, sustaining a mosaic of forest patches at different stages of their growth cycle.

One important consideration in patchy or spatially structured habitats, such as intensively managed production forests, is the role of metapopulation dynamics (Akçakaya *et al*. 2007). In its simplest form the metapopulation concept has only two requirements; populations are geographically discrete and mixing of individuals between populations is less than that within them – otherwise the assemblage of subpopulations within the landscape may be more appropriately described as a single panmictic population (Akçakaya *et al*. 2007). Subpopulations are distributed within a landscape through patches of suitable habitat, within a mosaic of unsuitable habitat. Patch occupancy in a metapopulation is dependent on habitat suitability, as well as colonisation ability and patch extinction. The important concept here is that these spatially discrete subpopulations within the landscape can be connected together through dispersal to form a metapopulation (Krebs 2001). Habitat suitability does not

only relate to a species habitat preferences, but also to survival and fecundity, which are further affected by prey abundance and predation.

Vertebrates respond particularly well to the range of habitats exhibited throughout the plantation cycle (e.g. reptiles, Dent and Spellerberg 1988; mammals, Fernandez *et al*. 1994; birds, Scott *et al*. 1998). Within the Forestry Commission, Forest Research have investigated the effects of habitat management on the conservation of a wide range of endangered species within the commercial forest landscape. Plantation forests have been shown to play a positive role in the conservation of red squirrels (*Sciurus vulagaris*) (Gurnell and Pepper 1991, Pepper 1993), kestrel (*Falco tinnunculus*) (Canham 1992), merlin (*Falco subbuteo*) (Petty 1994), goshawk (*Accipiter gentilis*) (Petty 1996) and golden eagle (*Aquila chrysaetos*) (McGrady *et al*. 1997). Conversely, both positive (Carter and Anderson 1987, Battles *et al*. 2001) and negative (Buse and Good 1993, Greatorex-Davies *et al*. 1993, Gardner *et al*. 2008) effects of plantation management has been recorded in invertebrate communities, with the conservation of deadwood a particularly important factor to species success (Ferris-Kaan *et al*. 1993). Although of primary concern to commercialism, it is possible to balance biodiversity conservation without threatening the production output of plantation forestry (Norton 1998).

Forestry plantations are highly spatially-structured man-made habitats, many planted on former heathlands, which provide a range of microhabitats suitable for adders. The growth of new grasses associated with newly planted or replanted areas support an

abundant small mammal fauna (Fernandez et al. 1994) that provides a substantial potential prey source; felled and discarded logs and the bases of tree stumps provide opportunities for hibernacula; growing trees provide protection from aerial predators. However, in plantations, these different beneficial features are rarely present at the same site and may not be within short-range dispersal distance of each other. Furthermore, patches of suitable habitat are likely to be isolated from others by a matrix of unsuitable habitat. This system provides an ideal research area to investigate the effect of human habitat management on the spatial ecology of extant adder populations at a landscape scale.

1.5.1 Study area and habitat descriptions

The focal areas for this research are a group of commercial production forests of varying sizes located in the North York Moors National Park, north-east England, UK. These primarily coniferous forests are commercially managed for timber production by the Forestry Commission, a public sector organisation, and are comprised of spatially complex matrix landscapes of managed plots, referred to by foresters as 'compartments', at different stages of growth in the plantation cycle. All 5 forests are known to support populations of adders (B Walker *pers. comms*); Dalby (54.2°N, 0.7°W – 34.2km^2), Langdale (54.3°N, 0.6°W – 23.5km^2), Wykeham (54.2°N, 0.6°W – 13.3km^2), Broxa (54.3°N, 0.5°W – 6.5km^2) and Harwood Dale (54.4°N, 0.5°W – 7.1km^2) (Figure 1.3).

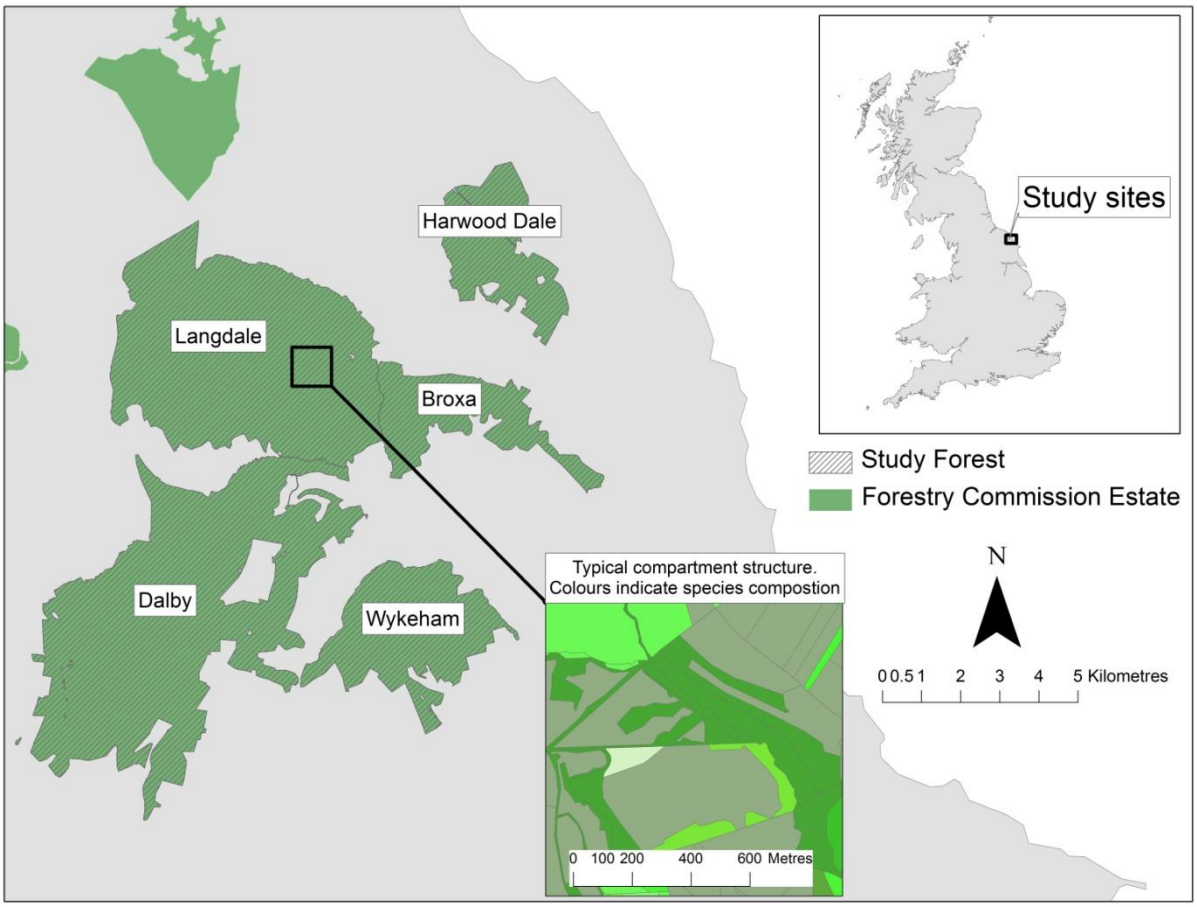


Figure 1.3. A diagrammatic review of the study sites. Forest location is shown at a national scale (top right), landscape scale (left), to demonstrate the spatial relationship between forests, and at a local scale (bottom right) to demonstrate typical intra-forest spatial structure of compartments.

Within the established infrastructure of each individual forest, each compartment generally houses a single species of tree. Although mixed compartments were present, they were infrequent and focus was not given to them in this study as their frequency is decreasing with commercial value. 7 species of conifer accounted for all of the plantation compartments used in this study (see Appendix H for detailed species descriptions), although sitka spruce (*Picea sitchensis*) are the dominant timber species.

1.6 Aims and Objectives

The overall aim of this research is to advance an understanding of the effects of human-influenced habitat change on adder distribution. I aim to investigate the spatial ecology of extant adder populations in commercial forestry plantations, which represent a model landscape to assess the effects of human-influenced habitat change in a dynamic landscape on a species distribution.

Specifically, within the context of spatial ecology and wildlife population monitoring of herpetofauna, the aims of this research are to:

1. Assess the suitability of patch occupancy modelling as a method for monitoring adder populations
2. Investigate the relationship between habitat, prey availability and predation levels on adder distribution
3. Examine the microhabitat characteristics of adder basking sites
4. Formulate recommendations for future monitoring, management and conservation of adders in commercial production forests

Extremely little research has been conducted on adders in forestry plantations, and how the commercial management of these plantations affect their distribution. This research will contribute to our understanding of adder ecology and also explore a method for monitoring the species; an element that is especially important considering

the broader decline in herpetofauna and in adders in particular (Gibbons *et al*. 2000, Wilkinson and Arnell 2011). Detailed knowledge of the spatial arrangement of populations will be important information for wildlife managers and conservationists alike.

*Chapter 2: Habitat selection and thermal ecology of the European adder (*Vipera berus*)*

2.1 Objective

3. Examine the microhabitat characteristics of adder basking sites

2.2 Introduction

The adder is arguably the most studied snake species in the world, however, while the ecology of the species is well studied, comparatively little is known about the factors that influence adder distribution at both a landscape and local scale. Although a wide range of ecological publications on adders exist (e.g. diet - Luiselli and Anibaldi 1991, Luiselli *et al*. 1995; phenology - Prestt 1971, Phelps 2008; reproduction - Andren 1982, Andren and Nilson 1983, Luiselli 1992, Madsen and Shine 1992, 1993, 1994, Hoggren and Tegelstrom 1995; survival - Forsman and Lindell 1997; and demography - Madsen *et al*. 1996, 2000, Phelps 2004), there has been relatively little published on the species' microhabitat requirements. Furthermore, as noted in Chapter 1, extremely little research has been conducted on adders in forestry plantations, and how the commercial management of these plantations affect their distribution.

All snakes are poikilothermic, as biological functions are dependent on the body temperature (T_b) of the organism (Seebacher 2005). Snakes manage T_b through behavioural and physiological processes to maintain basic biological functions. Due to

this limited control in keeping T_b constant, reptiles must rely on external heat sources (environmental temperature - T_e) (Pough *et al.* 2004). There are different approaches to thermoregulation; e.g. *homeothermy*, T_b is kept constant (within +/- 2°C) even with high levels of environmental temperature fluctuation, *ectothermy*, whereby energy is obtained from the environment to raise internal body temperature to allow normal metabolic activity, or *endothermy*, where heat is produced internally by the organism by metabolising carbohydrates, lipids and proteins from their diet (Pough *et. al.* 2004, Vitt and Caldwell 2009).

Adders adopt a form of ectothermy known as heliothermy, which means solar radiation is used as an external heat source to raise their internal temperatures through basking. The highest cost associated with heliothermy is time; time spent thermoregulating or waiting for suitable climatic conditions reduces the amount available for other activities and also increases the amount of time exposed to predators (Huey and Slatkin 1976, Ruxton *et al*. 2004). Therefore the availability of microhabitats offering suitable characteristics for heliothermy would be expected to be a prime factor influencing distribution. Sidorovich *et al*. (2007) highlighted the solar advantage of hills with a southerly aspect, with these sites gaining the longest hours of daily sunshine in the northern hemisphere. Previous research has investigated the internal temperatures of snakes using radio transmitters (e.g. Blouin-Demers and Weatherhead 2001) or temperature probes in both the cloaca (e.g. Forsman 1995) and the oesophagus (e.g. Rutskina *et al.* 2009) but these methods are invasive and there is therefore value in exploring non-invasive methods. Even though the temperature of the outer skin does differ from internal temperature (Rutskina *et al*. 2009), as would be expected in basking, it would be beneficial for adders to have a higher thermal

capacity than surrounding surfaces, allowing a rapid increase in thermoregulatory efficiency with limited exposure to predators.

The aim of this chapter is to investigate the habitat selection of adders at a small spatial scale, focussing on the specificity of basking site microhabitats in relation to local and surrounding habitats.

2.2.1 Aims

- To examine the difference between basking adder body temperature and ambient ground surface temperature
- To assess whether adders display basking site microhabitat selection

2.3 Methods

2.3.1 Data collection

Microhabitat analysis of adder basking sites was conducted by carrying out a series of vegetation surveys in plantation forest compartments. Adder basking sites were identified by walking transects in forest compartments. At each location where a basking adder was spotted, a $1m^2$ square quadrat was placed with the adder's basking position in the centre. Percentage cover of all plant species within the quadrat was recorded. Vegetation height was measured using the direct method (Stewart *et al.* 2001). Plants were identified to species level where possible, with some species (e.g. grasses, mosses) being grouped to increase surveying efficiency. Microhabitat data such as these will used to explore any vegetation selection pressures that are influencing adder site choice, and therefore distribution.

In all compartments where adders were found, the vegetation was assessed in 5 randomly placed $1m^2$ quadrats used to assess the specificity of adder basking site choice in relation to other areas within the compartment. In a subset of these compartments a further four $1m^2$ quadrats were placed at a 2m radius to the original adder basking site to assess the characteristics of habitat local to a basking site to try and explore the spatial scale that site selection may be working at (Figure 2.1).

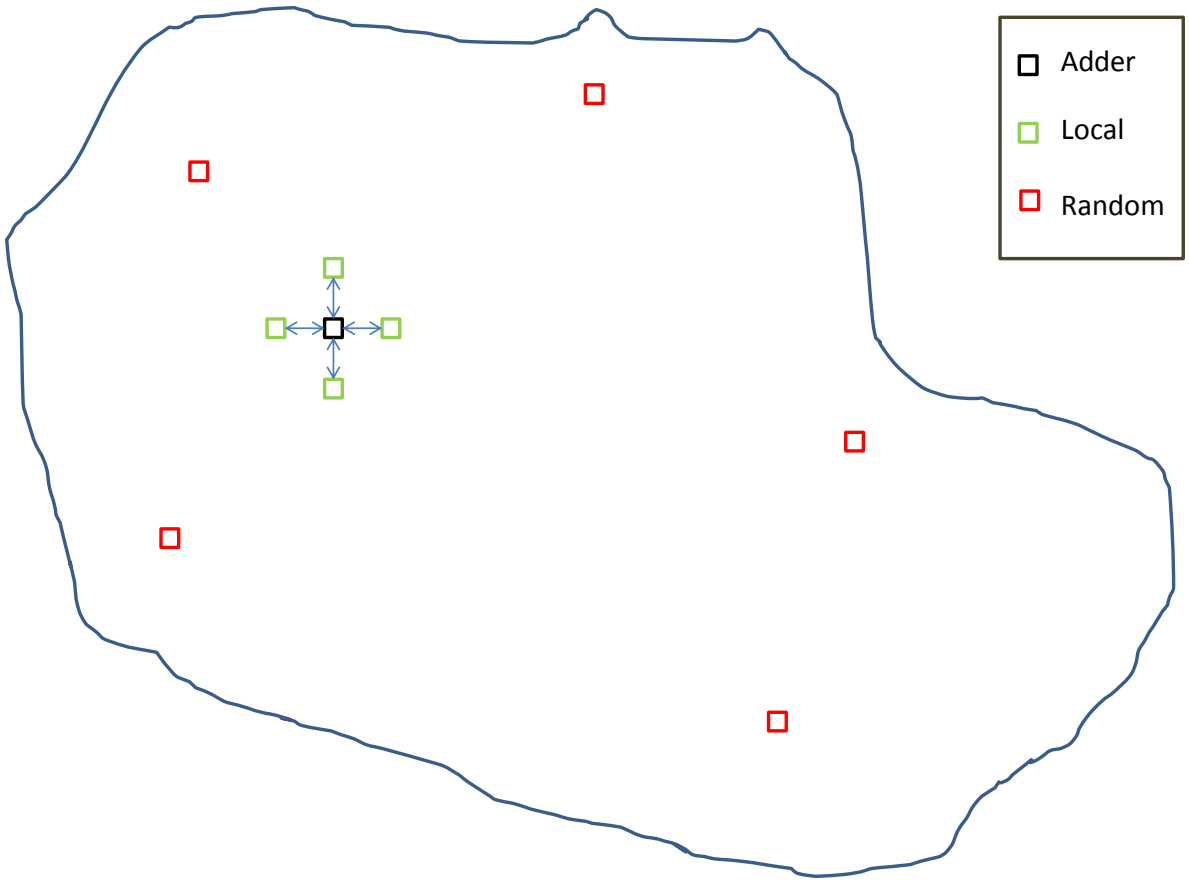


Figure 2.1. An example of the spatial configuration of the data collection design in a hypothetical forestry compartment; 4 'Local' quadrats (green) were arranged radially at a distance of 2m around a basking adder location (black). Vegetation data were also collected on 5 'Random' quadrats (red) which were located within the broader context of the compartment (blue line). Note this diagram is not drawn to scale.

Plantation compartments were classified into 5 distinct habitat types for adder surveying, following the recognised plantation stages outlined by Ferris *et al*. (2000) (Table 2.1):

Compartment type	*Description*
Felled	*Clear-felled*. Plantation compartments that have been clear felled and have not yet been replanted
Young	*Pre-thicket*. Compartments that have been replanted within the previous 1 to 3 years, trees are still very small (generally <1m) but undergrowth vegetation is more developed than in 'Felled' sites
Grown	*Thicket (mid-rotation)*. Replanted compartments that are 4 to 9 years old, by now ground vegetation is well developed and trees have grown significantly (>1m), however canopy is yet to close
Closed	*Pole (economically mature)*. Compartments are areas of mature trees where little to no sunlight is able to efficiently penetrate to the ground
Open	Unplanted areas, usually open heathland within the plantation with sparse self-seeded trees

Table 2.1. Habitat classification description

Categorising plantation stages was a valuable factor in this experimental design as habitat structure greatly differs between them. There is an associated decrease in habitat permeability as growth stage increases, however similarly there is an

associated increase in commercial value. This will be an important factor to consider when attempting to recommend future management plans.

Vegetation, or microhabitat variables, was classified into generic groups comprised of multiple species (Table 2.2.) to facilitate interpretation of the results.

Microhabitat variable	Description
Mosses	Moss species, largely within the genus *Sphagnum*
Bare Ground	Bare, uncovered ground with no vegetation
Wood	Dead wood, usually as the remnants of forestry clearances
Bracken (alive)	*Pteridium aquilinium*
Bracken (dead)	*Pteridium aquilinium*
Grass	Various assortment of grass species
Heather	*Calluna vulgaris*, *Erica cinerea*, *E. tetralix*
Sitka Spruce	*Picea sitchensis*
Scots Pine	*Pinus sylvestris*
Japanese Larch	*Larix kaempferi*
Stones	Stones, rocks, pebbles
Tree stump	Tree stump still rooted, remaining from previous forestry clearances
Bramble	*Rubus fruticosus*, *R. saxatilis*, *R. idaeus*, *R. chamaemorus*
Birch	*Betula pubsecens*, *B. pendula*, *B. nana*
Billberry	*Vaccinium myrtillus*

Table 2.2. Description of the microhabitat variables recorded as percentage cover (%) on all vegetation quadrats

The density of vegetation cover was analysed at 2 scales to assess ground-level solar exposure. Crown canopy cover was assessed using a canopy-scope as described in Brown *et al.* (2000). To assess undergrowth cover a novel piece of field equipment was trialled, adopting a similar basic method as used in the canopy-scope. Two 25cm canes were connected together to form a cross, with 25 black lines drawn on each at 1cm intervals (Figure 2.2). When placed on the ground, the number of black lines not

obscured by undergrowth was recorded from a height of 2m. Percentage cover of undergrowth canopy was then calculated. Using both of these methods allowed an index of total solar exposure to be recorded at two different scales, and analysis to be performed to calculate the importance of vegetation cover to adder site selection.

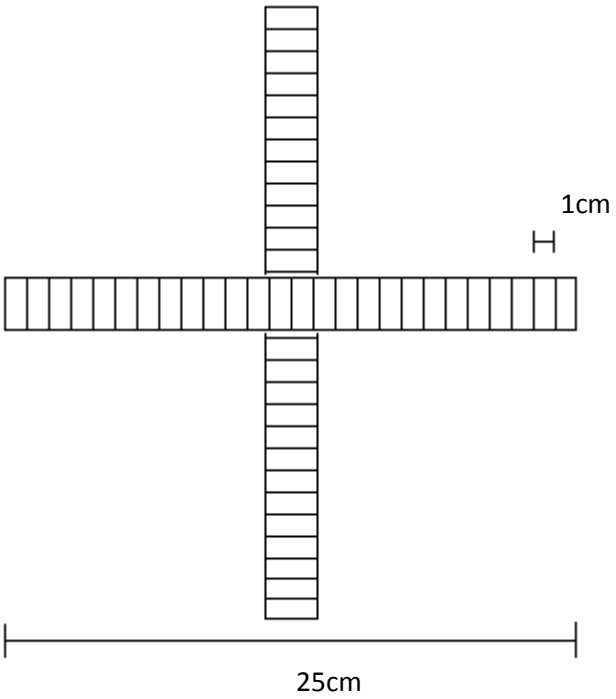


Figure 2.2. Undergrowth cover assessment tool

Microtopography of each basking site was recorded using a vertical marker positioned at exactly 90 degrees, with a protractor then used to measure the degree of slope against this mark (Figure 2.3). Slope direction was recorded using a compass. The importance of micro-slopes on local site selection by adders is poorly understood. Using this novel method it is possible to investigate the significance of microtopography within compartments, independent of macro-topography.

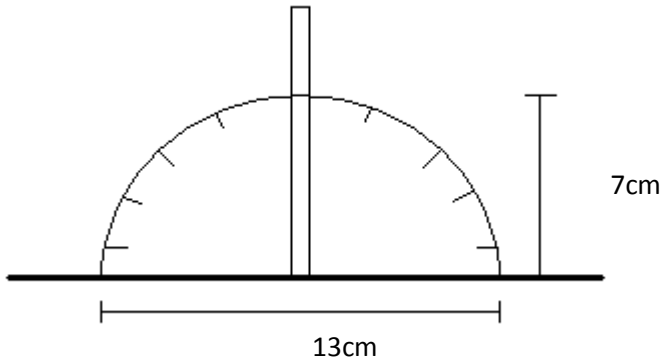


Figure 2.3. Equipment used to assess slope angle during microtopographical analysis

Tree density and tree height were recorded for all compartments. Tree density was estimated using the point-centred quarter method which is a commonly used tool in this area of research (Elzinga *et al*. 2001). Tree density within a plantation compartment was assumed to be similar throughout, as uniform management of tree distribution is adopted to maximise cost-efficiency for commercial growth. Tree height was recorded using a measuring tape where possible, and estimated when larger. It was important to measure the tree density and height so changes in vegetation macro-structure can be observed through the plantation growth cycle. Habitat measurements for adder basking sites were also taken for all locations of sloughed skins. Adders, like all snakes, regularly slough their skin through a process known as ecdysis. It is an important part of their natural history which allows growth, however next to nothing is known about the importance of habitat selection during this process. Sloughs relate to adder presence, although the significance of the sloughing location is unknown it was important to investigate the microhabitat specificity as its selection may impact the broader distribution of adders.

The location of each adder basking site was recorded with a GPS unit (Garmin GPSMAP® 76 or GPSMAP® 60Cx - Garmin (Europe) Ltd – Liberty House, Hounsdown Business Park, Southampton, Hampshire SO40 9LR, UK). Time of detection and altitude were also recorded. Adder basking sites were marked with a piece of flagging tape to allow relocation of a site for habitat data collection.

Snake and ground surface temperature was recorded for all basking adders and the closest uncovered section of ground using an Omega OS435-LS Non-Contact Infrared Thermometer (Omega Engineering Limited – One Omega Drive, River Bend Technology Centre, Northbank, Irlam, Manchester M44 5BD, UK). Snake and ground surface temperature data were also collected from a known population of adders on Fylingdales moor (SE 8897), between 10/03/2010 and 23/03/2010. These data were collected to investigate the thermal ecology of adders, of which very little is known on UK populations but which undoubtedly has an impact on site selection at both the local and landscape scale. It was important to also then collect ambient air temperature data, which was recorded in 4 different areas between 15/05/2010 and 18/10/2010. A datalogger was placed in a Grown (4-9 years since replanting) compartment within the core of Langdale forest, on the periphery of the forest and in Harwood Dale (representing a small forest). A fourth datalogger was placed in a 'Closed' (>9 years since replanting, corresponding with canopy closure) compartment in Langdale forest (~43 years since replanting). Due to availability restraints I was only able to record data from these limited sites. The first 10 days of temperature data were not used to allow dataloggers to settle to external ambient temperatures, therefore data was only used from 25/05/2010 to 10/10/2010. Dataloggers were

connected to the trunk of a tree (at ~50cm) in the centre of the compartment and programmed to record the temperature at 30 minute intervals.

Adder activity was recorded upon detection and split into two categories; basking, where no movement was observed or movement did not occur without a significant amount of disturbance, or moving, where the snake was first spotted already mobile. This permitted identification of true basking sites, distinguishable from temporary resting sites, or locations where adders were seen but had not been basking.

2.3.2 Data analysis

2.3.2.1 Tree density

Mitchell (2007) defines the absolute density (λ) of trees as the number of trees per unit area. In this study, tree density (tree.m^{-2}) was estimated using the equation detailed below from the data obtained via the point-centered quarter method:

$$\text{Absolute density} = \tilde{\lambda} = \frac{1}{\bar{r}^2} = \frac{16n^2}{\left(\sum_{i=1}^{n}\sum_{j=1}^{4} R_{ij}\right)^2}.$$

From Mitchell (2007)

Whereby:

n the number of sample points along the transect

4*n* the number of samples or observations (one for each quarter)

i a particular transect point, where *i* = 1, . . . , *n*

j a quarter at a transect point, where *j* = 1, . . . , 4

R_{ij} the point-to-tree distance at point *i* in quarter *j*

An estimate of trees per hectare (trees ha^{-1}) was calculated by multiplying the result of this equation by 10,000. This method allows compartment density to be estimated efficiently, without having to count every tree at a large spatial scale.

2.3.2.2 Microhabitat analysis

All microhabitat analysis was performed using PRIMER 5® for Windows (PRIMER-E 2002). Microhabitat quadrat data was transformed and standardised using a square root transformation to produce a Bray-Curtis similarity matrix. This method was used for all quadrat types separately, producing individual similarity matrices. Within both Basking and Slough group analyses, a cumulative analysis of similarities (ANOSIM) was performed to investigate the similarity significance between individual quadrats. The similarity of the quadrats between each type (e.g. basking and local, or local and random) was then analysed using a pairwise comparison (ANOSIM).

A SIMPER (similarity percentages within quadrat types and contribution per microhabitat variable) analysis was carried out to identify the microhabitat variables that produced the highest contribution to similarity between quadrats within each quadrat type, as well as calculating the total average similarity between quadrats.

An analysis of similarities (ANOSIM) between quadrat types calculated the average dissimilarity between quadrats of 2 quadrat types (e.g. Basking and Local) and then

extrapolated the microhabitat variables which contributed to the highest levels of dissimilarity. Non-metric multidimensional scaling (MDS) plots were used to graphically demonstrate the similarities between quadrat types for both Basking and Slough site analysis**.**

2.4 Results

A total of 77 adders were recorded throughout the study period (2009 n=9, 2010 n=67), from a total of 270 one hour presence-absence surveys of forestry compartments and further incidental observations. This presents a total surveying time for any adders of 270+ hours during the research period. 56 were detected whilst on surveys, while 21 were noted as incidental findings. Snake and ground surface temperature data were collected, where possible, for any snake encountered. Adders were detected between 31/03 and 11/09 in 2009 and between 29/04 and 07/10 in 2010. Time of detection varied from 08:21 (22/06/2010) to 18:40 (02/08/2010), n= 67 Mean= 12:49 SD= 2:43. Elevation ranged from 109m to 267m above sea level, n= 67 Mean= 188.46m SD= 44.24 (Table 3.2.). Incidental detections often took place whilst driving on forest tracks (n=12), although snakes were also found within forestry compartments when moving between surveys (n=9).

Of the 77 adders recorded in all study sites in both research seasons, there were 43 males, 28 females and 6 juveniles (2009 = 7:3:0, 2010 35:24:6). In 2010 activity was

classified into basking and moving, of which there were 52 and 11 individuals respectively. All basking adders were classified based on basking position; coiled or fully exposed. 17 adders were found in a coiled position and 34 were fully (laterally) exposed whilst basking, while 1 adder was basking whilst partially seeking cover underneath heather (Total n=52). A total of 9 gravid female adders were identified, detected between 23/06/2010 and 17/08/2010 (n=9, total females n=28).

2.4.1 Thermal ecology

Temperature recordings were collected between 06/05/2010 and 15/08/2010, and between 08:33 and 16:18. There was a significant difference between snake and ground surface temperature for snakes identified in forestry plantations (Table 2.3; Paired t-test n=19 p=0.026). At the known population of adders on Fylingdales moor, the difference was also significant (Paired t-test n=17 p=0.004). Combined surface temperature analysis also proved significant (Paired t-test n=36 p=0.001; Figure 2.4).

	Min	Max	Mean	Standard Deviation
Date:				
2009	31-Mar	11-Sep		
2010	29-Apr	07-Oct		
Time	08:21	18:40	12:49	02:43
Elevation (m)	109	267	188	44
Surface temperature (°C):				
*Snake (*Plantation sites*)*	5.0	37.4	22.4	9.2
Ground	4.1	43.4	20.2	8.7
*Snake (*Fylingdales moor*)*	8.8	35.3	23.6	7.6
Ground	6.7	35.6	21.8	7.0

Table 2.3. Adder encounter details

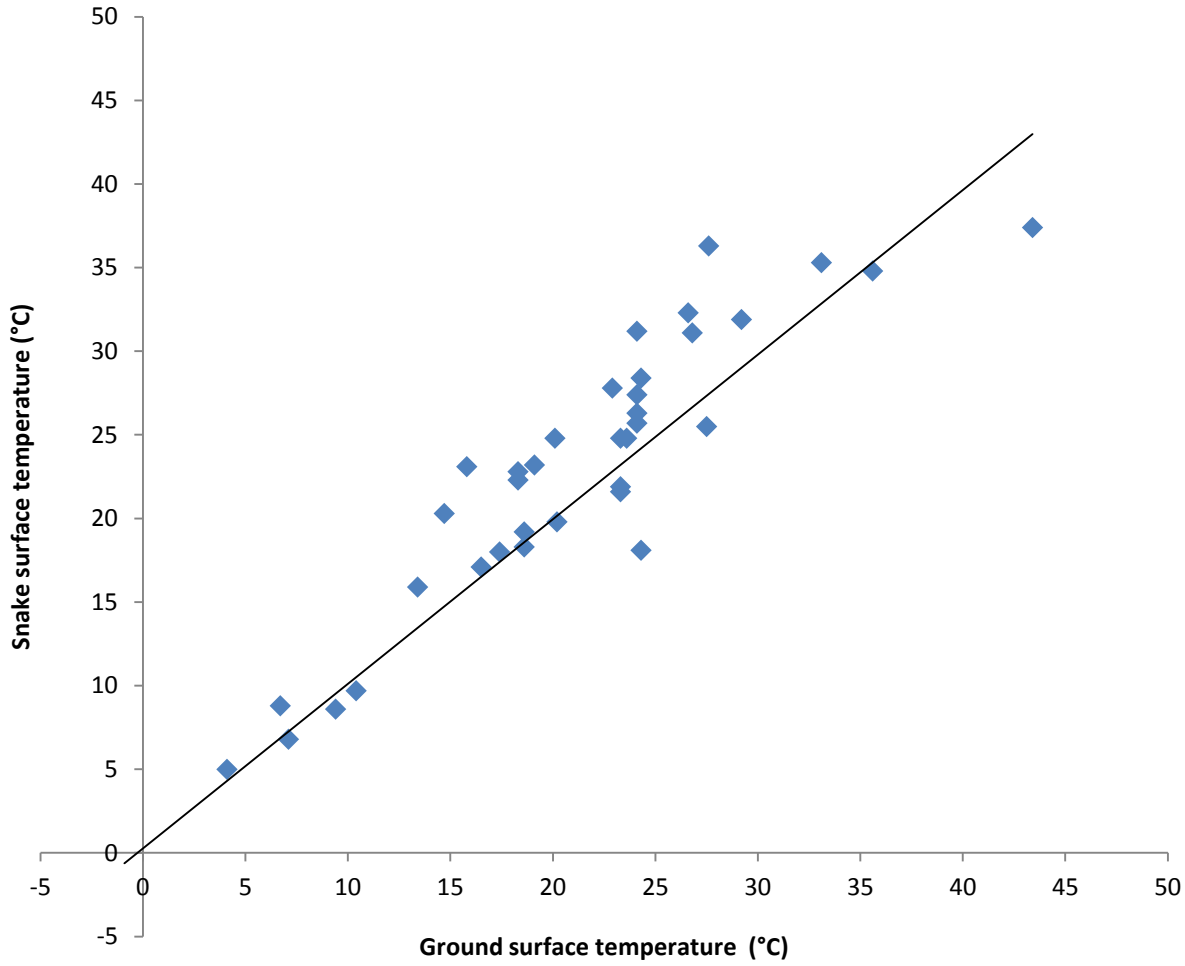


Figure 2.4. Snake temperature against Ground surface temperatures for snakes measured in forestry plantations and open moorland (Fylingdales moor). The straight line is the line of unity i.e. where snake temperature = ground temperature.

Temperature dataloggers demonstrated that ambient temperatures remained above those at which adders first emerged until mid-October (mean = 13.9 °C). The mature forest had consistently lower temperatures than other areas (Appendix E).

There was no significant difference between ambient air temperatures in Grown compartments (One-way ANOVA, F (2, 438) = 2.46, p = 0.09). The periphery habitat experienced the widest range of temperatures, while the datalogger in the Closed compartment recorded the most stable range (Table 2.4). Table 2.4 represents the

maximum daily temperatures for the dataloggers positioned in Grown compartments. Mature woodland (i.e. Closed) was found to be significantly cooler than younger compartments (One-way ANOVA, F (3, 584) = 16.1, $p < 0.001$).

Data logger location	Habitat	Min (°C)	SD	Max (°C)	SD	Mean (°C)	Range (°C)
Langdale (periphery)	Grown	-1.24	6.28	26.17	3.37	16.49	27.41
Langdale (core)	Grown	-0.58	3.02	25.73	3.60	12.64	26.31
Harwood Dale	Grown	0.27	2.91	25.22	3.64	12.63	24.95
Mature	Closed	0.81	2.63	23.33	3.41	11.80	22.52

Table 2.4. Ambient air temperature data collected from 4 dataloggers in the research area from 15/05/2010 and 10/10/2010

2.4.2 Microhabitat analysis

A total of 56 adder basking sites were surveyed (2009 n=11, 2010 n=45) – and a total of 646 habitat quadrats were completed in the entirety of the study. In 2009 basking site quadrats were surveyed with randomly placed habitat quadrats in each compartment data was collected (n=55), while in 2010, additional quadrats within 2m of each basking site ('local' habitat quadrats n=180) and randomly placed habitat quadrats (n=225) were collected. A total of 13 slough site microhabitats were investigated in 2010.

2.4.2.1 Microtopography

Microtopography of adder basking site was assessed for all basking adders in 2010 (n=45). Micro-slope within the microhabitat ranged from flat surface (90°) to 30° (mean=68.4°, SD=17.4°). Aspect of basking site micro-slopes, i.e. the direct $1m^2$ area the adder was positioned in at the time of basking, was significantly south-facing for all basking adders(Table 2.5; chi-squared = 86.9, df = 3, p<0.01). 11 adders were found on flat ground (i.e. 90°) and therefore no facing direction could be determined.

	No. adders
N	2
S	19
SE	5
SW	8
E	0
W	0
Flat ground	11

Table 2.5. Aspect of basking adders in 2010

2.4.1.2 Tree density and tree height

Tree density was recorded for all habitat quadrats. Tree density ranged from 70.14 trees ha^{-1} to 24996.5 trees ha^{-1} within quadrats (n=580). Tree height ranged between 0.29m and 7.8m (n=2320) (Table 2.6). There was no significant difference in tree heights (Two sample unequal variance T-test, p=0.115) or tree density (Two sample unequal variance T-test, p=0.152) between occupied and unoccupied compartments. There was no significant difference in tree density between quadrat types for both basking (One-way ANOVA, F (2, 337) = 0.69, p = 0.502) and slough plots (One-way ANOVA, F (2, 117) = 1.23, p = 0.295). There was also no significant difference in tree

height between quadrat types for both basking (One-way ANOVA, F (2, 337) = 0.041, p = 0.96) and slough plots (One-way ANOVA, F (2, 117) = 0.312, p = 0.732).

	Min	Max	**Mean**	SD
Tree density (trees ha^{-1})				
Basking site	145.1	8942.09	**3372.17**	2157.70
Local	70.14	1573.12	**3869.12**	3252.78
Random	318.88	19837.33	**3931.50**	1887.47
Slough site	154.32	5213.15	**3078.79**	1807.20
Local	148.72	24996.5	**4346.83**	3878.02
Random	812.84	12840.20	**4518.53**	2045.30
Tree height (m)				
Basking site	0.51	5.20	**2.40**	0.97
Local	0.29	6.40	**2.38**	0.96
Random	0.41	7.80	**2.40**	0.79
Slough site	1.00	5.40	**2.79**	0.90
Local	0.40	5.40	**2.64**	0.75
Random	0.45	6.20	**2.75**	0.82

Table 2.6. Tree density and tree height data for all quadrats for basking and slough sites

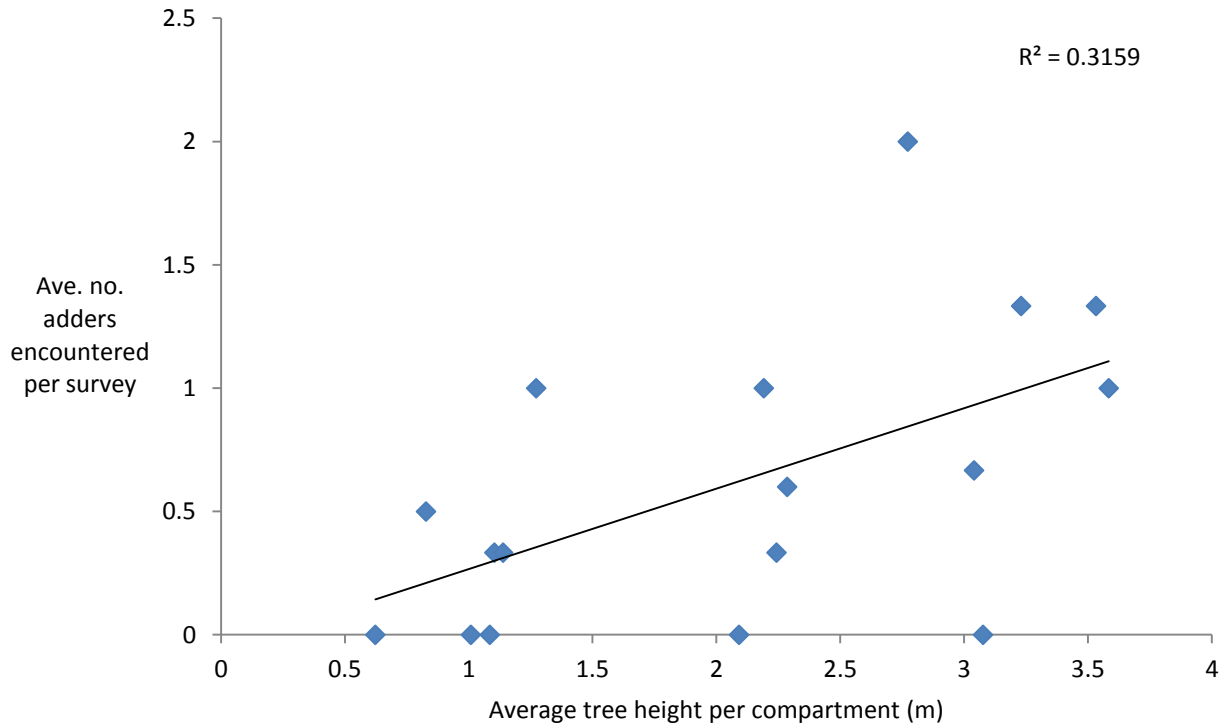


Figure 2.5. Average number of adders encountered per survey related to average tree height (m) per occupied compartment

The average number of adders detected per survey significantly increased with average tree height for all occupied compartments (Spearman rank correlation coefficient r_s = 0.53, p = 0.05, Figure 2.5). Conversely the average number of adders detected per survey significantly decreased with increasing tree density (Spearman rank correlation coefficient r_s = 0.59, p = 0.01, Figure 2.6).

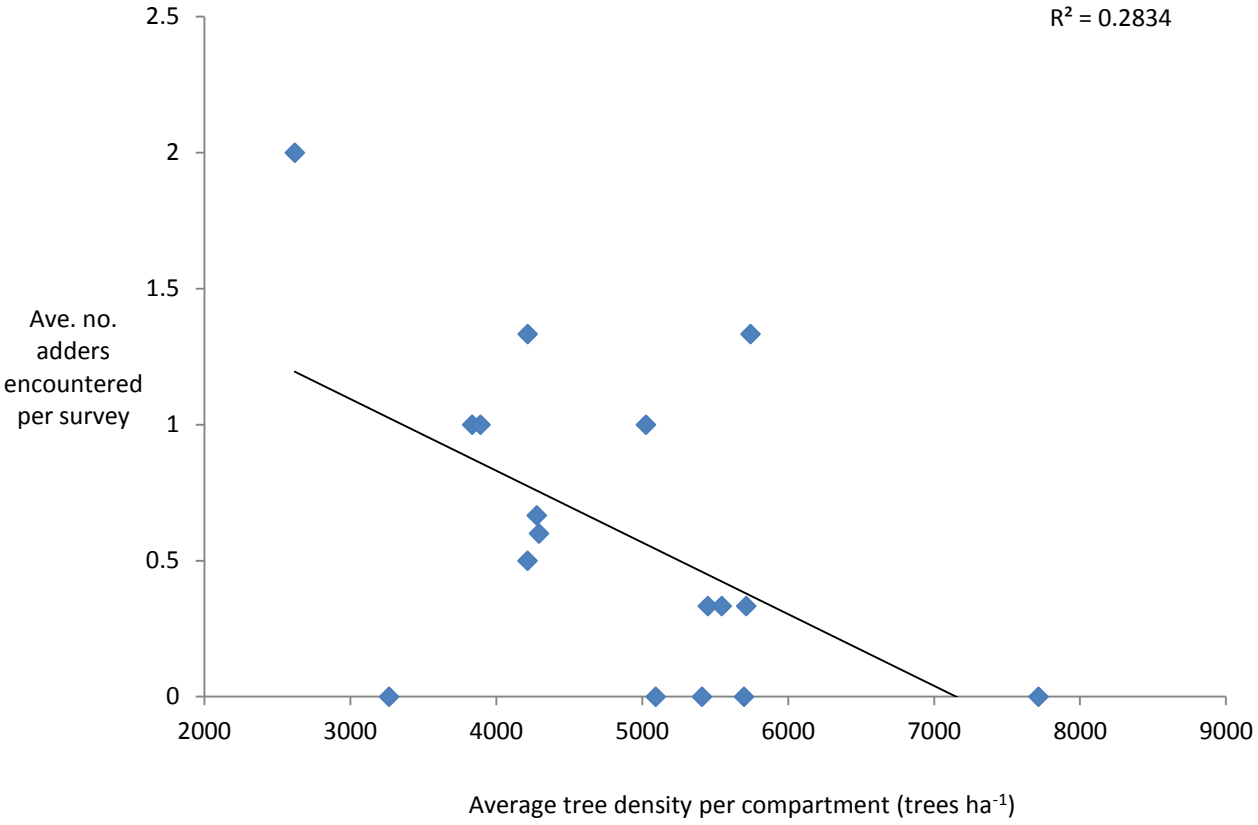


Figure 2.6. Average number of adders encountered per survey related to average tree density (trees ha^{-1}) per occupied compartment

2.4.1.3 Basking site habitat analysis

There was a significant difference between understorey vegetation height for basking sites and local and random quadrats (One-way ANOVA, F (2, 447) = 13.09, p < 0.001). There was also significant difference between quadrat types for understorey vegetation cover (One-way ANOVA, F (2, 447) = 25.5, p <0.001) and canopy cover (One-way ANOVA, F (2, 447) = 3.49, p = 0.03) (Table 2.7).

	Understorey vegetation height (mm)	Understorey vegetation cover (%)	Canopy cover (%)
Basking	47.3	18.6	4.4
Local	514.4	67.7	3.9
Random	306.5	64.9	0.5

Table 2.7 Average recordings for vegetation cover factors during quadrat surveys

Between basking, local and random habitat quadrats, vegetation assemblage was significantly different (ANOSIM Global R = 0.027, P = 0.3%). Pairwise comparison of the sites revealed that there was only a significant difference between Basking and Random quadrats (ANOSIM R = 0.08, P = 1.5%). Comparisons of both Basking and Local (ANOSIM R = 0.05, P = 8.4%), and Local and Random (ANOSIM R = 0.009, P = 6.4%) were not significant.

Four microhabitat variables accounted for 91.7% of the 20.6% overall similarity between the Basking quadrats. Grass had a mean percentage cover of 28.5% and contributed 42.5% of the similarity between quadrats, wood was the next most abundant microhabitat variable (mean % cover = 22.6, contributing 29.8% to overall similarity) followed by heather (mean % cover = 12.11, contributing 11% to overall similarity) and finally mosses (mean % cover = 10.98, contributing 8.6% of overall similarity) (Table 2.8).

Group: Basking
Average similarity: 20.61

Variable	Mean percentage cover	Mean similarity	Similarity/SD	Contribution (%)	Cumulative %
Grass	28.47	8.75	0.40	42.45	42.45
Wood	22.60	6.13	0.39	29.75	72.20
Heather	12.11	2.26	0.29	10.96	83.17
Mosses	10.98	1.77	0.23	8.60	91.77

Table 2.8. SIMPER analysis of all basking site quadrats

Two microhabitat variables accounted for 89.25% of the 22.35% overall similarity between Local quadrats. Heather had a mean percentage cover of 37.71% and contributed 66.3% of the similarity between quadrats, meanwhile Grass had a mean percentage cover of 21.25%, contributing 23% to overall similarity (Table 2.9).

Group: Local
Average similarity: 22.35

Variable	Mean percentage cover	Mean similarity	Similarity/SD	Contribution (%)	Cumulative %
Heather	37.71	14.81	0.50	66.25	66.25
Grass	21.25	5.14	0.30	22.99	89.25
Wood	7.45	0.70	0.13	3.12	92.36

Table 2.9. SIMPER analysis of all local habitat quadrats

The same two microhabitat variables were also the most important to Random quadrat vegetation cover, accounting for 88.22% of 24.31% similarity. Heather had a mean percentage cover of 42.41% and contributed 76.78% of the similarity between

quadrats, meanwhile Grass had a mean percentage cover of 15.29%, contributing 11.44% to overall similarity (Table 2.10).

Group: Random

Average similarity: 24.31

Variable	Mean percentage cover	Mean similarity	Similarity/SD	Contribution (%)	Cumulative %
Heather	42.41	18.67	0.57	76.78	76.78
Grass	15.29	2.78	0.23	11.44	88.22
Bracken (dead)	7.88	0.62	0.09	2.57	90.79

Table 2.10. SIMPER analysis of all random habitat quadrats

Table 2.11 illustrates the microhabitat variables which provide the highest contribution to the average dissimilarity (83.9%) between Basking and Local quadrats. Heather was far more abundant in Local quadrats than in Basking sites, whereas Grass and Wood was more commonly associated with the latter.

Variable	Mean percentage cover (%)		Contribution (%)
	Basking	**Local**	
Heather	12.11	37.71	23.31
Grass	28.47	21.25	21.39
Wood	22.60	7.75	15.32

Table 2.11. ANOSIM analysis of the dissimilarity between Basking and Local quadrats

Table 2.12 illustrates the microhabitat variables which provide the highest contribution to the average dissimilarity (84.31%) between Basking and Random quadrats. Similarly,

Heather was far more abundant in Random quadrats, while grass and wood more commonly associated with Basking sites.

Variable	Mean percentage cover (%)		Contribution (%)
	Basking	**Random**	
Heather	12.11	42.41	25.31
Grass	28.47	15.29	19.94
Wood	22.60	6.90	15.12

Table 2.12. ANOSIM analysis of the dissimilarity between Basking and Random quadrats

Table 2.13 illustrates the microhabitat variables which provide the highest contribution to the average dissimilarity (83.9%) between Local and Random quadrats. Heather was more abundant in Random quadrats, while Grass and Wood were more common in Local quadrats.

Variable	Mean percentage cover (%)		Contribution (%)
	Local	**Random**	
Heather	37.71	42.41	30.29
Grass	21.25	15.29	18.75
Wood	7.45	6.90	8.45

Table 2.13. ANOSIM analysis of the dissimilarity between Local and Random quadrats

2.4.1.4 Slough site analysis

There was a significant difference between understorey vegetation height for slough sites and local and random quadrats (One-way ANOVA, F (2, 127) = 5.23, p = 0.007). There was also significant difference between quadrat types for understorey vegetation cover (One-way ANOVA, F (2, 127) = 10.22, p <0.001), however no variation in canopy cover was recorded across all quadrat types for slough plots (n = 130, mean = 0).

However vegetation assemblage between slough, local and random habitat quadrats was not significantly different (ANOSIM Global R = -0.017, P = 77.7%). Pairwise comparison of the sites revealed that there was not a significant difference between any of the quadrat types; Slough and Local quadrats (ANOSIM R = -0.022, P = 60.7%), Slough and Random (ANOSIM R = -0.045, P = 76.3%), and Local and Random (ANOSIM R = -0.01, P = 75.6%).

2.5 Discussion

The annual period of activity that was recorded (31/03 – 07/10) coincides with previous phenological studies (Prestt 1971, Phelps 2008). A total of 77 adders found within plantation forests, when imperfect detection is acknowledged, suggest that this habitat can support large, healthy populations (see Appendix J) and could be of future conservation importance. Gravid females (n=9) were detected from 23/06/2010 to 17/08/2010, which also conservatively fell within the dates observed by Prestt (1971).

Investigation into the thermal ecology of basking adders revealed snake surface temperatures were significantly warmer than surrounding ground surface temperatures in all sites. A significantly higher temperature indicates that adders more efficiently engage solar radiation than the surrounding habitat, as would be expected of a heliotherm. These data allow us to confirm in this study that direct sun exposure through basking, which would lead to a higher body surface temperature, is an important element of this species' natural history and is therefore likely to influence habitat selection. It is beneficial for adders, as heliotherms, that an optimum body temperature can be rapidly reached so less time is spent basking and more time can be devoted to other activities, such as foraging or mating, as well as minimising the amount of time spent visually exposed to predators (Huey and Slatkin 1976). The importance of sun exposure was further highlighted as the microtopographical analysis of basking sites supported the prediction that southerly aspects would be favoured. Adders significantly chose to bask on microtopographical platforms with a southerly aspect over all other orientations (Table 2.5), a selection that would ensure maximum daily temporal solar exposure, as well as maximum solar intensity.

The results of the microhabitat analysis show that adders demonstrate very specific basking site selection within a plantation compartment. Although tree density or tree heights were not significantly different between quadrat types (section 2.4.1.2), basking sites had significantly less and significantly shorter ground vegetation cover. Furthermore results from the vegetation assemblage analysis revealed that basking sites had more open vegetation than those nearby or in the rest of the compartment, and also had more wood than all other types, representing a likely source of refuge from predators. Heather abundance increased from basking sites through local to random quadrats, while grasses follow the opposite trend (Tables 2.7-2.9).

Ground vegetation height, which was significantly shorter in basking sites, also underlined the importance of sun exposure, and correlated with a decrease in heather abundance and increase in grasses (section 2.4.1.3). These data indicate that adders rely on habitat patches that experience a certain level of disturbance to produce open patches, thus making them suitable for basking. It is possible that grazing by wild herbivores (principally deer) in plantations maintains open, grassy patches that could improve habitat quality for adders.

The significant difference between basking and random sites indicates selection of patches within a compartment. At a smaller scale the difference in vegetation assemblages between basking sites and local quadrats, as well as between local and random quadrats, approached significance. Although highly speculative based on this analysis, this suggests some very small scale selection within local patches of suitable

basking habitat and so highlights the importance of further data collection that would allow additional clarification of the selection processes.

There was no significant difference between quadrat types for slough sites for tree height and density, as well as vegetation assemblage, indicating that specific site selection does not occur for this process. However, slough sites did have significantly shorter ground vegetation, were less covered by ground vegetation and occurred only in plantation compartments with no canopy cover (section 2.4.1.4). This suggests that although slough sites are not selected for specific microhabitat characteristics, their location could be a factor of basking site location as sloughing occurs before or after basking. Little research has previously been published on the significance of slough sites on snake distribution. These results suggest that they are of no major importance to be considered in future studies of species distributions, however further ecological research should investigate slough location as a behavioural correlate of basking.

Analysis of microhabitat selection for both basking and slough sites has not previously been published for adders, and the significance of specific basking site selection indicates that this could be an important avenue of research for species conservation. Similarly, the novel non-invasive method used to investigate adder basking temperatures was successful and has identified it as a viable method for future studies in thermal ecology, particularly of heliotherms.

My data has shown that exposure to the sun is an integral aspect in habitat selection. Adders increase their exposure while basking by selecting south-facing, sloping patches with a clear selection for open ground level vegetation. Exposure to the sun also makes adders vulnerable to aerial predators, which may explain selection for sites with access to potential refuges such as dead wood piles. Subsequently, as basking is such an important element of the adder's life history, suitable basking site microhabitat availability ought to be key in determining broader habitat suitability for the species. In later chapters I explore the contrasting effects of habitat and predation on adder distribution.

Chapter 3: Predator-prey interactions: assessing the abundance and diversity of potential prey species and investigating potential predation levels using a novel method

3.1 Objective

2. *Investigate* the relationship between habitat, prey availability, predation levels and adder distribution

3.2 Introduction

The structure of animal communities, and changes in the abundance and spatial distribution of interacting populations of single species, are determined by a range of ecological processes (Inchausti and Ballesteros 2008, Howeth and Leibold 2010). For example, predator and prey dispersal distances (Cronin *et al*. 2000, Hammond *et al*. 2007, Howeth and Leibold 2010) and the variability in environmental gradients (Werner and McPeek 1994, Chase 2003) can collectively determine the spatial patterns of predator-prey co-occurrence (Howeth and Leibold 2010). In the natural world prey and predator abundances are rarely, if ever, constant over space (Inchausti and Ballesteros 2008), a factor accentuated in highly spatially-structured landscapes such as plantation forests (Gehring and Swihart 2003).

Predator-prey dynamics are a major structuring force in most ecosystems. Predator presence may affect prey species directly and indirectly, both having the potential to impact populations (Sih *et al*. 1985, Lima and Dill 1990), while habitat and diet selection can be extremely influential in determining community structure (Fryxell and Lundberg 1998). Although these factors will be especially pronounced in heterogenous landscapes (Lee 2010), the impact of spatial variability on ecological processes such as predator-prey interactions, as well as indirect species interactions, remain largely unexplored (Bull *et al*. 2006).

The role of adders within landscape-level predator-prey dynamics is unclear. Although prey abundance has been directly linked to body size (Forsman 1991, Lindell and Forsman 1996), as well as both reproductive and foraging success (Andrén 1982), no studies have investigated prey species distribution as a potential ecological correlate of adder distribution. Similarly, confounding effects of predation levels are likely to vary in highly heterogenous landscapes, and their impact on adder distribution is poorly understood.

Adder predators

Adder predation appears uncommon and largely opportunistic, with no ophiophagic specialists present in the UK. Commercial forests offer a wide range of habitats throughout the plantation cycle, and high levels of spatial heterogeneity within the landscape. There are potential benefits to aerial avian predators, such as corvids or buzzards (*Buteo buteo*) of foraging in habitats in early stage plantations, which provide maximum visual exposure. This might be expected to decrease with plantation growth as the ground level becomes obscured (Fernandez 1993).

Neumeyer (1987) and Andrén (1985) highlighted the potential mammalians; *Mustela erminea*, *Martes* sp., *Vulpes vulpes,* and avian; *Aquila chrysaetos, Buteo buteo*, *Buteo lagopus*, *Corvus corax*, *Corvus cornix , Corvus corone*, *Cuculus canorus*, *Falco tinnunculus* and *Pica pica* predators of adders. Other studies have identified a broad range of potential predators: hedgehogs, birds of prey, corvids, egrets and storks (Krapivny 1957, Wüster *et al*. 2004, Kowalewski and Profus 2007) were of primary concern, although rarer occurrences of predation were recorded, including finding an adder in the stomach of a European brown bear (*Ursus arctos*) (Jakuczan 1978). In the UK, the most consistent predators of adders have been identified as buzzards (*Buteo buteo*), kestrel (*Falco tinnunculus*), carrion crow (*Corvus corone*), magpie (*Pica pica*) and pheasant (*Phasianius colchicus*), as well as smooth snakes (*Coronella austriaca*) where range overlaps (Prestt 1971, Phelps 2004).

Adder prey

The variety of adder prey has been investigated in detail in several regions throughout the species total range (Tables 3.1, 3.2). Reports have been published from research in Poland, Czechoslovakia, western France, Italy and southern England (Prestt 1971, Luiselli and Anibaldi 1991, Luiselli *et al.* 1995), as well as attracting similar research interest in sympatric species, e.g. *V. aspis* (Canova and Gentilli 2008) and *V. seoneai* (Santos *et al.* 2007).

Prey species vary throughout the range of *V. berus* and differ with associated habitat transitions. The majority of studies suggest a primarily vertebrate diet, with specific prey choice varying depending on habitat and availability. The consistent trend

identifies small mammals (Soricidae, Muridae and Arvicolidae) as the dominant component of adder diet (Table 3.1). An ontogenetic shift from ecothermic to endothermic prey is recorded in other *Vipera* and is likely to also occur in *V. berus* (Luiselli and Agrimi 1991, Beat *et al*. 1992, Monney 1993, Luiselli *et al*. 1995).

Microtus (11)		*Myodes* (4)		*Apodemus* (6)		*Sorex* (6)	
Prestt	1971	Prestt	1971	Prestt	1971	Prestt	1971
Andrén	1982	Neumeyer	1987	Andrén	1982	Andrén	1982
Andrén and Nilson	1983	Luiselli *et al.*	1995	Andrén and Nilson	1983	Andrén and Nilson	1983
Forsman and Lindell	1991	Fey *et al.*	2006	Luiselli and Anibaldi	1991	Neumeyer	1987
Madsen and Shine	1993			Luiselli *et al.*	1995	Luiselli and Anibaldi	1991
Forsman *et al.*	1994			Kowalewski and Profus	2007	Kowalewski and Profus	2007
Lindell and Forsman	1996						
Forsman	1997						
Bonnet *et al.*	1999						
Fey *et al.*	2006						
Kowalewski and Profus	2007						

Table 3.1. Small mammal prey of *V. berus* gathered from a review of the literature and categorized by genus

Adders are generalist small mammal predators, primarily selecting species within the genera above (Table 3.1), although occasionally more unusual species are recorded (e.g. *Neomys fodiens* and *Micromys minutus* - Prestt 1971; *Glis glis* - Luiselli and Anibaldi 1991; *Talpa europaea* - Kowalewski and Profus 2007;). Species of all 4 genera in Table 3.1 are presently found within the research area.

Lacerta/Zootoca (4)		*Rana* (8)		*Bufo* (1)		*Triturus* (3)	
Neumeyer	1987	Andrén	1982	Kowalewski and Profus	2007	Andrén	1982
Prestt	1971	Andrén and Nilson	1983			Andrén and Nilson	1983
Luiselli *et al.*	1995	Neumeyer	1987			Luiselli *et al.*	1995
Kowalewski and Profus	2007	Luiselli and Anibaldi	1991				
		Luiselli *et al.*	1995				
		Lindell and Forsman	1996				
		Forsman	1997				
		Kowalewski and Profus	2007				

Table 3.2. Herpetofaunal prey of *V. berus* including only species found within the UK, gathered from a review of the literature and categorized by genus

In continental Europe lizards are an important prey group alongside small mammals (Mertens 1947, Pielowski 1962, Prestt 1971, Sebela 1978, Saint Girons 1980), with the most common being *Zootoca vivipara* and *Lacerta agilis*, although *Anguis fragilis* has also been recorded (Prestt 1971). Amphibians are also taken; three species of anuran (*Rana temporaria, Rana arvalis*, *Bufo bufo*) as well as further unidentified species (Lindell and Forsman 1996, Forsman 1997), and three species of caudate; *Salamandra atra* (Neumeyer 1987, Luiselli *et al*. 1995), *Triturus cristatus* (Andrén 1982, Andrén and Nilson 1983) and *Ichthyosaura* (*Mesotriton*) *alpestris* (Luiselli *et al*. 2005). Table 3.2 highlights publications that have identified predation events of species distributed in Britain. Although amphibians, especially *Rana temporaria*, are generally accepted as a potential prey species in the UK (Wüster 1998, Edgar *et al*. 2010), a review of the literature yielded no published accounts.

Among vertebrate prey birds are also recorded, however due to the low frequency and wide species diversity all occurrences are regarded as opportunistic predation, usually of nestlings (Prestt 1971). Only two species were recorded more than once, both of which are uncommon in Britain during the adder's 'summer' feeding period (section

1.2.4.2); *Anthus spinoletta* (Neumeyer 1987, Luiselli and Anibaldi 1991, Bollman *et al*. 1997, Rehsteiner *et al*. 1998) and *Phoenicurus ochrurus* (Neumeyer 1987, Luiselli and Anibaldi 1991). Many more are recorded as single occurrences (e.g. Neumeyer 1987; *Acanthis cannabina*, *Oenanthe oenanthe*, *Prunella modularis*, *Saxicola rubetra*, *Troglodytes troglodytes*).

The inclusion of species, such as adders, within a multiple predator-multiple prey system incorporates more complex dynamics than straight forward single predator-prey interactions (Krebs 2001). These complex systems have highlighted the importance of predation in the evolution of certain behavioural, morphological and physiological characteristics. The evolution of the dorsal zig zag band on the adder is a feature whose exact function has often been debated but is generally considered to aid in crypsis (e.g. Andrén and Nilson 1981, Luiselli 1992, Shine and Madsen 1994). Conversely, recent studies have experimentally demonstrated the development of *Vipera berus* morphology as an aposematic adaptation to aerial predators (Wüster *et al.* 2004).

This research aims to:

- Investigate the habitat-specific abundance and diversity of small mammal fauna in plantation forests, and assess its relationship to adder distribution
- Investigate the relationship between adder predation and habitat type in plantations

I hypothesise that small mammal abundance will increase with an increase in growth stage, before decreasing again as the canopy closes (as in Fernandez *et al.* 1994), and predation levels will decrease as sites mature, the canopy closes and the ground layer is obscured.

3.3 Methods

3.3.1 Prey – Small mammal surveying

Prey availability was assessed in each habitat type through live-trapping with Longworth small mammal traps (Chitty and Kempson 1949). Three sites of each of the five plantation stages were selected for trapping to ensure accessibility and spatial independence. Three trapping sessions were carried out with one site of each habitat type being surveyed concurrently during each session. All habitat types were surveyed so the relationship between plantation cycle and small mammal distribution could be investigated.

Session 1: 3rd–7th August 2010

Session 2: 8th–12th August 2010

Session 3: 14th–18th August 2010

Data were collected in August during the adder feeding period (see section 1.2.4.2) since this is when potential feeding is at its highest and has the greatest potential to influence adder distribution. Nevertheless a more comprehensive study of adder feeding would examine prey populations at different times of year and over a number of years. Such a study was not possible in this case because of time limitations.

Trapping was carried out using a series of 20 Longworth traps arranged at least 10m apart along a linear transect in each compartment (similar to Hansson 1967). A pilot study indicated best capture rates after 2 days of trap pre-baiting and so this approach was used. Traps were pre-baited and locked open for 2 nights, followed by 3 nights of trapping. A total of 900 trap nights were recorded. Traps included a bed of straw, and bait of mixed grain for any Rodentia, and blowfly (*Calliphora vomitoria*) pupae for the

Soricidae (*Sorex araneus* and *S. minutus*), which meant that any trapped individuals would be adequately provisioned in line with best practice (Gurnell and Flowerdew 1990). Traps were checked twice daily, approximately 12 hours apart so that there was minimal trap time for caught individuals, but also suitable time compensation for disturbance to not affect trapping success. Sex, age, reproductive condition, mass and external parasite load were recorded for each trapped individual. Animals were marked using a series of fur clips to determine capture day. Left shoulder indicated first trap night, left flank for second trap night and right shoulder for third trap night. Animals were marked so that recapture data could be compiled to estimate true number of individuals during a complete trapping. Multiple captures of the same individual may lead to incorrect population size estimates.

3.3.2 Predators - Plasticine adder models

Assessments of potential predation levels were completed in each of the plantation categories: open, felled, young, grown and mature. Data collection occurred between 27/07/2010 and 14/09/2010 corresponding with the period of annual activity highlighted in Chapter 1. Data was not collected after this date as there was potential for adders to begin to enter hibernation. Surveys were conducted in Langdale forest to allow easing monitoring of sites whilst other aspects of the research continued. Compartments used to assess predation levels were not surveyed for adders concurrently during the research period, and were assumed to have had little to no human disturbance within them during data collection.

Plasticine adder models were used to assess predation levels. Plasticine was obtained from Newclay Products Limited (1 Battle road, Heathfield industial estate, Newton

Abbot, Devon, UK). Models were made using a method adapted from Wüster *et al.* (2004). Sexual dichromatic models were made as in this previous study; male models were made using grey-coloured plasticine, and females using terracotta-coloured plasticine. All models measured between 30-35cm in length, and 3cm width, with a distinct head formed. The use of plasticine models in this instance allows for a low-disturbance but high-output method, where aside from the intial model production, very little time needs to be spent collecting the data. Although the method is still novel it provides an opportunity to examine if predation pressure changes with habitat type, and if so does this correlate with a change in prey distribution.

Figure 3.1. Plasticine adder models – male (left) and female (right), using the same method as Wuster *et al*. (2004)

All models were manipulated into an S-shaped curved to represent a resting adder (Fig 3.1., as in Wüster *et al.* 2004). Only models of adult snakes were used in this survey. A black dorsal stripe was drawn on each model using a permanent marker. Black masonry paint, as used in the method by Wüster *et al.* 2004, was not favoured over

marker pens after preliminary tests proved it ineffective. All models were made by the author personally.

A total of 250 plasticine adder models were made. Each habitat type was allocated 50 models. The models were placed singly at 10m intervals following a line transect, usually dictated by natural vegetation or physiogeographic features, in each plantation compartment. Model sexes were alternated along the transect. Models were left for 2 weeks to minimise disturbance after initial placement and then checked weekly for 6 weeks (10/08/2010-14/09/2010). A total of 2100 attack nights were available to predators. Each individual model location was recorded with a GPS. No physical identification was used to mark the position of each adder to avoid any positive or negative association for potential predator species.

Any physical disturbance to each model was recorded, and each mark photographed. Marks were removed as much as possible during each survey to provide typical undisturbed models for the next period. Disturbance events were split into 5 categories: rodents, deer, birds, carnivores and missing models. Markings were identified and grouped, with confirmation through photo analysis and field observations from P Wheeler. Models were deemed to be taken by a predator when they could not be located within a 5m radius of its GPS location. The classification of disturbance into these 5 categories was accepted to cover all the possible results of the marks observed.

Only one previous study has used this method for adders (W*ü*ster *et al*. 2004), however this is the first time it has been used in a basic ecological study to investigate

predation levels between a range of habitats. Attempts have been made to validate 'true' attacks from investigative disturbances by W*ü*ster *et al*. (2004), as well as by Brodie (1993), by recording mark location on snake models in their respective studies. A higher percentage of attacks were recorded on the head of patterned models, as oppose to plain control models. This suggests that although different model species were used (adders *Vipera berus* and coral snakes *Micrurus nigrocinctus* respectively) birds inferred the patterned venomous models as more 'hazardous', given the potential danger of biting by both species of venomous snakes, and therefore all recorded attacks on the patterned models could be inferred to as 'real'.

Predation pressure is assumed alongside prey availability to be one of the strongest potentially influential factors on species distribution (Franklin 2009). *Vipera berus* is the only snake within the study sites, and indeed within north-western Europe, to exhibit a solid dorsal zigzag band, so any predation attempts can be interpreted as species specific.

3.4 Results

3.4.1 Prey

A total of 115 individual animals were caught from 184 capture events in the 900 available trap nights, resulting in a trapping percentage of 12.78%. 115 individual animals were identified owing to 54 (46.95%) recaptured individuals (recapture events n=69 due to >1 capture of same animal). Session 1 yielded the fewest captures (n=25,

21.74%). The highest capture rates were recorded in Session 2 (n=48, accounting for 41.74% of all captures).

	Total capture events	Total individuals	Total recaptured animals	Total recapture events
Session 1	30	25	4	5
Session 2	76	48	21	28
Session 3	78	42	29	36

Table 3.4. Total number of trapped animals, individual animals, recaptured animals and recapture events for each trapping session

4 species were caught; *Apodemus sylvaticus*, *Myodes glareolus*, *Sorex araneus* and *S. minutus*. *Apodemus sylvaticus* was the most frequently caught species and made up 89.6% of captured individuals (n=103, total n=115), and 91% of all capture events (n=168, total n=184) (Table 3.4).

Species	Session 1	Session 2	Session 3	Total
A. sylvaticus	16 (19)	44 (71)	42 (78)	**102** (168)
M. glareolus	4 (6)	0 (0)	0 (0)	**4** (6)
S.araneus	3 (3)	2 (2)	0 (0)	**5** (5)
S. minutus	2 (2)	2 (2)	0 (0)	**4** (5)

Table 3.5. Total individuals (and total capture events) per species, per session

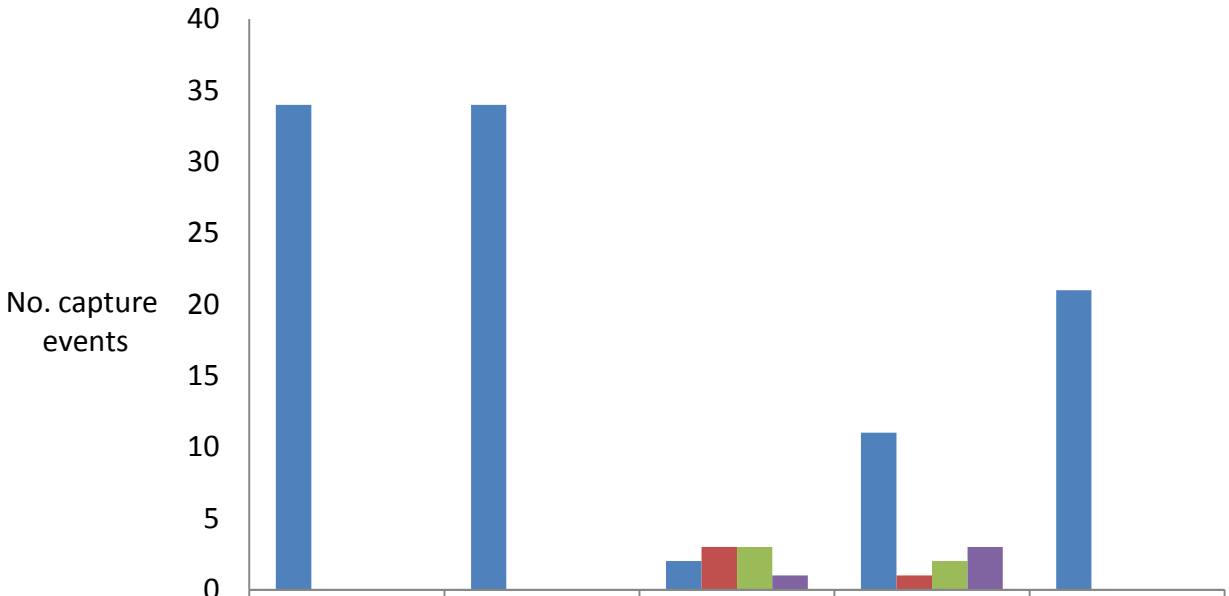
Felled and Young compartments had the highest number of captures (n=34, accounting for 29.57% in both sites). The fewest small mammals were captured in Grown compartments (n=9, 7.83%). There was a significant relationship between

numbers of individual animals caught per session and habitat type (chi-squared = 16.0, df. = 8, $p < 0.05$) (Table 3.6).

	Session 1	Session 2	Session 3	**Total**
Felled	5	16	14	**34**
Young	7	12	15	**34**
Grown	5	4	0	**9**
Closed	5	4	8	**17**
Open	3	13	5	**21**

Table 3.6. Total number of individual animals per habitat type per session. For each habitat type species composition is listed as follows; *Apodemus sylvaticus*, *Myodes glareolus*, *Sorex araneus*, *S. minutus*

In Felled, Young and Open habitats only *A. sylvaticus* was recorded. Grown and Closed habitats had equal α-diversity (4 species), however Grown (n=9) recorded far fewer individuals than Closed (n=17) (Figure 3.2).



	Felled	Young	Grown	Closed	Open
A. sylvaticus	34	34	2	11	21
M. glareolus	0	0	3	1	0
S. araneus	0	0	3	2	0
S. minutus	0	0	1	3	0

Figure 3.2. Total number of small mammal capture events per species per habitat type

3.4.2 Predation

A total of 524 disturbance events were recorded in all habitats which were significantly different (chi-squared = 108, df. = 16, p = < 0.001). The majority of disturbance events were recorded by Rodents (48.47% of all markings), followed by Birds (24.8%). Photographic examples of model disturbance from each group is supplied (Appendix G). 41 models (7.82% of all events) were lost over the study period. Open habitats recorded the highest number of disturbance events (n=198, 37.79% of total), followed by Felled (n=117, 22.33%). Grown had the fewest disturbance events (n=50, 8.54%) (Table 3.7).

	Birds	Carnivores	Missing	Rodents	Deer	Total	Contribution (%)
Felled	51	3	7	39	17	117	**22.33**
Young	25	8	3	46	12	94	**17.94**
Grown	12	3	0	28	7	50	**9.54**
Closed	3	7	1	54	0	65	**12.4**
Open	39	32	30	87	10	198	**37.79**
Contribution (%)	**24.8**	**10.11**	**7.82**	**48.47**	**8.78**		

Table 3.7. Total disturbance events per category per habitat

True predation was assessed as disturbance from just 3 categories: Birds, Carnivores and Missing models, which proved significantly different between habitats (chi-squared = 50.6, df. = 8, p = < 0.001). Birds accounted for over half of all predation events (58.04%). Missing models were recorded the fewest times (n=41, 18.3% of all predation events). Closed habitat had the fewest predation events (n=11, 4.91%), followed by Grown (n=15, 6.7%) (Figure 3.3). There were 51 recorded predation events by Birds in the Felled habitat, accounting for 39.23% of all Bird events. The fewest Bird predation events occurred in the Closed habitat (n=3, 2.3%). The highest number of predation events by Carnivores was recorded in Open habitat, where 32 events accounted for 60.38% of all Carnivore events. The fewest Carnivore predation events occurred jointly in Felled and Grown habitats (n=3, 5.67%). The highest proportion of Missing models were recorded in Open habitat (n=30, 73.17%). No missing models were recorded in the Grown habitat. (Table 3.7). Total predation events decreased with plantation age, with the majority occurring in Open habitat (45.09%) (Figure 3.3).

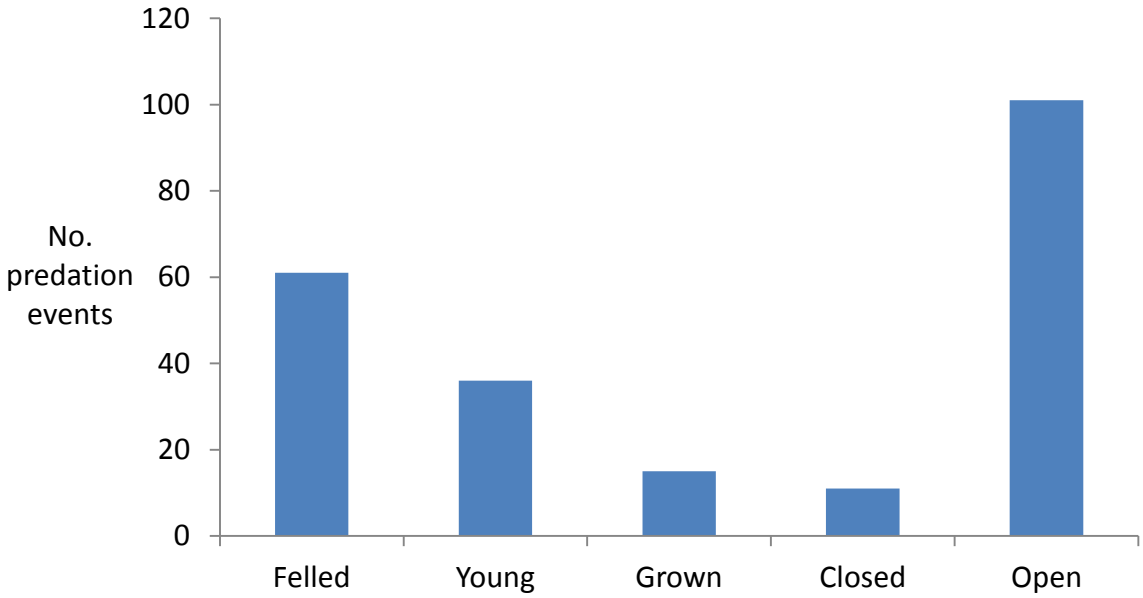


Figure 3.3. Total predation attacks per habitat type

Bird predation levels decreased with plantation establishment, a trend mirrored in Missing models. The highest number of bird attacks occurred in Felled habitats (51 models with predation marks, contributing 83.6% of all predated models within Felled). Carnivore attacks were relatively constant in all plantation stages. Open habitats experience the most predation events (101 models with predation marks, contributing 45.09% of all predated models), whilst also maintaining the most equal ratio between the three categories of predation (Birds 38.6%, Carnivores 32%, Missing 29.7%).

3.5 Discussion

3.5.1 Prey

The highest abundance of small mammals was recorded in compartments at the early stages of the plantation cycle (i.e. Felled and Young), where undergrowth had yet to mature and grasses dominated (Figure 3.2). Pooling data from all sessions indicated small mammal abundance declines rapidly as plantation compartments mature, with undergrowth succession and expanding canopy cover limiting the dominance of grasses, until eventual canopy closure shades out all vegetation (Fernandez *et al*. 1994).

Figure 3.2 illustrates the observed trend is mirrored by species diversity. *A. sylvaticus* dominates in early-stage compartments which are associated highest with vegetation dominance by grass communities. Closed habitats support a small but diverse population of small mammals, characterised by an increase in undergrowth permeability associated with increased shade from canopy closure.

There are two possible hypotheses to explain small mammal distribution in plantation forests; habitat suitability or colonisation dynamics. Open compartments provide a test between these hypotheses. Open compartments are well established, like Closed compartments, however are composed of established heath and scrubland with an associated absence of significant canopy cover, like Felled and Young compartments.

The succession through plantation stages from Felled to Closed sees the development of bare ground into a habitat dominated by grass and herb communities within a mosaic of planted trees, until eventual canopy closure shades out undergrowth vegetation. If small mammal presence within a compartment was accounted for by colonisation potential, we would expect high diversity and abundance in both Open and Closed habitat types. Open compartments only recorded one species presence (*Apodemus sylvaticus*), while Closed compartments recorded the highest levels of species diversity (jointly with Grown). This suggests that small mammal distribution is primarily determined by habitat suitability, i.e. plantation compartments, and secondly by colonisation dynamics, i.e. plantation stage. The exception is highly-dispersive, generalist species, such as *A*. *sylvaticus*, which have the ability to rapidly colonise and exploit young compartments (e.g. Felled and Young) (as in Morrison and Anthony 1989 and Fernandez *et al*. 1994). *A. sylvaticus* are the most mobile species in this study, capable of fully exploiting heterogeneity within dynamic habitats through rapid dispersal and adaptation (Halle 1993), and are also known to have significantly larger home range than sympatric *M*. *glareolus* (Crawley 1969). The absence of *M*. *glareolus*, *S*. *araneus* and *S*. *minutus* in exposed habitats (i.e. Felled, Young and Open), suggests that protection from predators, in this case by the establishment of canopy cover, is a significant factor in determining habitat suitability for the majority of small mammals.

Low capture rates of *M. glareolus*, *S. araneus* and *S. minutus* in Session 3 could have been due to limited trap availability due to high *A. sylvaitcus* captures. Further research should be conscious of this factor of trap dominance, potentially increasing the number of available traps if results are similar.

Alternatively, low capture rates of *M. glareolus* could be a factor of low population levels experienced during fluctuations within multiple-year breeding cycles (Wiger 1979), highlighting the importance of temporal data in future research.

3.5.2 Predation

Two direct forms of predation occurrence were recorded on plasticine models (Birds and Carnivores), as well as Missing models which were assumed to be predated. Levels of predation events were higher than similar studies using this method (see Wüster *et al*. 2004) suggesting that this is a suitable method for investigating potential predation levels in this landscape.

Total predation pressure decreases with plantation maturity, primarily because of a reduction in bird predation as the canopy closes (Figure 3.3). However, in this study all models were all placed fully exposed with no overhead undergrowth cover so as to represent a basking adder as closely as possible. This suggests that habitat-specific predation levels do truly follow this trend, as opposed to being a factor of model visibility from increased canopy cover. Compartments at the start of the plantation cycle are most closely associated with predation events and follow a decrease with plantation age, rather than decreased attacks being an artefact of model position.

Avian predation events contrast with those recorded for Carnivores, which remained relatively constant in all compartment types. The distribution of Missing models by

compartment type closely matched that of avian predation events (Table 3.7), perhaps suggesting a possible relationship between Missing models and removal by potential avian predators, however it must be noted that this is by no means conclusive. Felled compartments had high avian predation levels and high numbers of Missing models, despite few Carnivore predation events. This is further supported in Grown and Closed habitats, which had the fewest Bird predation events and numbers of Missing models. If Missing models are assumed to reflect avian predation, total potential predation from birds would equal ~76%, a significant majority of all predation events. This suggests birds are the highest potential predator of adders in plantation forests, concurring with studies in other landscapes in the UK (Prestt 1971, Phelps 2004). Birds could therefore represent the most likely animal group to have any sort of population limitation effect on adders from predation, however there is a shortage of literature relating to this topic with much previous research in this area instead choosing to investigate the danger imposed by prey dependence (Andrén 1982, Lindell and Forsman 1996, Forsman and Lindell 1997) or genetic viability (Madsen *et al*. 1996, 1999, 2000, 2004) and demonstrates a significant area of research that needs to be pursued.

Although mammals do predate on live adders, it is impossible in this study to separate the effects of genuine predation attempts from exploratory biting stimulated by curiosity rather than genuine predation. Also, the potential olfactory factor of model material type influencing disturbance events, much like rodents, should be acknowledged for carnivores. Avian attacks, which represent the majority of attacks by

likely predators (overwhelmingly so in 3 of 5 habitat classes), are probably not subject to the same source of error and may provide a clearer picture of true predation risk.

Total predation levels (Figure 3.3) follow the pattern of prey distribution (Table 3.7), except in Open habitats. As has previously been explained, Open compartments are old and well established much like Closed compartments. However unlike Closed compartments, Open compartments retain high levels of permeability and undergrowth vegetation is maintained due to few and sparsely distributed trees. Since Open habitats have relatively high small mammal abundance, and are more constant than Felled, Young or Grown habitats, they may be established components of predators' home ranges, resulting in high incidental predation on other species.

Although there are limitations to the use of plasticine models in this study, such as models probably being more conspicuous than real snakes potentially would be (as also noted by W*ü*ster *et al*. 2004), this method provides an exciting possibility to explore questions in predator-prey dynamics and further research should be conducted to further assess its validity. Another limitation that could have been highlighted in these data were the high levels of disturbance events attributed to Rodents (Table 3.7). Rodents have never been recorded predating on adders, and these events may not relate to true potential adder disturbance and could be a factor of the model material, which has been a factor in other studies using plasticine as a modelling material (e.g. Part and Wretenberg 2002). Similarly, model disturbance by deer decreased with growth stage, although causability in this case is thought to be incidental and more a factor of habitat permeability as would be expected with a large vertebrate, rather than intentional disturbance.

The role of adders within landscape-level predator-prey dynamics remains unclear. Adder survival has been directly correlated with prey density (Forsman and Lindell 1997), while predation levels are generally not high enough to be considered a potentially limiting factor of populations (Phelps 2004). The estimates of prey and predation levels of adders in this study could be important ecological correlates of adder distribution in plantation forests, and provide important implications for conservation management.

*Chapter 4: Distribution of the European adder (*Vipera berus*) in commercial forestry plantations*

4.1 Objectives

1. Assess the suitability of patch occupancy modelling as a method for monitoring adder populations
2. Investigate the relationship between habitat, prey availability and predation levels on adder distribution

4.2 Introduction

Assessing the status of elusive species, such as adders, is often difficult because they may frequently be present at sites but remain undetected (Mackenzie 2005). Monitoring of species such as this has often relied on presence-absence surveys. These can reliably indicate where species have been recorded, but cannot quantify the likelihood that recorded absences were indeed true absences. Furthermore the effects that habitat, season, or observer variability may have on detection probability cannot be quantified. Recent developments in occupancy modelling have established a statistical framework for wildlife monitoring based on presence-absence surveys. This has proved valuable for surveys of elusive species and herpetofauna in particular (see Chapter 1 for a review). These 'patch-occupancy' models rely on repeat sampling of sites over space or time. Repeat surveys allow the probability of detecting a species to

be modelled together with the probability of occupancy, such that occupancy can be reliably assessed independent of the confounding effects of uncertain detection. The two modelled parameters (detection probability *p* and probability of site occupancy ψ (*psi*) have associated confidence limits; it is therefore possible to indicate the certainty of observed changes in these parameters across space and time and include them as part of a management decision framework. Carrying out the same surveys in subsequent year's permits assessment of local patch colonisation and extinction rates and the environmental covariates associated with this (Mackenzie *et al.* 2006).

In the UK, adders are widely but patchily distributed with highest densities associated with southern heathlands (Reading 1997, Baker *et al*. 2006). The status of adders in Britain is unclear as there is no established monitoring method at both a local or national scale. There have been suggestions that the species may be declining due to a loss of habitat, mainly from landuse change and agricultural intensification (UK BAP 2009). Consequently adders have recently been added to the UK Biodiversity Action Plan (UKBAP) as a priority species.

Forestry plantations are highly spatially-structured man-made habitats, many planted on former heathlands, which provide a range of microhabitats suitable for adders. The growth of new grasses associated with newly planted or replanted areas supports an abundant small mammal fauna that should give a substantial food base (Chapter 3); felled and discarded logs and the bases of tree stumps provide opportunities for hibernacula (Edgar *et al*. 2010); and growing trees provide protection from aerial

predators (Chapter 3). However, in plantations, these different beneficial features are rarely present at the same site and may not be within short-range dispersal distance of each other. Furthermore, patches of suitable habitat are likely to be isolated from others by a matrix of unsuitable habitat. Anecdotal evidence suggests that adders are frequently found in forestry plantations, indicating they can be suitable habitats, but it is likely that informed management could enhance the suitability of plantations for the species. In the light of the likely effects that agricultural intensification has had on adders, forestry plantations represent a substantial potential safe haven, where with appropriate management the species could flourish.

Within a plantation forest there are discrete compartments of different tree species, clear fells and planted compartments at different years since replanting. A range of suitable and unsuitable habitats for adders are present. A challenge in assessing habitat suitability in densely vegetated habitats, and specifically with elusive species such as adders that exhibit clear season patterns in their behaviour (see Chapter 1), is disentangling the effect of differential detection probability from differential occupancy. One benefit of the patch-occupancy methods outlined above is that it is relatively easy to build models of occupancy and detection probability that include environmental and seasonal covariates, such that the factors that affect occupancy and detection can be assessed. Patch occupancy analysis is superior to traditional approaches that involve basic logistic regression as these latter do not take account of variation in detection probability associated with environmental covariates and can therefore produce misleading correlates of presence and absence (MacKenzie *et al*. 2005).

Sitka spruce (*Picea sitchensis*) is the most abundant tree species in Britain (Petty and Avery 1990, Forestry Commission 2010). Although mature stands of sitka spruce do not possess a large crown canopy like similar stands of deciduous species may, lateral growth of lower branches is extensive and established stands block light from the forest floor. This is especially evident in commercial plantation forests where tree densities are higher than in natural forests (Fernandez *et al.* 1994). Sub-canopy light levels are so low that the ground is bare, except for mosses, as all other vegetation is shaded out (Hill 1979). Consequently ground vegetation is largely absent at the time of clear-felling. A rich vegetation layer of grasses, heather, bramble, bracken and herbs is found amongst the mosaic of young conifers during the first five years of growth after replanting. However this habitat is short-lived and will begin to fade with tree growth and canopy closure (Fernandez *et al.* 1994).

The aim of this chapter is to use patch occupancy modelling to investigate the habitat associations of adders, and so attempt to understand the implications of the structure and dynamics of forestry plantations for the conservation of adders in this landscape system. Specifically I will test the hypothesis that adder distribution is dictated by habitat suitability, judged in plantation forests by the availability of potential basking sites. Youngest plantations (i.e. Felled) will have the lowest levels of undergrowth and canopy cover and therefore the most potential basking sites, while the reverse will be true for established plantations (i.e. Closed).

4.3 Methods

4.3.1 Study area and habitat descriptions

The spatial ecology of European adders (*Vipera berus*) was investigated in commercial production forests in the North York Moors National Park, UK. These primarily coniferous forests are commercially managed for timber production. Research was conducted in 5 forests in the North York Moors area that were known to support populations of adders (B Walker *pers. comms.*); Dalby, Langdale, Wykeham, Broxa and Harwood Dale (54°N, 0°W). In 2010 research was focussed specifically on 2 forests, after data from the first research season was evaluated. Good populations of adders existed in both Langdale and Harwood Dale, with the former being much larger than the latter. Surveys were conducted between 31/03 and 18/09 during 2009, and 29/04 to 10/10 in 2010 for the second research season. These dates were chosen based on an extensive review of relevant literature regarding the annual period of activity of adders (see Chapter 1 for a review).

The study areas each have an established infrastructure of commercially managed plantation compartments, with each compartment housing a single species of tree. Although mixed compartments were present, they were infrequent and not used in this study. 7 species of conifer accounted for all of the plantation compartments used in this study (see Appendix H for detailed species descriptions). The same method for habitat classification of plantation compartments was used as seen in the previous

chapter, with compartments classified into 5 distinct habitat types for adder surveying (see Table 2.1).

As noted previously, 5 forest blocks were surveyed in 2009, with research then focussed on 2 forests in 2010. In 2009 53 compartments were surveyed, whereas in 2010 only 36 compartments were surveyed. (Table 4.1)

Forest	**2009**	**2010**
Dalby	16	0
Broxa	6	0
Wykeham	5	0
Langdale	15	24
Harwood Dale	11	12
Total	**53**	**36**

Table 4.1. Number of sites (compartments) surveyed in each forest for both 2009 and 2010

In 2010 research was focussed specifically on 2 forests; Langdale and Harwood Dale, both of which were known to harbour adders. These 2 forests were split into 3 forest sections to account for accessibility from surrounding heathland, a known optimal habitat of adders. Langdale, due to its larger size, was partitioned into a 'Core' and a 'Periphery', while Harwood Dale was classified as a small forest. An equal number of plantation compartments were surveyed in each of the forest sections (n=12) to investigate the effect of accessibility from surrounding habitats on adder populations. The levels of accessibility were assumed to be of importance when considering the limited dispersal ability of the study species.

4.3.2 Presence-absence surveying

Surveys were conducted to record presence of adders using a timed visual survey approach. This method of monitoring was chosen as it allowed presence-absence data to be collected with low resource use. Other methods of snake monitoring were considered (and previously discussed in), however visual surveys were chosen as the suitable data collection method in this study. Adders are an easy species to identify by a trained fieldworker and so presence data is reliable. As noted in the previous chapter, this species is sexually dichromatic which allows for visual sexual identification by the observer. Although initially highly cryptic, at least to the human eye, when observed, adders are easy to identify from the surrounding habitat. Only two sympatric legless reptiles occur within or near to the study sites; the non-venomous colubrid *Natrix natrix* and the lizard *Anguis fragilis*, neither of which bear any resemblance to *Vipera berus* (Arnold and Ovenden 2002).

Surveying was restricted to days of suitable basking conditions, characterised by humid, dry, warm or sunny weather (Reading 1996, Luiselli and Capizzi 1997). Surveys were not carried out when climatic conditions were assumed to yield no snake activity (e.g. rain) as incorrect data, i.e. false absences due to decreased basking, foraging or mating behaviour in suboptimal conditions, may be recorded. Surveys were constrained to 1 hour visual surveys of each compartment. Line transects were not practical due to variation in vegetation density and topography. All snakes were recorded using a slow, ambling walk (as described by Kéry 2002). Surveys commenced 15m inside each compartment to reduce potential edge effects on adder presence which meant that all detections could be inferred as compartment occupancy. Survey

transects were not identical for repeat surveys of each compartment. In 2009 only adders detected on transects were recorded by GPS, however in 2010 all adder locations were marked to provide an overview of total adder distribution within the study sites.

Survey order was randomised during both years to avoid temporal site bias. Compartments were categorised into groups of 3 based on similar geographic location. This would ensure minimal time spent travelling between them to survey whilst still maintaining an unbiased sampling schedule. Only one forest was surveyed on any one day to maximise potential surveying opportunities.

During each survey, presence or non-detection plus compartment (i.e. habitat) type was recorded following Mackenzie *et al.* (2003). Adder presence was classified by both adder and fresh slough detection (i.e. slough still complete, with no damage) as these both provide indications of adder presence within the compartment.

Each adder basking site location, time of encounter and altitude was recorded with a GPS (either Garmin GPSMAP® 76 or GPSMAP® 60Cx; Garmin (Europe) Ltd – Liberty House, Hounsdown Business Park, Southampton, Hampshire SO40 9LR, UK). The location was marked with a piece of flagging tape to provide a visual notification for future surveys or as a location confirmer when returning to collect habitat data.

4.3.3 Patch Occupancy Modelling

Presence-absence data obtained from repeat surveys of the same sites were fitted to a series of models representing combinations of environmental variables using program PRESENCE2 (Hines 2006). Model selection was used to identify the variables that affected occupancy and detection probability. Best fitting models were identified on the basis of AIC (Akaike's Information Critereon) (MacKenzie *et al.* 2002, 2003, Finley *et al.* 2005, Kery and Schmidt 2008).

Patch occupancy modelling was chosen as the analysis toll for the presence-absence data as it allows occupancy to be estimated while accounting for imperfect detection which invariably occurs when surveying cryptic species. Practically it also allows monitoring to occur at a large spatial scale with an associated low cost in time

Additionally, two seasonal analyses were conducted, firstly as a single sampling covariate with levels (1, 2 and 3, representing Spring, Summer and Autumn respectively), and secondly as separate sampling covariates. Seasons were categorised as Spring (01/09-14/05), Summer (15/05-31/07) and Autumn (01/08-15/10). These analyses were conducted to investigate if estimates of occupancy probability changed with season throughout the year.

4.4 Results

A total of 270 surveys were carried out in the 89 compartments over the two years, with 57 adders being detected. Adders were present in 41 surveys (15.2%). Habitat-specific survey data can be seen in Table 4.3. Grown compartments produced the most presence surveys (24, 38.7%) and also the most adders (34). Closed compartments provided the fewest presence surveys (2, 1.9%) and also the fewest adders (2). Individual compartment survey records can be viewed in Appendix K.

Habitat	Sites	Surveys		No. presence surveys		No. adders		% surveys present	
Felled	14	**38**	(10/28)	**5**	(2/3)	**7**	(2/5)	**13.2**	(20/10.7)
Young	12	**37**	(14/23)	**6**	(0/6)	**7**	(0/7)	**16.2**	(0/26.1)
Grown	19	**62**	(28/34)	**24**	(5/19)	**34**	(6/28)	**38.7**	(17.9/55.9)
Closed	34	**104**	(104/-)	**2**	(2/-)	**2**	(2/-)	**1.9**	(1.9/-)
Open	10	**29**	(-/29)	**4**	(-/4)	**7**	(-/7)	**13.8**	(-/13.8)

Table 4.2. Total data for presence-absence surveys. Numbers in brackets indicate split of adder detections between years: 2009/2010

Grown compartments recorded the most presence surveys (24), while Closed compartments recorded the fewest (2), despite having the highest survey effort (104 surveys) (Table 4.2).

Grown habitats had the highest percentage of sites recorded as occupied (12/19, 63.2%), while Closed had the fewest (2/34, 5.9%) (Figure 4.1). Felled, Young and Open

compartments all had relatively similar proportions of occupied compartments (5/14, 35.8%, 4/12, 33.3% and 3/10, 30% respectively).

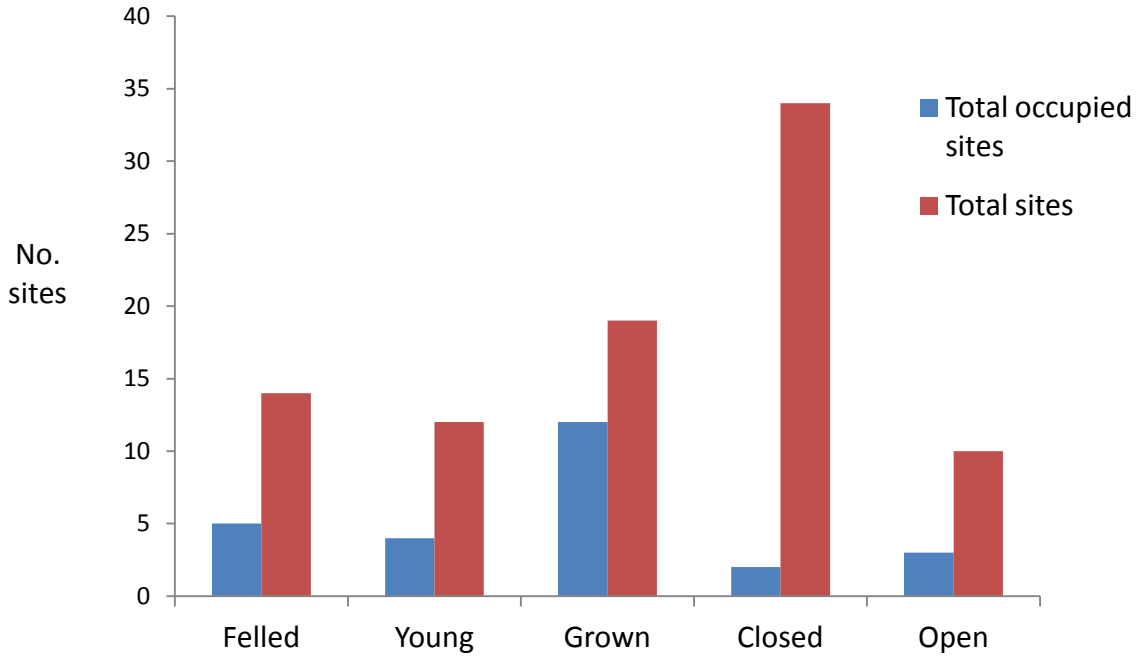


Figure 4.1. Blue bars indicate total number of occupied sites per habitat, red bars demonstrate total number of sites per habitat

There was no significant difference between occupied and unoccupied compartments for both tree height (Two sample unequal variance t-test n=17, p=0.115) and tree density (Two sample unequal variance t-test n=17, p=0.152).

The percentage of presence surveys per habitat type changed during the research season (Figure 4.2). While Grown compartments maintained high levels throughout (31-46%), other habitats, such as Young and Open, varied (0-50% and 0-30%, respectively). Only two habitats (Felled and Grown) had adder presence recorded in all seasons. Closed habitats only recorded adders in Spring, where presence surveys only accounted for 5% of all surveys.

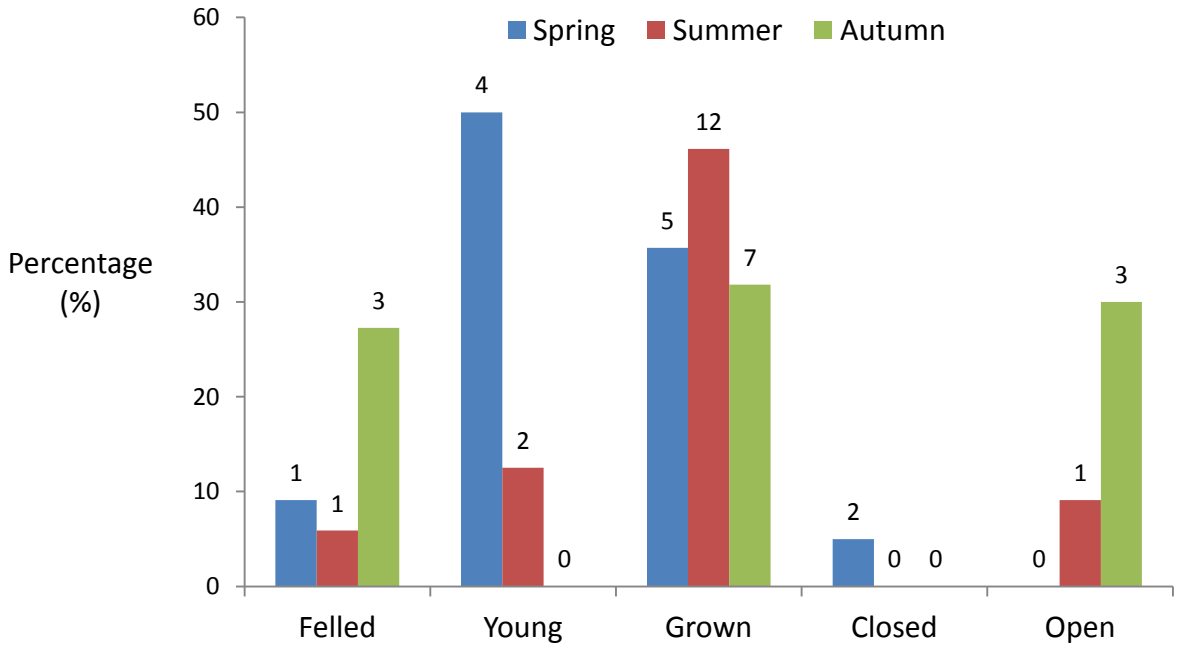


Figure 4.2. Percentage of present surveys per habitat type, per season, with associated number of present surveys above each bar

Table 4.3 presents the results from the patch occupancy analysis using PRESENCE. Model selection is based upon AIC, an information-theoretic approach to model selection, whereby lower values indicate higher parsimony (Burnham and Anderson 2002). Models are presented in a system similar to those commonly used in mark-recapture analyses, with two terms in parentheses indicating the factors present for each associated parameter (Lebreton *et al*. 1992) – in this case the influence of habitat type on estimates of occupancy (psi) and detection (p) probabilities

Model reference	Model description	AIC	Delta AIC	AIC weight	Model likelihood	No. parameters
1	psi(.),p(habitat)	197.97	0.00	0.6358	1.0000	7
2	psi(seasons*),p(habitat)	199.72	1.75	0.2650	0.4169	8
3	psi(seasons),p(habitat)	203.50	5.53	0.0400	0.0630	10
4	psi(habitat),p(.)	203.68	5.71	0.0366	0.0567	7
6	psi(habitat),p(habitat)	207.04	9.07	0.0068	0.0107	12
8	psi(.),p(.)	215.86	17.89	0.0001	0.0001	2

Table 4.3. Patch occupancy analysis for total data from presence-absence surveys calculated using PRESENCE. Analyses are arranged in order from lowest delta AIC value, i.e. the model which best fits the data. Delta AIC is the difference in AIC values between each model and the low-AIC model.(See Appendix I for full table of models)

Models with estimates of detection probability (p) varying by habitat type best fitted the data, while there was no good support for an effect of habitat type on estimates of occupancy probability (Table 4.3). A likelihood ratio test between models 1 and 7 was not significant (chi-squared = 0.93, df. = 5, $p > 0.25$) therefore indicating that adding the habitat term to psi does not significantly improve the fit of the model to the data.

The most parsimonious model (Table 4.3, model 1) suggested that estimates of detection probability varied with habitat, ranging from between 0.027 (Closed) to 0.5162 (Grown) (Figure 4.3). Detection probability increased with plantation growth stage until canopy closure (i.e. Closed), at which point it declined to near zero. The naïve estimated occupancy remained constant (=0.2921) across all habitat types, as did the modelled occupancy estimate (=0.7137).

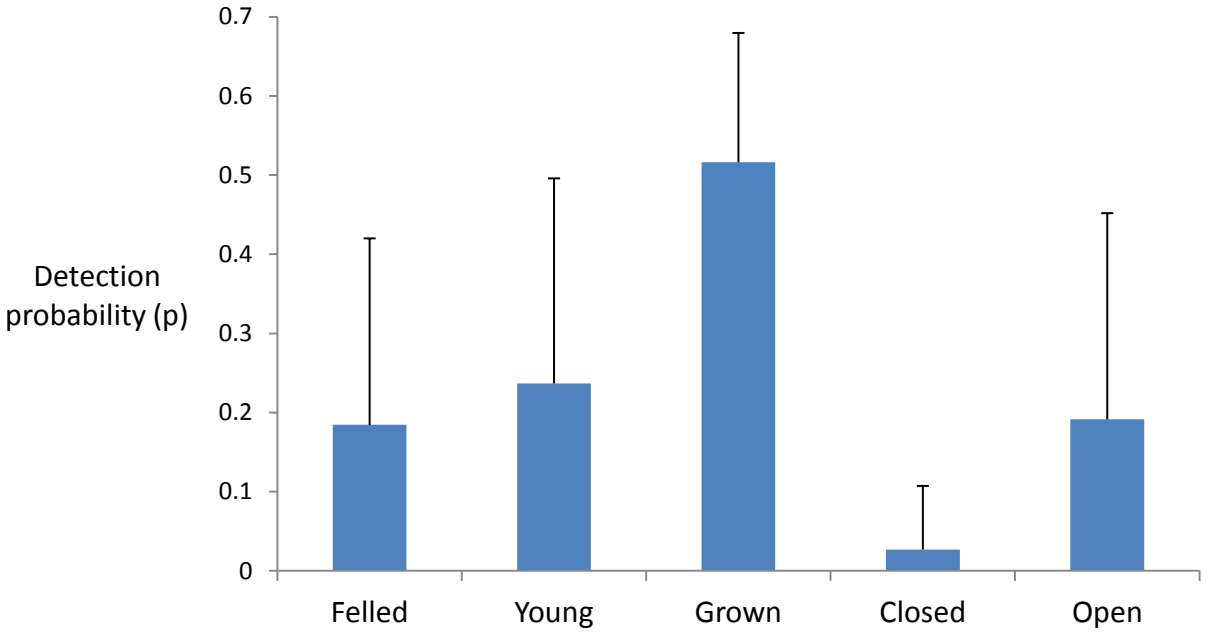


Figure 4.3. Adder detection probability per habitat calculated using PRESENCE, errors bars indicate 95% confidence intervals

Including additional sampling covariates to the data did not produce more parsimonious models than model 1 (see Appendix I). The models investigating the effect seasons as covariates of detection probability (models 2) strongly suited the data.

It was possible that the large number of 'closed' sites surveyed and the very low number of encounters associated with them skewed the results of the PRESENCE analysis. The same models were therefore run with 'closed' sites removed, but the results did not differ qualitatively from those obtained with the full dataset and are therefore not presented.

4.5 Discussion

The distribution of adders within this dynamic, spatially structured landscape was widespread, although habitat preferences were evident. Adders were found in all habitats and in all seasons surveyed, although not in all habitats in all seasons.

The basic data obtained from presence-absence surveying indicated that adder distribution varied with habitat type (Table 4.2). If we take the trend of % of present surveys per habitat as an indicator of adder distribution, it suggests an increase in adders through the plantation cycle until eventual canopy closure (i.e. Closed). This does not agree with the original hypothesis that habitat suitability will be based on basking site availability, except that Closed habitats had the fewest basking site opportunities which was supported by the fewest presence surveys.

Established plantation compartments that still provided basking opportunities (e.g. Grown) recorded the highest number of adders as well as the highest number of occupied sites, however the proportion dramatically declined with canopy closure as potential basking sites became increasingly limited (e.g. Closed) (Fig 4.1). Grown compartments recorded more presence surveys, more adders and the highest percentage of occupied sites of all habitat types (Table 4.3, Fig 4.1).
Grown sites provide the highest potential for colonisation whilst still maintaining suitable habitat structure to sustain adder populations, i.e. pre-canopy closure. These data suggest that adder distribution is driven by colonisation dynamics from compartment establishment and not by habitat suitability based on basking site availability.

However these data, unlike patch occupancy analysis, do not account for the confounding factor of imperfect detection. Patch occupancy analysis using PRESENCE resulted in a best-fitting model that suggested probability of detection varies by habitat, but that occupancy probability was not affected by any of the environmental variables examined, meaning adders are equally as likely to occupy any habitat in the plantation matrix (Table 4.3). Estimates of detection probabilities from this model follow the same trend as shown in the basic data previously; an increase with plantation age before decreasing sharply with canopy closure (Fig 4.3).

Detection probability increasing with plantation age could be associated with basking site availability. Basking site opportunities are highest in Felled sites as undergrowth is undeveloped and canopy cover non-existent, and decreases with compartment establishment as tree and undergrowth cover increase. The rise in detection probability could be due to a decrease in the total viable area within compartments in which to survey for adders as patches of suitable basking habitat increasingly become smaller and isolated. The detection probability dramatically declines with full canopy closure because of decreased habitat permeability, decreased visual ability due to low light and thick branches and increased disturbance from the surveyor. It is also possible that detection probability is a function of population density and the pattern observed relates to differences in density between compartment types.

The models that explored the effect of seasons and habitat as categorical variables of occupancy fitted the data particularly well (model reference 2). This suggests there may be seasonal differences in occupancy however there is not enough data to be conclusive and represents an area of analysis that would benefit from further research.

Although site surveys were not evenly distributed between months or seasons, the data suggest that this could be an important factor in confirming adder occupancy. This analysis has identified this subsection as being of particular interest to future research, as temporal effects on distribution may be more important than habitat.

The seasonal differences in adder encounter rate observed between habitats (Fig 4.2) and the support for models incorporating differences in occupancy with season (Table 4.3) pointed to a potential interaction between the effects of season and habitat on occupancy. However, models with psi(habitat*season) terms proved unstable, probably because of the relatively small amount of data and large number of model parameters.

Very limited data were collected for tree height and density of all compartments, of which there was no significant difference between occupied and unoccupied. Although this study has not fully clarified the relationship between these factors and adder distribution, these parameters will be particularly important to further investigate in future studies as habitat management is becoming increasingly used as a conservation tool.

Closed compartments recorded the fewest presence surveys and also the fewest adders, both equalling just 2 (Table 4.4). Interestingly, both adders detected in Closed compartments were restricted to canopy gaps created by natural tree falls, which significantly increased solar exposure through the canopy opening. In mature forests,

breaks in the canopy through natural tree falls, or similar localised patches created by habitat management, could represent an important refuge for adder populations.

All analysis for the investigation into the spatial ecology of the adder in this landscape was conducted using site-specific presence-absence data. Although plantation compartments form the majority of the forest landscape, smaller peripheral and fragmented habitat patches should not be discounted as potential viable adder habitat. The use of 'Open' areas that were not surveyed, such as roads, rides and habitat verges could be valuable corridors for dispersal, but also should be regarded as potential habitat in their own right (Edgar *et al*. 2010).

Presence-absence data was obtainable in all habitats and at all times throughout the research period, although this was dependent on suitable climatic conditions. Future research should also attempt to incorporate data collection using individual identification of adders. This would enable further investigation into the movements, habitat associations, range and ecology of adders, whilst also allowing wider parameters to be investigated, such as population fluctuations, reproductive ecology and community structure. Individual marking has been widely used with this species, with both invasive (e.g. PIT tags – Reading 1997) and non-invasive methods available (e.g. scale-sclipping – Prestt 1971, Luiselli *et al*. 1995, individual patterning – Sheldon and Bradley 1989, Benson 1999). Radio telemetry would provide clear data for individual dispersal and movements, and is a method yet to be fully exploited with this species in this landscape, although it has previously been used in others with relative success (Forsman 1995, Olsson and Madsen 2001, Krupitz 2009).

The use of the novel method of patch occupancy analysis in this study has identified a new avenue for research into the spatial ecology of snake species. Previous similar research has relied on time-expensive methods such as capture-mark-recapture (Mills *et al*. 1995, Whiting *et al*. 1997) and radio telemetry (Johnson 1995, Roth 2005, Kapfer *et al*. 2008, Wasko and Sasa 2009). Although this data does have its own equal value, when used in conjunction with patch occupancy analysis a more comprehensive evaluation of the species landscape ecology can be achieved.

The reasons for the utilisation of a wide range of habitats by adders within the landscape are unclear within the context of this research. It is therefore likely that a combination of improved management of local habitat patches and increasing landscape connectivity is important in maintaining adder populations in plantation forests.

Chapter 5: Final discussion, conclusions and implications for conservation

5.1 Patch occupancy modelling: suitability for future monitoring

This study has demonstrated that patch occupancy modelling is a viable approach for the monitoring of adders, and for studies their spatial ecology. My data suggest that detection probabilities for adders vary with habitat, emphasising the importance of accounting for detection probability in surveys of this species. This highlights an important aspect of patch occupancy analysis, as it provides a clear demonstration that methods that do not take account of detectability could be confounded by the effects of imperfect detection. This is further supported in my analysis which suggests no clear differences in occupancy probability between habitats, therefore patterns in encounter rate are better explained by detectability, which itself may be a function of other factors, e.g. populations size or climatic conditions. Modelled occupancy in the best supported model was high (71%) but detectability was low across all habitat types, i.e. only 52% in Grown which recorded highest detectability, and much less in others. There was also relatively high variability in the estimate of occupancy, ranging between 42-89% for the 95% confidence interval. Variability in the null model was much lower (25-53%), although estimated occupancy was also substantially lower (39%). Habitat type was favoured over other factors, such as survey seasons, in explaining adder detectability or distribution in plantation forests. Additional surveying, sampling and site-specific data, would allow further clarification using the

patch occupancy modelling technique to explain the factors most influencing adder distribution in this landscape.

A recent report by the Amphibian and Reptile Conservation Trust reported an alarming national decline in adder populations in recent years, stating it is now the rarest widespread reptile species in the UK (Wilkinson and Arnell 2011). Currently, no monitoring protocol for adders is well established in the UK at either a local, regional or national scale. This study has identified patch occupancy methods, using presence-absence data, as a potential framework for establishing a simple and functional monitoring method in the UK. However, the practical suitability of extensive presence-absence surveying in future monitoring is debateable. Large survey effort in the plantation forests that I studied resulted in relatively low numbers of adder detections in both research seasons. Surveying is time-consuming and physically demanding in some habitat types, particularly 'Grown' compartments where irrigation ditches are commonly masked by a thick layer of heather. Ease of movement varies hugely between habitats, meaning that adopting time-constrained surveys often resulted in differences between total distance covered within compartments. Nevertheless, it is clear that methods similar to those employed in this study would provide appropriate data for widespread monitoring of adders. The strong evidence that my data provide for clear differences in detectability between habitats indicates the importance of accounting for habitat-specific differences in detectability in any method adopted for distribution surveys of the species. Furthermore, the evidence that habitat occupancy may vary seasonally suggests that it may be important to repeat surveys seasonally, or stratify survey effort by season.

My data demonstrate that Closed compartments are largely unsuitable for adders; although dispersal through them is not necessarily blocked, the very low encounter rate of adders in this habitat suggests that they must limit dispersal in some way. Surrounding compartments could also be factored into a more complex analysis of the factors determining occupancy, as surrounding permeability would undoubtedly affect colonisation potential.

5.2 Determinants of adder distribution

Adders were found in all habitats surveyed within plantation forests. Basking site microhabitat analysis demonstrated that basking sites are significantly different to the surrounding habitat and therefore basking site availability may influence distribution (in terms of site occupancy) and abundance. At a landscape scale, the distribution of adders within the highly spatially structured habitat matrix can be explained by either habitat factors or colonisation dynamics. I assessed habitat suitability for adders in different plantation growth stages as follows:

- Adder distribution within a site is determined by basking site availability (Chapter 2)

- Small mammal prey abundance increases with an increase in plantation growth stage, before decreasing again as canopy closes (Chapter 3)

- Predation levels decrease as sites mature, the canopy closes and the ground layer is obscured (Chapter 3)

Habitat suitability is a complex mixture of, but not restricted to, the factors that I investigated in this research, and these change through the stages of the plantation cycle (Fig 5.1).

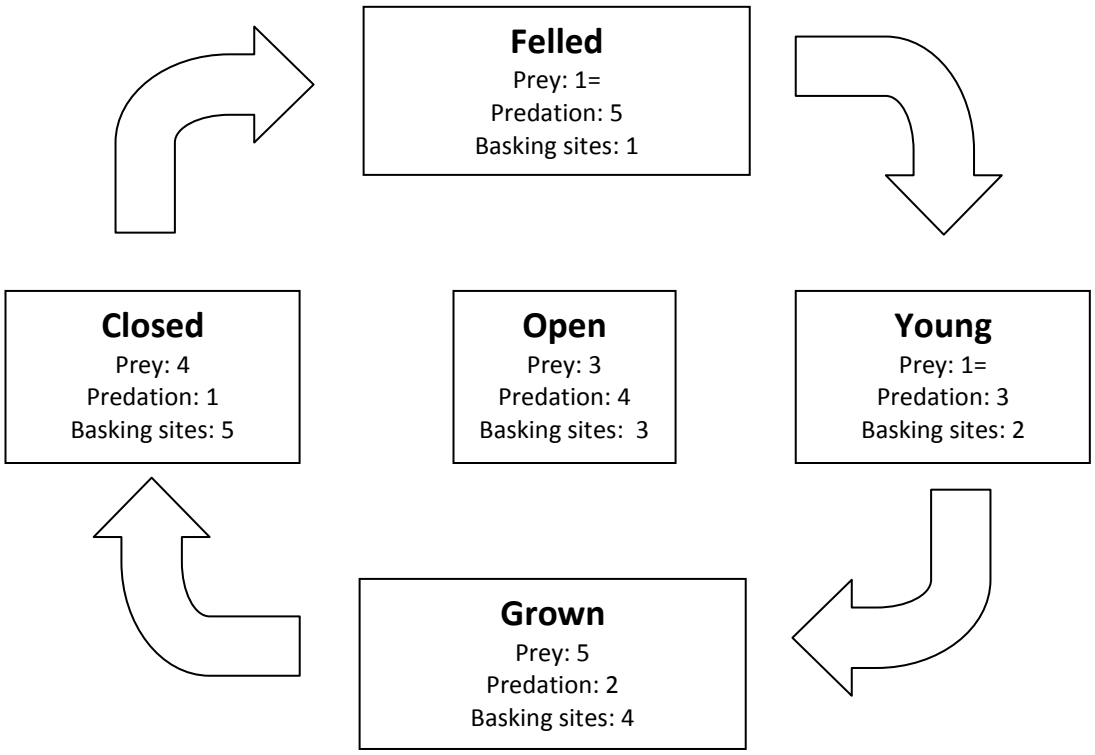


Figure 5.1. Flow chart demonstrating the plantation cycle stages, with accompanying prey/predation rates as calculated in Chapter 3 and habitat suitability governed by availability of potential basking sites (demonstrated in rank order, 1 = optimum levels)

Fig 5.1 demonstrates a ranking system based on assessments of the factors assumed to affect habitat quality in the previous chapters. This figure suggests that the most suitable habitat type is Young, judged by the balance of suitability based on prey, predation and basking sites, as it provides the highest levels of prey abundance, high levels of basking site opportunities and moderate levels of predation. The least suitable is Grown, as it has the lowest recorded prey abundance and low basking sites,

as a closing canopy increasingly limits opportunities, though there is also low predation.

Although patch occupancy analysis suggested no habitat-specific difference in occupancy, the basic surveying data, alongside the review of adder in ecology in chapter 1, suggest it would be reasonable to assume that there were more adders in some habitats and fewer in others. There are well established links between abundance and detection probability (Royle and Nichols 2003, Wenger and Freeman 2008) and the patterns in detection probability highlighted by my PRESENCE analysis could be interpreted as differences in abundance between habitats. It is important to clarify that I am not going to attempt to estimate abundance or examine abundance-detection relationships here, however if we are to assume there is a direct relationship between abundance and detection, this data suggests clear patterns in (inferred) abundance that can be related to the habitat suitability ranks in Fig 5.1. The estimates of detection probability from the PRESENCE analysis (Fig 4.3) suggest that there is a progressive increase in detectability, and therefore inferred abundance, with growth stage. However, the variability in estimates of *p* is such that there is only clear support for Closed habitats supporting fewest adders and Grown supporting most, with Felled, Young and Open all relatively similar to each other.

If we classify Closed as predominantly unsuitable, the remaining habitat types demonstrate that prey availability and basking site availability do not correlate with detectability/abundance, but the pattern in predation does. This suggests that abundance may be limited by predation, or conversely that predation may affect detectability. It is possible that the patterns in inferred abundance from the PRESENCE analysis could be determined directly from predation, or conversely that detection

probability is influenced by behavioural adjustments to variable predation pressures, or that there are joint effects of these two factors. It is also possible that it is best explained by a combination of these factors alongside colonisation potential, which increases with growth stage.

Open sites may provide a test of these possible explanations of the observed patterns in adder abundance: habitat suitability (i.e. predation risk) or colonisation dynamics. Open compartments are well established, like Grown compartments, however are composed primarily of heath and scrubland without significant canopy cover, like Felled and Young compartments. Open compartments recorded high levels of predation and low levels of prey availability, however the large confidence limits on the estimates of *p* (Fig 4.3) preclude any assessment of real differences in abundance between Felled, Young and Open compartments. The observed pattern could be a product of both processes, though restrictions on dispersal would be expected to affect occupancy more than detection probability.

The fact that adders are highly philopatric may pre-dispose them to be limited by dispersal in habitats like plantation forests, however low dispersal in patchy landscapes can bring new problems to population persistence. Fragmented landscapes, such as in the patchy matrix within plantation forests, is often associated with species living in metapopulations (Lawes *et al*. 2000, Akçakaya *et al*. 2007). In the context of plantation forests, the fact that I detected adders in all habitat types, but that there was not 100% occupancy indicates they may exist in a metapopulation in a broad sense, i.e. a subdivided population that has spatial structure (as in Griffiths *et al*. 2010). Within a metapopulation, habitat patches vary in quality and may be sources, those with

positive population growth, or sinks, which record negative growth (Pulliam 1988). The evidence that predation is demonstrably higher in some habitats and may be a significant factor affecting abundance, suggests that some habitats (particularly Young plantations) may be sinks.

An important factor to also consider with metapopulation systems is the difference between habitat attractiveness and habitat quality. Habitat attractiveness can be such that individuals are attracted to superior habitats (creating a source-sink system) or inferior ones (creating an ecological trap) (Battin 2004). The separation of these two factors within the plantation landscape could be further complicated by seasonal shifts in distribution as alluded to in the analysis.

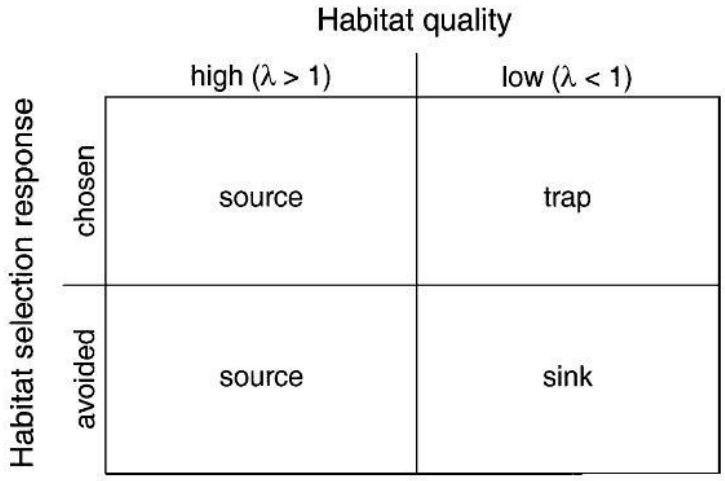


Figure 5.2. From Battin 2004: "Representation of the relationship between sources, sinks, and traps, illustrating the four possible combinations of habitat selection and habitat quality in a landscape containing one habitat of high quality in which the population growth rate is positive (habitat quality > 1) and one of low quality in which population growth is negative (habitat quality < 1). All high-quality habitats, whether selected or avoided, are considered sources. Sinks occur when low-quality habitat is avoided, and traps occur when low-quality habitat is selected."

Although the concept of ecological traps is nearly four decades old (Dwernychuk and Boag 1972), and has been investigated in a range of species (Gates and Gysel 1978, Chasko and Gates 1982, Flaspohler *et al*. 2001, Ries and Fagan 2003), theoretical work

is still relatively novel. An ecological trap represents a patch of low-quality habitat that is selected over other available, high-quality habitats, meaning a trap is simply a sink habitat that is preferred rather than avoided (Delibes *et al*. 2001). It is possible that Grown habitats represent an ecological trap, where low habitat quality is represented by low prey abundance and low basking site availability but it experiences high selection due to high colonisation potential. It is essential that the potential existence of traps is recognised in this landscape to both researchers and managers alike, and begin to understand how they might be distinguished from true sinks to assist future conservation plans (Battin 2004).

Alternatively, as adders exhibit relatively low feeding rates compared to endotherms (Andren 1982, Andren and Nilson 1983) the conservative approach to population success characterised primarily by survivability (i.e. low predation levels) suggest that Grown habitats represent a significant source patch within the forest matrix. Younger plantations (i.e. Felled and Young) that experience high prey/high predation dynamics are likely to represent sink patches, meaning that as a patch matures it is likely to improve for adders. It is possible that, unintentionally, current plantation management results in a system that is suitable for adder populations, which is further supported by the high modelled occupancy (>70%) in the best supported model. The problem that faces conservation management for adders comes during the transition from Grown to Closed habitat as suitability is significantly decreased.

If dispersal is a major determinant of distribution and abundance in plantation forests, the changing suitability of habitat over time may produce a transient, nonequilbrium (declining) system, as has been described in other low-dispersal vertebrates (e.g.

Lawes *et al*. 2000). High philopatry encourages the isolation of (sub)populations when dispersal is limited, one of the results of which can be inbreeding depression, a phenomenon already well documented in adders (Madsen *et al*. 1996). Inbreeding depression leads to a rapid loss of genetic diversity and reduced reproductive fitness, culminating in localised extinctions (Madsen *et al*. 1996, Frankham 2005). Although Madsen *et al*. (1999) showed that the effects of inbreeding depression can be rapidly reversed through the introduction of novel genes, therefore restoring population viability.

It must also be noted however that compartments within plantations are not absolute, and it is possible that habitat selection (and therefore population regulation) happens at a much larger spatial scale, with plantation forests as a whole representing a singular patch in the landscape.

5.3 Recommendations for future management of plantations for adder populations

My study has provided some indications of suitable habitat management for adder populations in plantations. There is good evidence that microhabitat selection is an important determinant of distribution within a patch, but that predation may affect abundance at the patch scale. Therefore providing basking opportunities while reducing predation risk will be important to adder success. Habitat connectivity within the landscape may also be important, however as adders were found in all habitats, the case is less clear. Although my data suggest that current management does not restrict dispersal, it is possible that if dispersal is increased than population success (in terms of patch

occupancy and abundance) would also increase. If adder distribution is limited by dispersal, improving landscape connectivity may be more important than site-specific habitat management in improving commercial plantation forests for adder populations.

However, in recommending an increase in habitat connectivity as a potential management plan its suitability must first be evaluated. Corridors are an increasingly used tool in landscape management as they are known to aid dispersal when it is previously limited (Hilty *et al*. 2006, Akçakaya *et al*. 2007), but the extent to which they effectively contribute to habitat connectivity depends on corridor type, matrix characteristics and the response of the species to both (Rosenberg *et al*. 1997, Beier and Noss 1998, Tischendorf and Fahrig 2000).

Habitat corridors have successfully acted as landscape connections for a variety of mammal (Haddad *et al*. 2003, Pardini *et al*. 2005), amphibian (Mazerolle 2005), reptile (Tiebout and Anderson 1997, Garcia *et al*. 2007), butterfly (Haddad *et al*. 2003, Townsend and Levey 2005) and bird (Bolger *et al*. 2001, Gillies and St. Clair 2008) species, and their general effectiveness widely reviewed (Simberloff *et al*. 1992, Beier and Noss 1998). Corridors aid in increasing individual dispersal (Haddad 1999, Mech and Hallett 2001), gene flow (Aars and Ims 1999, Hale *et al*. 2001, Mech and Hallett 2001), population size (Dunning *et al*. 1995, Haddad and Baum 1999) as well as generally buffering the effects of fragmentation (Pardini *et al*. 2005).

Increased landscape connectivity is not always good for species that exist in metapopulations, potentially causing 'anti-rescue effects' (Harding and McNamara 2002). Increased dispersal can negatively affect total population viability by spreading infectious diseases, parasites or predators (Hess 1996, Grenfell and Harwood 1997), increasing impacts of catastrophes (Akçakaya and Baur 1996) or losing individuals to sink habitats (Akçakaya *et al*. 2007).

Following the assessments of habitat quality, my data suggest that connecting Felled compartments should be the most successful option for improving plantations for adders. It has been observed in previous studies that patches experiencing high predation levels often create sinks (Wilcove 1985, Wilson *et al*. 1998, Rosenheim 2001), and so the connection of Felled sites may be counterproductive. Using habitat types that sustain commercial value, i.e. Young or Grown habitats, would require additional management to maintain their suitability due to canopy closure with site establishment. The most suitable habitat type to use for corridors in plantations would be Open. Open patches require little to no management, and are known to support adders. Additionally, the use of Open habitat corridors along forest rides have been successfully used for both butterfly (Carter and Anderson 1987) and sand lizard (Dent and Spellerberg 1988) populations in UK plantation forests. Unlike fast reproducers such as small mammals or invertebrates, corridors are likely to affect adder populations in the longer term, so corridors designed for adder conservation should reflect this (Hudgens and Haddad 2003). Although the importance of corridors has long been recognized, future studies would need to use metapopulation models to fully quantify their effects. Models would allow a comparison to be made between

alternative strategies, so that their effects on increased species persistence or population viability can be evaluated (Akçakaya *et al*. 2007).

Although habitat connectivity may increase adder dispersal, my data suggest that there is already dispersal across plantation landscapes. A more cost-effective conservation management scheme could instead focus on forest management as a whole, ensuring a sufficient matrix of habitat types is present to maintain heterogeneity. A large amount of forest estate in Britain is currently reaching maturity, and the rate of harvesting has been steadily increasing in recent years (Forestry Commission 2010). There is little experience of using methods other than patch clear-felling in British forests, therefore its continued use would lead to a wide-scale increase in the number of Felled and Young compartments within plantation forests, and less Closed, than has been recorded in the recent past. This younger matrix could benefit adder populations as it leads to the (eventual) formation of optimum habitat patches and a potential increase in dispersal opportunities, however this relies on population persistence in the preceding years as the number of sink patches would increase exponentially, threatening to destabilise metapopulations as a whole.

Continuous cover forestry is an increasingly used management tool in silviculture, which involves the maintenance of a forest canopy during the re-planting growth phase of younger trees, therefore avoiding the need to clearfell large tracts of forest (Mason *et al*. 1999, Forestry Commission 2004). Although commercial limitations may occur compared to other approaches, it can be balanced by the provision of enhanced, non-market benefits as more diverse forests can have multi-purpose benefits (Mason *et al*. 1999). The use of continuous forest cover could be a viable landscape-level

management method for increasing the suitability of plantation landscapes for adder populations.

The primary focus of this conservation management should be to provide suitable local habitat patches within compartments for basking. Small scale recommendations to current forestry procedures could further improve this and increase their presence and abundance within compartments. For example, during site preparation for replanting, foresters should aim to dig drainage ditches from East-West where possible. This would present a range of suitable microtopographical sites for adder basking, as southerly aspects would remain exposed for longer during the day. Development of localised, linear habitat patches such as this will extend compartment-suitability as canopy closure increases elsewhere in the compartment but basking sites are maintained.

5.4 Conclusion

Commercial plantation forests could represent a significant conservation refuge for adders, as habitat is increasingly being lost elsewhere through land use change and agricultural intensification (UK BAP 2009). Adder presence despite high heterogeneity within plantation landscapes highlights the species resilience and persistence. Future reviews (e.g. Baker *et al*. 2006) and regional to national scale conservation plans should include plantation forests as important habitat for adders in the UK.

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Appendix A – Literature review of adder morphometrics - *Males*

Authors	Year of Publication	Study Area	Study Year	Adult Male At Sexual Maturity (mm) Max Length	Min Length	Mean	SD
Prestt	1971	South England (Dorset)	1971	440	153	359.1	
Bonnet *et al.*	1999	Western central France	1999			480	49
Madsen and Shine	1993	South Sweden	1993	540	400	473.1	
Kowalewski	2007	Poland	2007	684	298	525	
Madsen	1988	South Sweden (recaptured)	1988			455	32
		South Sweden (not recaptured)				471	29.8
Forsman	1993	Baltic Sea islands (E. Sweden coast)					
			1986			488	58
			1987			478	74
			1988			462	76
			1989			486	87
			1990			478	88
Lindell *et al.*	1993	Ängskär (All south east Sweden)				494	48.8
		Infredeln				517	64.2
		Röder				499	42.1
		Svenska hörgana				496	50.6
		Uppsala				451	38.8
		Västmanland				466	37.9
Average				554.7	283.7	**475.2**	55.4

Appendix B – Literature review of adder morphometrics - *Females*

Authors	Year of Publication	Study Area	Study Year	At Sexual Maturity (mm) Max Length	Min Length	Mean	SD	No. Offspring (Mean)
Prestt	1971	South England (Dorset)	1971	496	355	434.2		7.9
Bonnet et al	1999	Western central France	1999			527	41	
Madsen and Shine	1994	South Sweden	1994					6.2
Madsen and Shine	1993	South Sweden	1993	600	470	553.4		6.7
Neumeyer	1987	Swiss Alps	1987					
Madsen and Shine	1992	South Sweden	1992	512	485	509.5		6.5
Kowalewski	2007	Poland	2007	858	545	575		
Madsen	1988	South Sweden	1988			504	33.5	
		South Sweden				504	30.2	
Andren and Nilson	1983	South Sweden	1974	750	610	671		
			1984	730	540	665		
Forsman	1993	Baltic Sea islands	1986			511	114	
			1987			534	68	
			1988			496	93	
			1989			523	88	
			1990			478	133	
Lindell *et al.*	1993	Ängskär	1993			525	61.9	
		Infredeln				592	66.7	
		Röder				546	74.5	
		Svenska hörgana				519	59.8	
		Uppsala				546	67.3	
		Västmanland				544	52.7	
Average				657.7	500.8	**537.9**	70.3	6.8

Appendix C – Literature review of adder morphometrics - *Juveniles*

Authors	Year of Publication	Study Area	Study Year	Juveniles At Birth (mm) Max Length	Min Length	Mean	SD
Prestt	1971	South England (Dorset)	1971	200	120	144.333	
Madsen and Shine	1992	South Sweden	1992			153	
Kowalewski	2007	Poland	2007	165	140	152.5	
Forsman	1997	Baltic Sea islands (E. Sweden coast)	1997	200	150		
Andren and Nilson	1983	South Sweden (island)	1983				
			1974	215	175	195	10.1
			1984	207	168	190	11.7
Average				197.400	150.600	**166.967**	10.900

Appendix D - Literature review of the methods of used to survey snake species

Font key: Normal - All species, **Bold - Viperidae**, ***Bold Italic - Vipera berus***

Transects		Time-constrained		Pitfall traps		Roads	
Andren	***1982***	Bonnet *et al*	2002	Gibbons and Semlitsch	1981	***Bonnet et al***	***1999***
Andren and Nilson	***1983***	Ryan *et al*	2002	Crosswhite *et al*	1999	**Nilson *et al***	**1999**
Mills *et al*	1995	Gillespie *et al*	2005	Enge	2001	Enge and Wood	2002
Lindell and Forsman	***1996***	Ribero-Junior *et al*	2008	Ryan *et al*	2002	Stevenson *et al*	2003
Reading	***1997***			Jenkins *et al*	2003	Jochimsen *et al*	2004
Sun *et al*	**2001**			Diffendorfer *et al*	2005	Andrews and Gibbons	2005
Lind *et al*	2005			Gillespie *et al*	2005	Diffendorfer *et al*	2005
Ribero-Junior *et al*	2008			Todd *et al*	2007	Andrews *et al*	2006
Sidorovich et al	***2008***			Cagle et al	2008	Jochimsen	2006
				Ribero-Junior *et al*	2008	Andrews and Jochimsen	2007
						Row *et al*	2007
Spotlight searches		Plots				***Herczeg et al***	***2007***
						Martinez-Freiria *et al*	**2008**
Engeman and Vice	2001	Ribero-Junior *et al*	2008			Langen *et al*	2009
Gillespie *et al*	2005						

Appendix D - Literature review of the methods of used to survey snake species

Visual Surveys	
Prestt	***1971***
Kent *et al*	2001
Altwegg *et al*	**2005**
Diffendorfer *et al*	2005
Martinez-Freiria *et al*	**2008**
Tyrrell *et al*	2009

Coverboards	
Reading	***1997***
Bonnet et al	***1999***
Kjoss and Litvaitis	2001a
Kjoss and Litvaitis	2001b
Ryan *et al*	2002
Cagle *et al*	2008

Glue traps	
Ribero-Junior *et al*	2008

Opportunistic	
Stevenson *et al*	2003
Roth	2005
Wisler *et al*	2008
Sperry and Weatherhead	2009

Questionnaire	
Reading	***1996***
Baker et al	***2006***

Flap Traps	
Engeman and Linnell	1998
Linnell *et al*	1998
Vice *et al*	2005
Tyrrell *et al*	2009

Monkey tracking	
Penner *et al*	**2008**

Funnel traps	
Prestt	***1971***
Whiting *et al*	1997
Enge	1998
Crosswhite *et al*	1999
Engeman and Vice	2001
Kjoss and Litvaitis	2001a
Prior *et al*	2001
Ryan *et al*	2002
Jenkins *et al*	2003
Vice *et al*	2005
Todd *et al*	2007
Cagle et al	2008
Ribero-Junior *et al*	2008

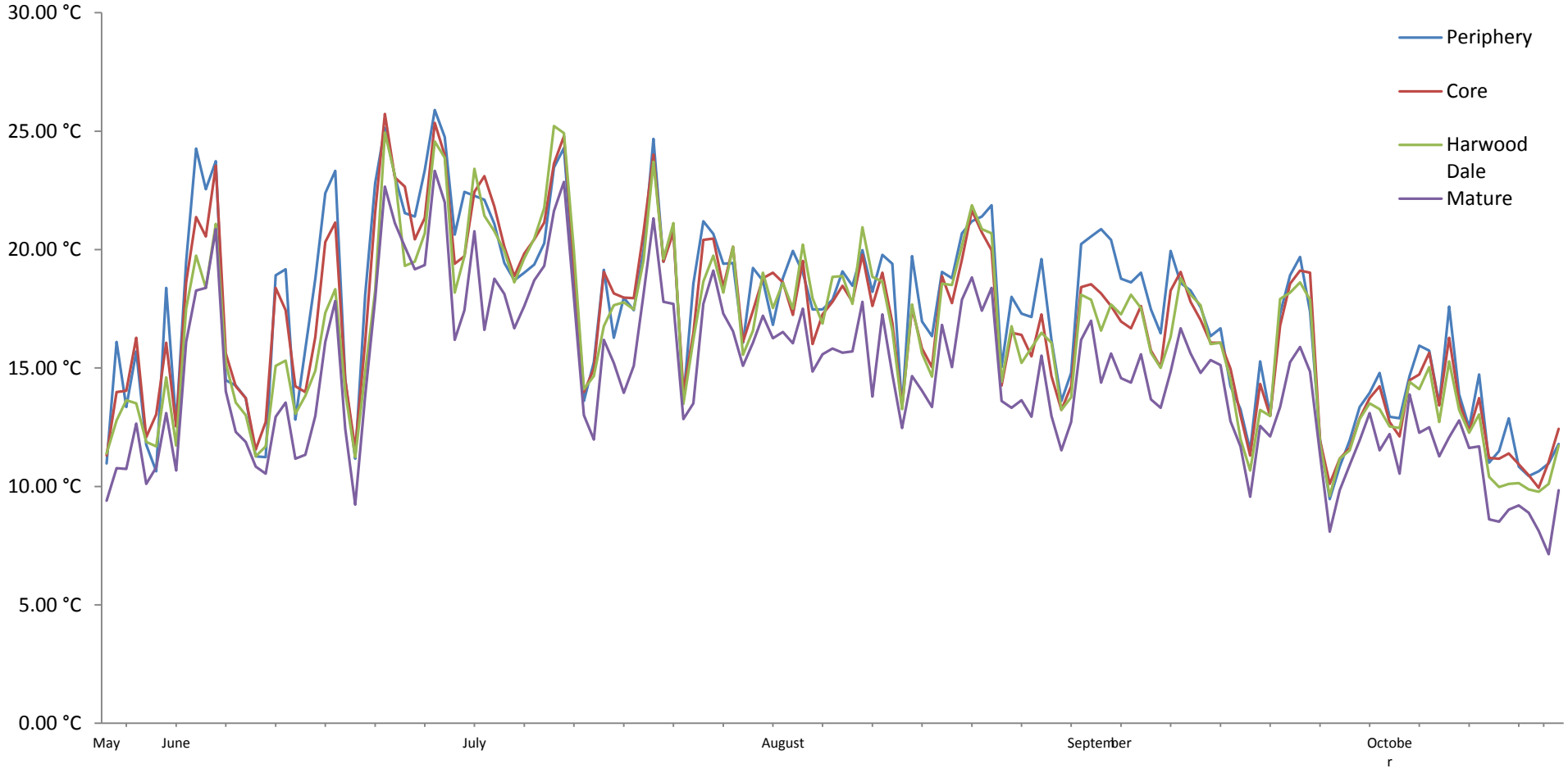
Appendix D - Literature review of the methods of used to survey snake species

Known population

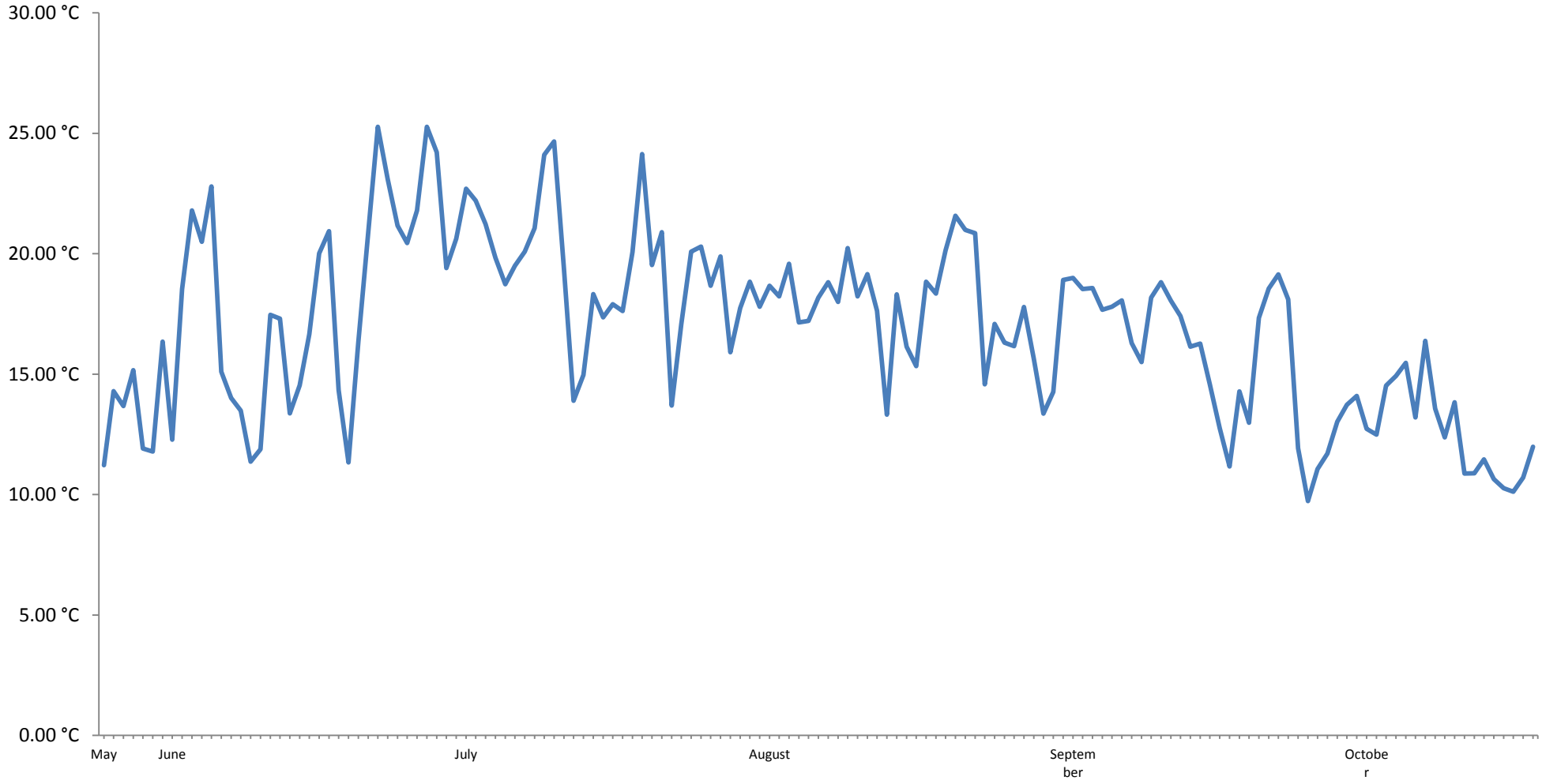
Stille et al	***1986***	**Nilson *et al***	**1999**	***Prestt***	***1971***	***Madsen et al***	***2004***
Forsman and As	***1987***	Zuffi *et al*	1999	***Andren***	***1982***	***Phelps***	***2004***
Neumeyer	***1987***	**Jaggi *et al***	**2000**	***Forsman and As***	***1987***	***Thomas***	***2004***
Madsen	***1988***	**Lourdais *et al***	**2002**	***Neumeyer***	***1987***	**Luiselli *et al***	**2007**
Madsen and Stille	***1988***	***Kasewieter et al***	***2004***	***Madsen***	***1988***	***Ursenbacher et al***	***2008***
Sheldon and Bradley	***1989***	***Madsen et al***	***2004***	***Madsen and Stille***	***1988***		
Forsman	***1991***	***Phelps***	***2004***	***Sheldon and Bradley***	***1989***		
Forsman and Lindell	***1991***	***Thomas***	***2004***	***Forsman***	***1991***		
Luiselli and Agrimi	**1991**	**Altwegg *et al***	**2005**	***Forsman and Lindell***	***1991***		
Luiselli and Anibaldi	***1991***	Luiselli *et al*	2007	***Madsen and Shine***	***1992***		
Madsen and Shine	***1992***	**Canova and Gentilli**	**2008**	***Forsman***	***1993a***		
Merila et al	***1992***	Kapfer *et al*	2008	***Forsman***	***1993b***		
Forsman	***1993a***	***Ursenbacher et al***	***2008***	***Lindell et al***	***1993***		
Forsman	***1993b***			***Luiselli***	***1993***		
Lindell et al	***1993***			***Madsen and Shine***	***1993***		
Luiselli	***1993***			***Forsman et al***	***1994***		
Madsen and Shine	***1993***			***Madsen and Shine***	***1994***		
Forsman et al	***1994***			**Johnson**	**1995**		
Madsen and Shine	***1994***			***Luiselli et al***	***1995***		
Johnson	**1995**			***Lindell and Forsman***	***1996***		
Luiselli et al	***1995***			***Forsman and Lindell***	***1997***		
Lindell and Forsman	***1996***			***Olsson et al***	***1997***		
Forsman and Lindell	***1997***			***Benson***	***1999***		
Olsson et al	***1997***			**Nilson *et al***	**1999**		
Benson	***1999***			**Zuffi *et al***	**1999**		
Jaggi and Baur	**1999**			**Lourdais *et al***	**2002**		

Capture-Mark-Recapture

Appendix E. Ambient air temperature (°C) across Grown compartments in all locations, including data for mature Closed woodland



Appendix F. Mean ambient air temperature (°C) across all Grown compartments in all locations



Appendix G. Adder plasticine model: typical placements and disturbance evidence

Typical placement:

Rodents

Deer

Carnivores

Birds

Appendix I – Patch occupancy analysis models using PRESENCE

Model reference	Model description	AIC	Delta AIC	AIC weight	Model likelihood	No. parameters
1	psi(.),p(habitat)	197.97	0.00	0.6358	1.0000	7
2	psi(seasons*),p(habitat)	199.72	1.75	0.2650	0.4169	8
3	psi(seasons),p(habitat)	203.50	5.53	0.0400	0.0630	10
4	psi(habitat),p(.)	203.68	5.71	0.0366	0.0567	7
5	psi(habitat),p(seasons*)	205.68	7.71	0.0135	0.0212	8
6	psi(habitat),p(habitat)	207.04	9.07	0.0068	0.0107	12
7	psi(habitat),p(seasons)	209.36	11.39	0.0021	0.0030	10
8	psi(.),p(.)	215.86	17.89	0.0001	0.0001	2
9	psi(seasons*),p(.)	217.85	19.88	0.0000	0.0000	3
10	psi(.),p(seasons*)	217.86	19.89	0.0000	0.0000	3
11	psi(seasons*),p(seasons*)	219.84	21.87	0.0000	0.0000	4
12	psi(seasons),p(.)	220.08	22.11	0.0000	0.0000	5
13	psi(.),p(seasons)	221.06	23.09	0.0000	0.0000	5
14	psi(seasons),p(seasons)	225.64	27.67	0.0000	0.0000	8

Appendix J – A review of adder population sizes from relevant literature

Authors	Publication year	Location	Habitat type	Population size
Prestt	1971	South England	Heathland	166
Andren and Nilson	1983	South Sweden	Heathland/	200
		South Sweden	Rough Grassland	18
		South Sweden		10
Neumeyer	1987	Swiss Alps	Moorland - Subalpine	108
Madsen	1988	South Sweden	Rough Grassland	138
		South Sweden	Rough Grassland	49
Forsman and Lindell	1991	Baltic Sea islands	Heathland/Woodland	87
Luiselli and Anibaldi	1991	Italy	Coniferous Woodland	64
Madsen and Shine	1992	South Sweden	Rough Grassland	48
Lindell *et al.*	1993	South East Sweden	Not stated	69
		South East Sweden	Not stated	51
		South East Sweden	Not stated	33
		South East Sweden	Not stated	40
		South East Sweden	Not stated	21
		South East Sweden	Not stated	85
Luiselli	1993	North Italy	Rough Grassland	58
Madsen and Shine	1993	South Sweden	Dune - Coastal	86
Madsen and Shine	1994	South Sweden	Dune - Coastal	72
Lindell and Forsman	1996	Baltic Sea islands	Rough Grassland	33
Reading	1997	South England	Heathland/Agriculture	6
Reynolds *et al.*	1999	South Sweden	Dune/Coastal	50
Madsen *et al.*	2000	South Sweden	Not stated	15-40
		North Sweden	Not stated	30-50
		South West Sweden	Not stated	60-200
		South Sweden	Not stated	50-250
		Central Sweden	Not stated	>100
Kowalewski	2007	Poland	Heathland/Moorland	100
		Poland	Mixed Woodland	
			Mean	**69.2**

Appendix K – Individual compartment survey data

Compartment	Study year	Habitat	Section	Presence-absence survey data				
1	2009	Grown	n/a	0	0	-	-	-
2	2009	Closed	n/a	0	0	-	-	-
3	2009	Closed	n/a	0	0	-	-	-
4	2009	Closed	n/a	0	0	0	-	-
5	2009	Felled	n/a	0	-	-	-	-
6	2009	Closed	n/a	0	0	0	-	-
7	2009	Closed	n/a	0	0	0	0	-
8	2009	Closed	n/a	0	0	-	-	-
9	2009	Closed	n/a	0	0	0	-	-
10	2009	Closed	n/a	0	0	0	-	-
11	2009	Grown	n/a	0	0		-	-
12	2009	Closed	n/a	0	0	0	-	-
13	2009	Closed	n/a	0	0	0	-	-
14	2009	Closed	n/a	0	0	0	-	-
15	2009	Closed	n/a	0	0	0	-	-
16	2009	Closed	n/a	0	0	0	0	-
17	2009	Grown	n/a	0	0	1	-	-
18	2009	Felled	n/a	1	-	-	-	-
19	2009	Grown	n/a	0	0	-	-	-
20	2009	Grown	n/a	0	0	0	0	-
21	2009	Closed	n/a	0	0	0	-	-
22	2009	Closed	n/a	0	0	0	-	-
23	2009	Closed	n/a	0	0	0	-	-
24	2009	Closed	n/a	0	0	0	-	-
25	2009	Closed	n/a	0	0	0	-	-
26	2009	Closed	n/a	0	0	0	-	-
27	2009	Closed	n/a	0	0	0	-	-
28	2009	Grown	n/a	0	1	1	0	0
29	2009	Felled	n/a	0	0	0	-	-
30	2009	Closed	n/a	1	0	0	-	-
31	2009	Closed	n/a	0	1	-	-	-
32	2009	Closed	n/a	0	0	-	-	-
33	2009	Closed	n/a	0	0	-	-	-
34	2009	Closed	n/a	0	0	-	-	-
35	2009	Closed	n/a	0	0	-	-	-
36	2009	Grown	n/a	0	0	0	-	-
37	2009	Felled	n/a	0	0	0	-	-
38	2009	Felled	n/a	1	0	-	-	-
39	2009	Young	n/a	0	0	-	-	-
40	2009	Closed	n/a	0	0	0	0	-
41	2009	Closed	n/a	0	0	0	-	-
42	2009	Young	n/a	0	0	0	0	-
43	2009	Young	n/a	0	0	0	-	-
44	2009	Closed	n/a	0	0	-	-	-

45	2009	Grown	n/a	0	0	0	1	0
46	2009	Closed	n/a	0	0	-	-	-
47	2009	Closed	n/a	0	0	-	-	-
48	2009	Closed	n/a	0	0	0	-	-
49	2009	Closed	n/a	0	0	-	-	-
50	2009	Closed	n/a	0	0	-	-	-
51	2009	Grown	n/a	1	0	-	-	-
52	2009	Grown	n/a	0	0	0	-	-
53	2009	Young	n/a	0	0	-	-	-
54	2010	Grown	Core	0	0	0	-	-
55	2010	Grown	Core	1	1	1	1	-
56	2010	Grown	Core	1	0	1	1	0
57	2010	Young	Core	1	1	0	-	-
58	2010	Young	Core	0	0	0	0	-
59	2010	Young	Core	1	0	1	0	-
60	2010	Open	Core	0	0	0	0	-
61	2010	Open	Core	0	0	-	-	-
62	2010	Open	Core	0	1	0	-	-
63	2010	Felled	Core	0	0	0	0	-
64	2010	Felled	Core	0	0	1	-	-
65	2010	Felled	Core	0	0	0	-	-
66	2010	Grown	Periphery	1	1	0	-	-
67	2010	Grown	Periphery	1	1	1	-	-
68	2010	Grown	Periphery	0	0	1	-	-
69	2010	Grown	Periphery	0	0	0	0	-
70	2010	Young	Periphery	1	0	0	-	-
71	2010	Young	Periphery	0	0	0	-	-
72	2010	Open	Periphery	0	0	0	-	-
73	2010	Open	Periphery	0	1	0	-	-
74	2010	Open	Periphery	0	0	-	-	-
75	2010	Felled	Periphery	0	0	1	-	-
76	2010	Felled	Periphery	0	0	0	-	-
77	2010	Felled	Periphery	0	0	1	-	-
78	2010	Grown	HWD	0	1	1	-	-
79	2010	Grown	HWD	0	0	1	-	-
80	2010	Grown	HWD	1	1	1	-	-
81	2010	Young	HWD	0	1	0	-	-
82	2010	Young	HWD	0	0	0	-	-
83	2010	Open	HWD	0	1	1	0	-
84	2010	Open	HWD	0	0	0	-	-
85	2010	Open	HWD	0	0	-	-	-
86	2010	Open	HWD	0	0	0	-	-
87	2010	Felled	HWD	0	0	0	-	-
88	2010	Felled	HWD	0	0	-	-	-
89	2010	Felled	HWD	0	0	0	0	-