

**The Influence of Aspect and Forest Edge Effects on the Ecology of
the Wood Ant, *Formica rufa* L. (Hymenoptera : Formicidae).**

**A Thesis Submitted to the University of Leicester for the degree of Doctor of
Philosophy**

By

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three edge to interior transects, a total of 82 sample nests and five control points were located around the wood. Nest location and characteristics, wood structure, and the phenology of activities were also recorded. Overall, south-facing nests received more light but lower wind speeds than the other aspects and also supported a greater diversity of tree species. Southern nests also received significantly more light in the late parts of the year than nests in other aspects. At the random sampling locations, south-facing nests received significantly more light and lower wind speeds than the controls. Controls, nests supported a higher plant species richness, but in terms of abundance, sycamore (*Acer pseudoplatanus*) and elder (*Sambucus nigra*) were found in greater numbers at nest sites than controls. The south also supported significantly higher nest densities and had a higher percentage of polydomous colonies than the other aspects. The results suggest that aspect mediated edge effects caused differences in wood ant phenology. South-facing colonies left hibernation earlier, began reproduction earlier, and had completed their life cycle before colonies in the other aspects had begun theirs. Overall, these results demonstrate to show the impacts of aspect and distance related forest edge effects on *F. rufa*.

Declaration

I hereby declare that no part of this thesis has been previously submitted to this or any other university as part of the requirements for a higher degree. The work described here, unless otherwise acknowledged in the text or by reference, was conducted by the undersigned who is fully responsible.

Signed : P.A. Clarke Date: 13/7/2005

Dedication

This thesis is dedicated to two very special people. Firstly, to the memory of my grandfather, Robert Jay, who introduced me to the wonder of the natural world during our frequent walks and fishing trips. You are truly missed; my love and thanks always. Also to Andrea, without whose constant love and support I could not have completed this work. I am eternally thankful.

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Chapter 1: Introduction

1.1 Background

Habitat fragmentation is a significant threat to the maintenance of biodiversity in terrestrial ecosystems (Young *et al.* 1996; Sih *et al.* 2000). By decreasing the size of habitat patches, fragmentation leads to the increased isolation of populations, disrupting both individual and population behaviour, the genetic make up of populations and a host of other key ecological processes (Margules 1996; Young *et al.* 1996; Clarke & Young 2000). With both taxonomic and population extinction running at perhaps 100 to 1000 times the 'normal' background rate due to habitat destruction, understanding what drives these losses is vital for future conservation efforts (May *et al.* 1995; Pimm *et al.* 1995; Hughes *et al.* 1997; Gonzalez 2000).

Fragmentation tends not to be a uniform process, but in the majority of cases, results in the formation of a mosaic of habitat fragments, which contain only a small sample of the organisms which once occupied the original continuous landscape (Saunders *et al.* 1987; Burgman & Lindenmayer 1998; Gonzalez 2000). According to Andr en (1994), in these disjointed and fragmented landscapes extinction is the dominant population process.

The impact of edge effects (including the influence of edge aspect) is particularly evident in remnant forest fragments (Forman & Godron 1986), where exposure to edge effects threatens the survival of many woodland species (Harris 1984; Murcia 1995; Didham 1997). In Britain, the clearance of forests by humans over the millennia has left the landscape severely altered, and most forests now persist as 'islands' in a sea of agricultural or urban land use (Forman & Godron 1986; Rackham 1986, 1990; Sutcliffe & Thomas 1995). As these remaining forest patches have become smaller, the relative area of 'edge' influenced habitat which they possess has increased. Hence, in many smaller fragments the entire area of the forest is influenced by 'edge- like' conditions, all interior habitat having been lost. This places interior species and communities, which are not adapted to edge conditions, under severe pressure, increasing competition for the limited resources which remain, and bringing many to the brink of localised extinction (Nicholson & Bailey 1935; Cole 1954; MacArthur 1958; Hairston *et al.* 1960; Kruess & Tsharntke 1994; Morris 1996; Bender *et al.* 1998; Huxel & Hastings 1998; Pimm 1998; Root 1998; Saurez *et al.* 1998; Laurance *et al.* 2000). For this reason,

understanding the impact of edge effects has been recognised as a key issue for conservation and has subsequently become an increasingly important focus of ecological research during the last few decades.

Research on edge effects *per se* largely emerged in the early part of the 20th century, notably with the work of Geiger (1936). At this point, interest focused mainly on the impact of microclimatic edge effects on aspects of forestry, although Leopold (1933) had noted that biodiversity tended to increase in edge habitats. It was not until the 1950s and 1960s that research on edge effects once again came to the fore, largely in response to the recognition of the impacts of habitat fragmentation. Notable works by Gysell (1951) and Wales (1967 & 1972) highlighted the potential impact of edge effects in relation to orientation and the consequent responses of edge vegetation. These works especially, recognised the effect of edge structure on observed species richness.

Edge effects have consequently been found to occur as a result of two adjacent, but quite different habitats, being separated by an abrupt divide (Geiger 1936; Matlack 1994; Murcia 1995; Fox *et al.* 1997; Gehlhausen 2000). The review by Murcia (1995) divided the processes associated with edge effects into two major categories, physical edge effects and biological edge effects.

1.2 Physical Edge Effects.

Physical edge effects are changes in the environmental conditions due to the modification of the microclimatic regime in the areas adjacent to the habitat discontinuities (Murcia 1995). In forests isolated within an agricultural mosaic, conditions between the two contrasting habitats tend to be extreme (Forman & Godron 1986; Cadenasso *et al.* 1997). Due to their relatively simple structural complexity, agricultural fields allow much greater solar radiation to penetrate to ground level during the day, but suffer higher levels of heat loss at night. Therefore, temperature fluctuation at ground level is relatively extreme (Murcia 1995). In contrast, the microclimatic conditions within a forest are much less variable, tending to be cooler and more moist than the surrounding landscape (Geiger 1965; Fraver 1994; Murcia 1995). Due to these differences, microclimatic variables such as air temperature, air and soil moisture, vapour pressure deficit, light intensity, and wind penetration can be very different between the surrounding landscape and the interior of a woodland (Geiger 1965; Marquis 1965; Wales 1967 & 1972; Whitney & Runkle 1981; Kapos 1989; Matlack 1993, 1994; Young & Mitchell 1994; Camargo & Kapos 1995; Murcia 1995).

These differences give rise to a microclimatic gradient which runs across the edge, from the extreme conditions of the surrounding landscape to the stability of the forest interior (Harris 1984; McNaughton 1989; Brothers 1993; Chen *et al.* 1995; Cadenasso *et al.* 1997). It is generally accepted that this transitional zone or gradient extends for a distance of up to three times the canopy height into the forest (Fritschen *et al.* 1971; Harris 1984; McNaughton 1989; Murcia 1995; McCollin 1998). In reality, the actual width of an edge is a product of both spatial and temporal factors, and may vary in response to diurnal rhythms, the age of the edge, seasonality, physiognomy, orientation, and successional development (Geiger 1965; Lee 1978; Whitney & Runkle 1981; Kapos 1989; Matlack 1993; Young & Mitchell 1994; Camargo & Kapos 1995; Murcia 1995; McCollin 1998; Didham & Lawton 1999).

1.2:1 Microclimatic Responses in Relation to Orientation and Solar Input.

The orientation of an edge is a very important factor in determining the extent of physical edge effects, directly influencing the amount of incoming solar radiation which is received (Chen *et al.* 1992; Fraver 1994). For example, in the northern hemisphere, north facing edges receive less direct solar radiation and are therefore cooler, and possess narrower edge gradients, than those with a southerly aspect (Kapos 1989; Fraver 1994; Matlack 1994). Those oriented to the east or west are intermediate between the two (Fraver 1994). Working in the southern hemisphere, Young & Mitchell (1994) reported that north facing edges had very distinct microclimatic regimes during the summer, with much larger edge gradients than their southerly counterparts, but that these gradients broke-down during the winter months. These findings are not unusual, being a product of the physical attributes of forested areas.

Forest surfaces have a low albedo, and therefore besides reflecting solar radiation, the forest canopy traps a large amount of energy (Oke 1987; Packham *et al.* 1992; Veen *et al.* 1996), the amount of energy absorbed by the canopy being linked to the season. Geiger (1965) reported that during the summer on a sunny day, the canopy of a dense stand of *Fagus sylvatica* can trap as much as 80% of the incoming solar radiation; only 5% reaching the forest floor. For this reason, the temperature in the canopy may be several degrees higher than at the forest floor. In contrast, most deciduous forests in winter allow over 70% of this solar radiation to penetrate to the ground, breaking down the vertical temperature profile (Sukachev & Dylis 1968; Hutchinson & Matt 1977; Barry & Chorley 1992; Kuuluvainen 1992; Morecroft *et al.* 1998).

However, the amount of energy reaching beneath the canopy may also be influenced by the local weather conditions prevalent on a particular day. In the summer months when the canopy is fully developed, on clear sunny days the greatest trapping of solar radiation occurs in the canopy itself (Oke 1987; Barry & Chorley 1992; Morecroft *et al.* 1998). Some direct solar energy, in the form of diagonal beam radiation, is able to penetrate to the forest floor, but this tends to be limited to the edges facing the sun at certain times of the day (Marquis 1965; Wales 1967). Alternatively, when the sky is overcast, greater amounts of energy, in the form of diffuse radiation, are able to penetrate laterally into the trunk space for longer periods of time (Barry & Chorley 1992). Morecroft *et al.* (1998), after a three year study in Oxford, UK, reported that the input of diffuse radiation was sufficient to warm the air beneath the canopy to the extent that the vertical temperature profile between the canopy and forest floor was broken down. They also found that temperatures within the forest on a cloudy summer's day were close to exterior grassland conditions, thus removing the impact of edge width with respect to temperature. Therefore, microclimatic edge effects may be influenced by season and weather conditions on a particular day, in response to the angle of incidence of incoming solar radiation, the number of daylight hours an edge receives and the type of incoming solar energy which is received (Marquis 1965; Barry & Chorley 1992; Murcia 1995; McCollin 1998; Morecroft *et al.* 1998).

1.2:2 The Impact of Air Flow on a Fragmented Forest.

Forested areas act to produce surface roughness which impedes both the lateral and vertical movement of air on its journey across the landscape (Oke 1987; Barry & Chorley 1992; Veen *et al.* 1996). Forest edge vegetation is therefore vulnerable to the effects of turbulence as a result of high winds striking abrupt edges. This may lead to windthrow and elevated tree mortality, an especially common feature in newly created forest edges (Williams-Linera 1990; Chen *et al.* 1992; Murcia 1995; Laurance *et al.* 1998; McCollin 1998).

Although the surrounding open landscape experiences higher mean wind speeds than the forest interior, the actual extent of wind penetration across an edge remains variable and difficult to predict (Morecroft *et al.* 1998). In fact, the degree of variability is substantially increased as the vertical structuring of edge vegetation becomes more complex (Sigmon *et al.* 1984). For example, in the rainforests of Panama, wind velocity within the tree crowns (23m) was 75% of that outside, whilst in the understorey (2m) it was only 23% (Barry & Chorley 1992).

Seasonality is also a key element. According to Sigmon *et al.* (1984), the summer foliage of deciduous forests severely reduces the mean wind speed through the canopy; flow through is also reduced where dense understorey vegetation exists. In the mixed oak forests of Tennessee, USA, Barry & Chorley (1992) report that during the winter, wind speeds inside the forest were 12% of those outside, whereas in August the figure had dropped to only 2%. In the UK, Morecroft *et al.* (1998) found similar results. Species vulnerable to wind damage are therefore in severe danger close to newly created or recently disturbed forest edges.

1.2.3 Edge Induced Air and Soil Moisture Gradients.

Relative humidity values of the forest interior and the surrounding landscape are very different from one another (Murcia 1995). Typically, the forest interior will experience much less evaporation from the forest floor, due to the lower amounts of solar radiation which reach that zone (Hutchison & Matt 1977; Oke 1987; Matlack 1993; McCollin 1998; Morecroft *et al.* 1998). The forest interior also tends to experience lower wind speeds and has lower maximum temperatures than the exterior. This leads to relative humidity being higher within the forest interior than the surrounding open landscape (Barry & Chorley 1992; Murcia 1995; Morecroft *et al.* 1998).

The humidity within the forest is, nevertheless, very much linked to the degree of evapotranspiration which is occurring, itself a product of the type and density of the vegetation found in a particular zone (Oke 1987; Chen *et al.* 1992, 1993, 1995; Murcia 1995; Gehlhausen *et al.* 2000). Therefore, according to Barry & Chorley (1992), the general increase in mean relative humidity inside a forest is in the region of 3-10% over outside values and is particularly marked in summer. The forest edge experiences quite different conditions to the interior however (Murcia 1995). According to Matlack (1993) and Malcolm (1998), edge zone temperature, elevated as it is on many occasions by the increased advection of air heated outside the forest, leads to lower relative humidity. The humidity in the edge zone may also be influenced by the increase in wind velocities which are able to penetrate into these areas, which together with increased temperature, brings about 'near edge' drying (Wales 1967; Kapos 1989; Matlack 1993; Murcia 1995; Malcolm 1998).

In fact, lower air moisture as a result of high temperature and wind velocity, together with increased evapotranspiration of edge vegetation, may seriously deplete soil moisture (Morecroft *et al.* 1998). Kapos (1989) and Camargo & Kapos (1995), working in the Brazilian rainforest, found that at the end of the dry season, edge soil moisture was seriously

depleted, with many plants at wilting point. Certainly, a severe depletion of soil and leaf litter moisture may have a serious effect on the water use efficiency of edge vegetation, as well as insects and other invertebrates living in this zone, and may reduce rates of decomposition thus lowering the quantities of available nutrients (Kapos 1989; Williams-Linera 1990; Murcia 1995; Didham 1997; Majer *et al.* 1997; Carvalho & Vasconcelos 1999; Cadenasso & Pickett 2000). Varying degrees of reduced soil moisture have been found to lead to elevated water stress in some species resulting in higher mortality rates (Kapos 1989; Williams-Linera 1990; Camargo & Kapos 1995; Murcia 1995; Laurance *et al.* 1998). It would appear that the severity of the impact of edge related changes to air and soil moisture regimes are dependent upon latitude, season and the orientation of the edge (Matlack 1993; Murcia 1995; Morecroft *et al.* 1998; Friedland *et al.* 2003).

1.3 Biological Edge Effects

Biological edge effects can be divided into two further categories, direct and indirect biological edge effects (Murcia 1995).

1.3.1 Direct Biological Edge Effects.

Direct biological edge effects occur as a result of the changed physical conditions at, or close to an edge and may have serious consequences for many species that inhabit woodland habitats (Wales 1967; Murcia 1995). The most common response of edge vegetation is an altered physiognomy, due to a proliferation of growth amongst edge plants (Matlack 1994; Murcia 1995; Malcolm 1998; Saunders *et al.* 1998 a&b; Mourelle *et al.* 2001).

In southerly facing forests dense secondary growth tends to occur, which together with the production of adventitious limbs by the remaining mature trees, acts to effectively seal the edge by way of a 'side canopy' (Gysell 1951; Wales 1967; Brothers & Spingarn 1992; Matlack 1993; Murcia 1995; Didham & Lawton 1999). These 'closed edges', although helping to reduce the severity of physical edge effects, do not produce conditions entirely comparable to those of the forest interior, although they do produce greater microclimatic stability than newly created edges (Geiger 1965; Matlack 1993). According to Camargo & Kapos (1995), changes in the microenvironment in these 'closed' edge zones may not be linear due to the nature of the vegetation behind the edge. It has been found that a 'competition induced wave of biomass' (Reichman *et al.* 1993) can occur, as some edge plants receive much greater quantities of light than others (Murcia 1995). Therefore, in edges

in receipt of higher solar radiation, microclimatic edge effects may not vary simply with distance into the patch (Williams-Linera *et al.* 1998).

In addition to a proliferation in the growth of existing species of vegetation, many studies have also reported changes in species composition within the edge zone, over various temporal scales (Gysell 1951; Wales 1967; Chen *et al.* 1992; Matlack 1993, 1994; McCollin 1998). That physical edge effects are likely to produce a different vegetation structure along the edge to interior gradient is a key factor (Murcia 1995; Fox *et al.* 1997). For example, Young & Mitchell (1994) found that many dominant trees of the forest interior were either absent, or survived with reduced abundance at forest edges. At the edge it seems that many of these interior species, unable to tolerate edge conditions, give way to earlier successional species, and to exotics not normally associated with forest habitats, but which are able to exploit this region (Brothers & Spingarn 1992; Brothers 1993; Fraver 1994; Murcia 1995; Benitez-Malvido 1998; Laurence *et al.* 1998; Mesquita *et al.* 1999). However, according to Matlack (1994) as an edge becomes older and the canopy closes (over periods in excess of 50 years), many of the invading species tend to be lost and most components of the original species composition are restored (see also Kapos 1989; Williams-Linera 1990; Didham & Lawton 1999). Therefore, the response of edge vegetation to increased light availability at the forest edge is dynamic and affects many ecological processes which occur there (Didham & Lawton 1999; Kupfer & Runkle 2003).

In evaluating direct biological edge effects it appears that common features of forest edges globally are that in comparison to the woodland interior, they have a higher species richness, an overall increase in biomass and a greater structural complexity (Matlack 1993; Fraver 1994; Young & Mitchell 1994; Fox *et al.* 1997).

1.3:2. Indirect Biological Edge Effects.

Indirect biological edge effects occur due to changes in species interactions as a result of the influences of both physical and direct biological edge effects, and cover such factors as predation, competition, herbivory, brood parasitism, pollination and seed dispersal (McClanahan & Wolfe 1987; Reese & Ratti 1988; Burkey 1993; Murcia 1995; Laurance *et al.* 1998; McCollin 1998). According to Murcia (1995) these changes tend to occur as a 'cascade' of inter-related events. For example, the greater complexity of edge vegetation may attract herbivorous insects able to take advantage of the leaf flush produced in response to elevated light intensity (Murcia 1995). This may attract insectivorous birds to the forest edge,

which in turn may attract more predators, both of which are able to maintain higher than normal densities (Reese & Ratti 1988). The subsequent increase of predation, brood parasitism and overall competition for the limited resources in these fragmented habitats, may lead to a reduction of both opportunist and traditional woodland edge species, but also to the loss of specialist interior birds (Reese & Ratti 1988; McCollin 1998). Studying edge related seed and egg predation in Belize and Mexico, Burkey (1993) found well defined effects, where predation rates remained higher close to the edge but diminished with distance into the interior.

Indirect biological edge effects are themselves potentially destructive, for their impacts largely go unnoticed by all but a few specialist biologists, focusing on a single or small groups of organisms. Although for many years it was thought beneficial to maintain forest edges in order to promote higher species richness, more recent research argues that these actions were misguided (Chen *et al.* 1992, 1995; Reese & Ratti 1998). Species interactions hold the key to ecosystem stability, and it is clear that edge effects may have serious impacts on these valuable relationships (Murcia 1995; Krebs 1994; Begon *et al.* 1996). It would appear that without a thorough understanding of the impact of physical edge effects on key aspects of the ecology of the flora and fauna of edge zones, including their interactions with one another, many conservation strategies may struggle to succeed.

1.4 Edge Effects, Fragmentation and the Regulation of Nest Microclimate by Insects.

Research into edge effects has gained momentum over the last 20 years. Studies on the impact of edge effects have covered a wide variety of factors; for example, the response of edge vegetation, species composition, avian behaviour and nest predation, seed predation, seed dispersal, and the invasion of exotic species (McClanahan & Wolfe 1987; Brothers & Spingarn 1992; Burkey 1993; Fraver 1994; McCollin 1998). However, recent evidence suggests that edge effects are a major driving force behind changes in insect populations in forest fragments (van Dongen *et al.* 1994; Didham *et al.* 1996; Berwaerts *et al.* 1998).

Although influencing all species, edge effects are particularly important for insects which inhabit woodlands, and especially those found around the woodland edge. The negative effects of fragmentation on the genetic structure of insects has revealed worrying trends (Kearns & Inouye 1997; Lewis *et al.* 1997; Fisher 1998; Frankham & Ralls 1998; Saccheri *et al.* 1998). Less work exists on the problems faced by insects from the changes in species

interactions in edge regions, especially those concerning predation and parasitism (Thomas *et al.* 1991). However, the effect of microclimate on woodland insects has been recognised for some time as a key ecological factor and is one which continues to pose significant problems for the conservation of vulnerable species (Heinrich 1974; Oke 1987; Thomas 1994; Mousson *et al.* 1999). The situation is exaggerated by the fact that many insect species require different microclimatic conditions at different stages of their life cycle. Therefore, any efforts to conserve these species must be linked to a thorough understanding of the requirements of a species at each stage of development, as well as the impacts on these organisms when these conditions are not freely available (Thomas 1994).

As poikilotherms, insects have developed a wide variety of techniques to ensure that suitable thermoregulatory control can be maintained for themselves and their offspring at all stages of development (Oke 1987; Gullan & Cranston 2000). This is particularly evident amongst the social Hymenoptera (Wilson 1971). The technique of 'fanning,' which involves using the turbulence created from rapid wing beating to regulate nest microclimate, is employed with great efficiency by some bees, notably of those of the genus *Augochlorella* (Michener 1969) and *Bombus* (Himmer 1933). For example, according to Himmer (1933) the bumblebee *B. agrorum* maintains inner temperatures within one degree of 30°C in larger nests during the summer, through a combination of nest construction techniques and fanning.

In many social wasps the technique of fanning is combined with the habit of water transport, a method used to regulate nest temperature via evaporation (Wilson 1971). Colonies of the genera *Polistes*, *Polybia*, *Vespa* and *Vespula* employ these combined techniques to maintain an equitable nest microclimate (Steiner 1930; Himmer 1933; Gaul 1952; Kemper & Döhring 1967). Wilson (1971) quotes the example of members of *Polistes* whose simple nests are composed of a single brood comb exposed to the air. Using both fanning and water transport these organisms maintain comb surface temperatures close to 34°C during the summer, the optimal temperature for brood development.

However, ants face a different set of challenges in providing a suitable environment for themselves and their brood (Wilson 1971). As workers lack wings they cannot employ the technique of fanning to regulate nest microclimate (Hölldobler & Wilson 1990). For the same reason, they cannot rely on the rapid deployment of workers to the nearest source of water for transportation to the nest to regulate nest temperature via evaporation (Wilson 1971; North 1996). Ants must rely instead on the careful location and construction of their nests to ensure that a suitable microclimate is automatically maintained (Wilson 1971; Brian 1977; Dumpert

1981). According to Hölldobler & Wilson (1990), ants achieve these requirements by utilizing a combination of strategies:

- i) nest location (placement of nests to ensure that a beneficial microclimate is obtained, e.g. direct sunlight etc) ;
- ii) efficient nest construction (utilisation of the thermal properties of various materials, e.g. soil, rocks, vegetable matter etc so as to maintain an equitable microclimate);
- iii) migration within the nest (moving the brood around the nest to meet the requirements of each stage of development);
- iv) migration among multiple nests;
- v) regulation of metabolic heat (increase or reduce the temperature within the nest locally by clustering or dispersion).

Ants in general are strongly thermophilic, which is reflected in their biogeography (Hölldobler & Wilson 1990; North 1996; Folgarait 1998). Ant diversity steadily declines along a gradient running from the tropics through the temperate zones and on to the boreal forests of Northern Europe (Hölldobler & Wilson 1990). In the UK for example, there are less than fifty species (Skinner & Allen 1996), about the same number that has been found on a single tree in Peru (Wilson 1987; Alonso & Agosti 2000). The wide range of climatic zones in which ants exist require that they utilise a variety of nest types to ensure that a suitable microclimate is maintained (Wilson 1971; Brian 1977; Dumpert 1981; Hölldobler & Wilson 1990). Nest construction varies accordingly, from the simple underground chambers of many Mediterranean and desert species, which take advantage of the stable year round temperature and humidity found a few centimetres below the surface (North 1996; Gordon 1999), to the complex construction of leafcutter colonies (genus: *Atta*), whose nests may cover an area of up to seven square metres and must provide conditions suitable for both the ants and the extensive fungus gardens within (Wilson 1971; Hölldobler & Wilson 1990; Hoyt 1998).

In Northern Europe, ants use a variety of techniques to elevate nest temperatures, from either exploiting the thermoregulatory properties of the soils, rocks or concrete surfaces, to the stability of rotting logs and stumps, or the interior of tree trunks (Donisthorpe 1927; Pontin 1961 & 1996; Brian 1977; Skinner 1987; Skinner & Allen 1996). However, by far the most striking nests among the northern species are those of the mound building ants of the genus *Formica*. Nests of the true wood ants, the *Formica rufa* group, are often up to a metre in height and several metres in circumference (Skinner 1998), the thermoregulatory properties of

which have long been acknowledged (Hölldobler & Wilson 1990). These impressive structures provide an ideal opportunity to measure the impact of forest fragmentation and edge effects on a northern species of ant.

Ants have received some attention with respect to fragmentation, but to date the study of the impacts of edge effects has been extremely sparse. Table 1.1 provides a brief overview of a sample of previous studies on ants and habitat fragmentation and/or edge effects. It is notable that only a single paper deals solely with the impact of edge effects on ants (Majer *et al.* 1997). Forest edge effects lead to changes in both the biotic and abiotic conditions of a woodland, including changes in species interactions (Murcia 1995). This study sets out to determine the influence of edge effects, including aspect, on a generalist woodland species, the red or southern wood ant, *Formica rufa* L. (Hymenoptera: Formicidae). Of particular interest will be why the wood ants select particular nest sites and how differences in the microclimate around a woodland, caused by all aspects of edge effects, impact upon key aspects of the ecology of this species.

1.5 Aims and Objectives of the Thesis.

Many of the important aspects of the general ecology of *F. rufa* colonies are likely to be affected by edge effects related to both aspect and distance behind an edge. As this is an area which has received little attention this research will set out to address a number of key questions. A detailed breakdown of these research questions and where they are answered within this thesis is provided in Table 1.2.

Table 1.1: An overview of notable research on the effects of fragmentation and/or edge effects on ants.

Subject	Location	Author (s)
Fragmentation & urban expansion.	Scandinavia	Vepsäläinen & Wuorenrinne (1978).
Impact of slash and burn on ants.	Amazonia	MacKay <i>et al.</i> (1991).
Fragmentation on genetics (wood ants).	Europe	Pamilo <i>et al.</i> (1992).
Forest disturbance of leaf litter ants.	Ghana	Belshaw & Bolton (1993).
Fragmentation on wood ants.	Europe	Mabelis (1994).
Fragmentation.	Scandinavia	Puntilla <i>et al.</i> (1994; 1996).
Fragmentation on wood ants.	Scandinavia	Puntilla (1996).
Ant litter fauna and forest edges.	Brazil	Majer <i>et al.</i> (1997).
Fragmentation on litter dwelling ants.	Amazonia	Carvalho & Vasconcelos (1999).
Fragmentation on the invasion of ants.	USA	Saurez <i>et al.</i> (1998).
Forests disturbance (fragmentation).	Amazonia	Vasconcelos (1999).
Fragmentation.	USA	Golden & Crist (2000).
Fragmentation.	Amazonia	Vasconcelos & Delabie (2000).
Fragmentation and species composition.	Amazonia	Sobrinho <i>et al.</i> (2003).

Table 1.2: Key research questions and where these are addressed within this thesis.

Research Question	Variables of Interest	Chapter
To what extent do physical edge effects modify the microclimate around the study aspects?	Temperature (°C) Relative humidity (%) Wind speed (ms ⁻¹) Light Intensity (lux)	4
Is wood ant nest location influenced by edge effects?	Microclimate & Vegetation	4
What role does microclimate play in nest location?		4
Is there a relationship between the location of nests and their proximity to both external and internal 'edges' and the orientation of nests?		4
Do edge effects determine nest density and colony persistence?	Microclimate & Vegetation	4
Is nest density within the four study aspects related to edge effects?		4
Does <i>A. pseudoplatanus</i> bud development vary around the wood?	Microclimate	5
How are activity phases (phenology) in <i>F. rufa</i> affected by edge effects?	Microclimate Food Resource	5
Date of first activity after the winter diapause		
Date of spring mass in individual colonies		

Research Question	Variables of Interest	Chapter
Date of first foraging activity.		5
Timing of nuptial flights around Harlestone Firs.		5
Date at which colonies cease activity for the season.		5
Length of active period.		5
Does edge vegetation show variation in response to edge effects around the study aspects?	Species composition Vegetation structure Vegetation density	6
Are there specific associations between species of tree and ground flora at nest locations?		6
Is there a pattern of foraging dependence of a particular species of tree(s) at nest locations and do these patterns change with location around the wood?		6
Is colony structure determined by edge effects?	Microclimate Food resource Nest densities	6
How stable are nest sites in time? Do colonies move nests regularly due to edge effects?		6

Chapter 2:

The Wood Ant, *Formica rufa* L. (Hymenoptera: Formicidae) : Taxonomy, Biology and Ecology.

2.1 The Basic Taxonomy and Ecology of *F. rufa*.

2.1:1 Wood Ant Taxonomy

Ants are grouped into a single family, the Formicidae, in the Order Hymenoptera. The taxonomic status of ants, and their evolutionary relationships with other members of the Hymenoptera, is long established and, for the most part, retains taxonomic stability (Hölldobler & Wilson 1990). However, the taxonomy of the *F. rufa* group was confused from the beginning, due mainly to the original description of an ant as *Formica rufa* by Linnaeus in 1758 (Yarrow 1955; Vepsäläinen & Pisarski 1981). Due to the ongoing difficulty of identification, it became commonplace for researchers to either apply the name *F. rufa* L. to all wood ants, or to use a complicated combination of names to describe the particular species that they studied (Yarrow 1955; Skinner 1998). In Britain, the notable works of Donisthorpe (1927), Nelmes (1938), Sweeney (1950) and Morley (1953) characterised this habit in the first half of the 20th Century. Major revisions in Britain by Yarrow (1955) and in continental Europe by Betrem (1960), finally brought some stability, but it should be noted that early work, especially from Europe, should be treated with caution, as it is not always clear to which species the research applies (Skinner 1976, 1980 a&b, 1998; Pamilo *et al.* 1979; Rosengren & Cherix 1981; Collingwood 1987; Pamilo *et al.* 1992).

It is now widely accepted that four sub-genera exist within the genus *Formica*: *Raptiformica*, *Coptoformica*, *Serviformica* and *Formica sensu stricto* (Dlussky 1967). Although originally controversial, based solely on morphology (early allozyme work failing to confirm the classification - see Pamilo *et al.* 1979), the validity of the systematic relationships of these sub-genera have now been confirmed by Goropashnaya (2003) (Table 2.1).

Table 2.1 : Some European *Formica* ants: classification of *sub-genera*
(Adapted from Collingwood 1964; Pamilo *et al.* 1979; Goropashnaya 2003).

Sub-Genus : *Formica sensu stricto*

F. aquilonia Yarrow.
F. lugubris Zett.
F. paralugubris Nov Spec.
F. polychtena Först.
F. pratensis Retzius. (formerly known as *F. nigricans* Emery)
F. rufa L.
F. truncorum Fabr.
F. uralensis Ruzky.

Sub-Genus : *Coptoformica*

F. exsecta Nyl.
F. pressilabris Nyl.

Sub-Genus : *Serviformica*

F. candida Smith. (formerly known as *F. transcaucasica* Nasonov & *F. picea* Nyl.)
F. cinera Mayr.
F. cunicularia Latr. (formerly known as *F. glebaria* Nyl. & *F. rubescens* Förel.)
F. fusca L.
F. lemani Bond.
F. rufibarbis Fabr.

Sub-Genus : *Raptiformica*

F. sanguinea Latr.

The *Formica rufa* group (the true wood ants), is composed of six species from the sub-genus *Formica s. str.*; *F. rufa*, *F. pratensis*, *F. polychtena*, *F. lugubris*, *F. paralugubris* and *F. aquilonia*, which phylogenetically represent a tight cluster of species (Goropashnaya 2003; Gyllenstrand *et al.* 2004). The cluster splits into two main groups (Fig. 2.1), although *F. pratensis* is a sister species of one of these groups.

In Britain, with the recent loss of *Formica pratensis* Retz. from the mainland (Skinner 1998), there are three species of the *F. rufa* group; *F. rufa* L., *F. lugubris* Zett., and *F. aquilonia* Yarrow (Yarrow 1955; Collingwood 1964; Brian 1977; Skinner 1987; Skinner & Allen 1996; Skinner 1998).

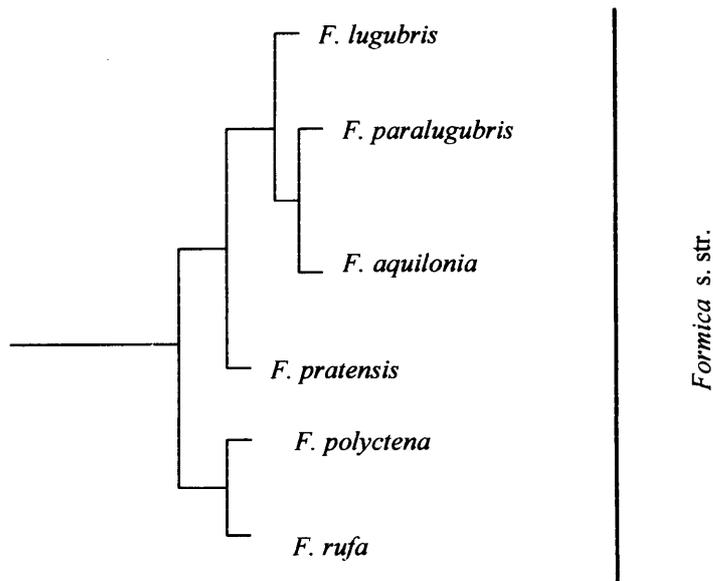


Figure 2.1: Phylogenetic tree of the *Formica rufa* group of the sub-genus *Formica* s. str (Adapted from Goropashnaya 2003).

2.1:2 Identification of the British Wood Ants and the Division of Castes.

Because the *F. rufa* group of wood ants are morphologically very similar (Douwes 1981), the easiest method of identifying the three British species is by their distribution (Skinner & Allen 1996; Skinner 1998). Where there is an overlap, in the case of *F. rufa* and *F. lugubris* in parts of England and Wales, it is virtually impossible to determine the species without the aid of a hand lens (Skinner 1987). With a hand lens, one needs to focus on the number of hairs on the head and around the eyes. *F. rufa* has no, or very few, short hairs on the top or sides of the head, or around the eyes. Alternatively, *F. lugubris* has many long hairs on the top and sides of its head, often giving the appearance of a ‘fringe’ below the eyes (Brian 1977; Skinner 1987; Skinner & Allen 1996). Great caution should be taken when identifying these two species because these hairs tend to be lost with age. Therefore, any identification should ideally be carried out after viewing a number of samples from a single nest.

A typical ant colony contains three basic castes: queens, males and workers (Brian 1977). Queens are reproductive females whose basic function is colony foundation (in many, but not all species), and the subsequent laying of eggs. The queen produces both fertilised and unfertilised eggs. The fertilised (diploid) eggs give rise to other (mostly winged) reproductive females or to the predominant sterile female worker caste. The unfertilised (haploid) eggs,

produce winged males. Males are normally very short lived members of the colony which have the single role of reproduction; they die very shortly afterwards. The sterile worker caste, which comprise the vast majority of the colony, obtain food, feed and nurse the larvae (and queen), build and maintain the nest and defend the colony (Brian 1977; Dumpert 1981).

In *F. rufa*, the three basic castes (queens, males and workers) are the components of the colony (Figure 2.2); unlike many ant species around the world, no sub-castes exist. However, although not truly polymorphic, workers may show great size variation, which in many cases may determine the function that they fulfill within the colony (Skinner 1976; Oster & Wilson 1978).

According to Dumpert (1981) wood ant workers can live for up to four years (although this is rare). However, some workers do over-winter for one and maybe even two seasons, making the identification of workers more problematic (Rosengren 1970; Brian 1977; Rosengren & Pamilo 1978; Zakharov 1980; Dumpert 1981; Rosengren & Fortelius 1986).

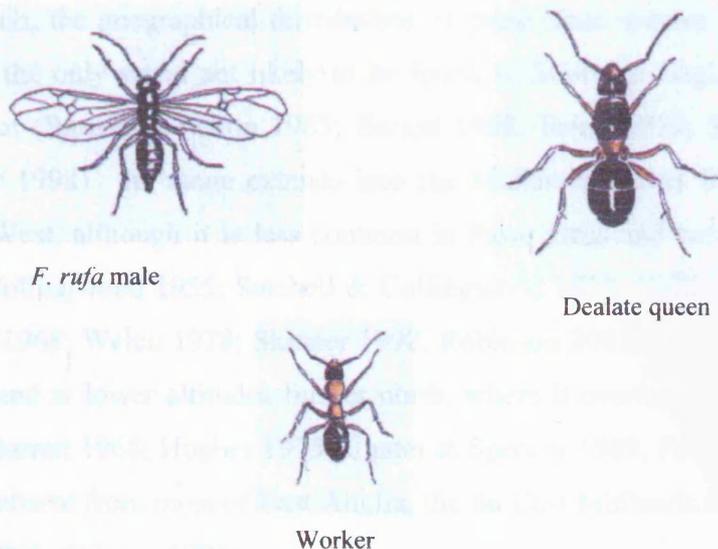


Figure 2.2 : Three basic castes of *F. rufa* (after Skinner & Allen 1996).

2.2 : The Distribution and Habitat Preference in the *F. rufa* Group.

Wood ants are common across the entire Holarctic region, with taxonomically similar species exploiting the same types of habitats on each continent (Fowles 1994). The geographical distribution of *F. rufa*, *F. lugubris* and *F. aquilonia* across mainland Europe gives an

indication of the impact of climate on colony structure, a factor discussed in more detail in Section 2.3.

F. rufa is considered to be a lowland species, exploiting woodlands or scrubby heath (Wells *et al.* 1983). Although tending to have a continuous distribution across Europe, it does not occur in northerly regions (above 64°N latitude) or at altitudes greater than 1200m (Yarrow 1955; Pamilo *et al.* 1992). This species extends as far south as Northern Italy and the Pyrenees to the west, although according to Yarrow (1955) it is found as far south as Central Spain (Kutter 1977; LeMoli *et al.* 1982; Zahrádnik & Severá 1998).

F. lugubris is a boreoalpine ant (Gösswald *et al.* 1965) found throughout Fennoscandia and central Europe, especially at higher altitudes (Collingwood 1979; Wells *et al.* 1983; Pamilo *et al.* 1992). It forms especially striking colonies in many areas of Europe (Cherix & Gris 1977; Wells *et al.* 1983; Goropashnaya 2003). *F. aquilonia* is another highland species, although its range is restricted to more northerly areas, especially Fennoscandia and the states of the former USSR (Collingwood 1979; Pamilo *et al.* 1992).

In Britain, the geographical distribution of these three species follows a similar pattern. *F. rufa* is the only wood ant likely to be found in Southern England, where it remains locally abundant (Barrett & Felton 1965; Barrett 1968; Brian 1977; Skinner 1987; Edwards 1997; Skinner 1998). Its range extends into the Midlands and as far as the Lake District in the North-West, although it is less common in these areas and has been lost from many former sites (Collingwood 1955; Satchell & Collingwood 1955; Collingwood & Barrett 1964, 1966; Barrett 1968; Welch 1978; Skinner 1998; Robinson 2001). *F. rufa* is also found in Southern Wales and at lower altitudes further north, where it overlaps with *F. lugubris* (Collingwood 1955; Barrett 1968; Hughes 1975; Chater & Spencer 1989; Fowles 1993, 1994). However, *F. rufa* is absent from most of East Anglia, the far East Midlands and the North East (Skinner & Allen 1996; Skinner 1998).

The overlap between *F. rufa* and *F. lugubris* extends north from Wales into the north west of England (Skinner 1998). *F. lugubris* is then found alone across the remainder of northern England and up into eastern Scotland (Collingwood 1964; Skinner & Allen 1996), occurring also at limited sites in southern Ireland (Breen 1979a). *F. aquilonia* again has the most northerly distribution, being found in the Scottish Highlands, and on into north eastern Scotland, where it overlaps with *F. lugubris* (Yarrow 1955; Collingwood 1964; Skinner 1998). It also exists in a single location in Ireland (Breen 1979a).

F. rufa is most commonly found in, or very near to woodland habitats, where it generally prefers more open areas, often utilising edge zones or those areas which receive high amounts of sunlight (Andrews 1927; Scherba 1958; 1959; Brian 1977; Breen 1979a; Punntila & Haila 1996; Hofener *et al.* 1996; Pontin 1996). This species is found in a variety of woodland habitat types, but seems to do particularly well in areas of coppice or in well managed plantation (Adlung 1966; Sudd *et al.* 1977; Welch 1978; Wells *et al.* 1983; Fowles 1994). A common held belief was that colonies died out when mature woodland shaded nests, although Adlung (1966) found that *F. rufa* was able to utilise shaded interior habitats much more effectively than the other species of the wood ant group. Long term observations from all over the Holarctic suggest that members of the *F. rufa* group are able to utilise apparently inhospitable habitats due to the unique thermal qualities of their nests (Brian 1977; Brandt 1980; Coenen-Stass *et al.* 1980; Martin 1980; Horstmann & Schmid 1986; Rosengren *et al.* 1987). Important factors in this ability are the construction and location of the nest mounds and diet (Brian 1977; Skinner & Allen 1996). This is considered later in section 2.3 and Chapter 5.

Within these parameters, *F. rufa*, as with most species of ant, tends to be more abundant in warmer regions or in warmer habitats (Brian 1977; Skinner & Allen 1996). Traditionally, the species was associated with sandy soils (Nelmes 1938; Brian 1977), which are free draining and have a low heat capacity, warming quickly on receipt of quite limited amounts of solar radiation (Barry & Chorley 1992; Ahrens 1994). Nelmes (1938), from extensive observations, concluded that wood ants preferred acidic substrates and avoided areas dominated by base rich bedrock. However, Satchell & Collingwood (1955) showed that *F. rufa* was found extensively on limestone rich areas of the Lake District and that therefore other factors were the dominant determinants of wood ant habitat preference. A review of the literature highlights that soil temperature and moisture, air temperature, humidity, rainfall, vegetation, and daylight hours at key periods of the year, are very important factors in determining *F. rufa* distribution (McCook 1877; Andrews 1927; Dreyer 1932, 1942; Dreyer & Park 1932; Scherba 1958, 1959; Brian 1977; North 1991, 1993 a&b; Bristow *et al.* 1992; Skinner & Allen 1996; Robinson 2001).

2.3 : Adaptations to Life in the Northern Temperate and Boreal Zones.

Wood ants have evolved several unusual adaptations which allow them to survive, and indeed thrive, in quite extreme habitats (Heinze & Hölldobler 1994). These adaptations, shaped as

they are by the environment, have profound effects on the very fabric of colony organization, from nesting biology, reproductive strategy to overall colony structure (Rosengren & Pamilo 1983; Pamilo & Rosengren 1984; Coenen-Stass *et al.* 1980; Hölldobler & Wilson 1990; Heinze & Hölldobler 1994).

In describing ‘alternate strategic solutions’ to life in extreme environments, both Hölldobler & Wilson (1990) and Heinze & Hölldobler (1994) use the contrasting habits of the *F. rufa* group species and *Camponotus herculeanus* L. The two live in similar habitats and are adapted very well to the harsh climate of northern latitude regions, with their prolonged very cold winters and short warm summers (Gregg 1972; Francoeur 1983). Here, the ants must not only survive the long cold periods of the winter hibernation, where temperatures may drop to -40°C , but must still be able to become fully active very early in spring to allow them to reproduce, and give new queens time to found new colonies before the cold sets in again (in extreme cases the active period lasting a maximum of five months) (Heinze & Hölldobler 1994). As temperature is a key factor in determining the speed of brood development, in extreme boreal regions there is a real danger that a newly founding queen will not have sufficient time to mate, find a nest, and produce the first worker crop before the end of the short period of summer activity. The queen therefore faces the prospect of a winter hibernation alone (Heinze & Hölldobler 1994).

The main distinction between the two strategies lies in the properties of their nests; *F. rufa* group species build large mound nests, which are recognised for their thermoregulatory properties, whilst *C. herculeanus* typically makes its nests under the bark of a tree, and thus has no special nest adaptations that might enhance the thermal conditions within. The differences in nesting strategy have a profound effect on the reproductive cycles of both (Hölldobler & Wilson 1990).

Hölldobler (1961, 1962) carried out extensive research on the life history of *C. herculeanus*. His findings, together with accounts published by Hölldobler & Wilson (1990) and Heinze & Hölldobler (1994) have been used to contrast the different strategies of this species and members of the *F. rufa* group in the following paragraphs.

C. herculeanus, without the benefit of being able to control nest microclimate, solves the problem of the need to reproduce early in the year by over-wintering with mature male and female reproductives. In late summer, the queen produces an ‘eclosion guild’ of young workers, and male and female reproductives, which remain in the nest until the nuptial flight

the following year. The males in most ant species are not normally known for their social attributes. However, *C. herculeanus* males, although receiving food from storage workers, also donate resources to other nestmates. By over-wintering with brood the colony is able to ensure that their nuptial flights can occur in May or June the following year; normally as soon as climatic conditions allow.

At this point, newly mated queens found nests. Living on their body reserves, those queens that mated very early in the season, may raise the first worker brood before the onset of winter. However, late breeding queens may over-winter with second instar larvae, extending the perilous stage of colony founding to two seasons. The strategy of over-wintering with mature reproductives seems a strange choice given the need for the colony to provide these individuals with valuable food resources for a much longer period of time than is normally usual in ants. However, according to Heinze & Hölldobler (1994) this strategy represents a 'storage economy', and is probably offset by the fact that the mature males participate in food distribution.

However, members of the *F. rufa* group have long been noted for their conspicuous and long lived nest mounds (Mayr 1855; Forel 1874; Escherisch 1906; Steiner 1923; Wellenstein 1928; Kato 1939; Gösswald 1942, 1951; Yarrow 1955; Skinner 1976; Brian 1977; Laakso & Setälä 1998). These mounds form the above-ground portion of the nest, called the solarium and can be as much as one metre in height, and several more in circumference (Brian 1977; North 1991, 1996; Skinner 1998). The actual height and form of the mound will vary according to the size of the colony, the age of the nest, the degree of shading, the nest material used and the substrate on which it is built (Figure 2.3) (Dreyer 1942; Gosswald 1942, 1951; Yarrow 1955; Scherba 1958; Zahn 1958; Skinner 1976, 1980a; Sudd *et al.* 1977; Fowles 1994; North 1996; Gilev 2000; Robinson 2001). The nest itself may extend between 0.5 metres and two metres below the surface, and contains a network of chambers which house the resident queen(s), eggs and young larvae, which are maintained in stable conditions of temperature and humidity (Brian 1977; North 1991, 1993 a&b, 1996; Skinner & Allen 1996; Skinner 1998). This is generally where the colony spends the winter months of hibernation (Rosengren 1970; Rosengren & Pamilo 1978).

The mound (solarium) is constructed from organic matter from locally derived material such as *Pinus* spp and *Larix* spp needles, twigs and leafy petioles, together with quantities of conifer resin (Yarrow 1955; Skinner 1976; Collins & Wells 1987; Skinner & Allen 1996; Laakso & Setälä 1998; Lenoir *et al.* 1999). Mounds may be located on the forest floor, or in

some cases, built around the trunk of a tree which the ants use for foraging (Brian 1977; Skinner 1998). Some may even be built around old tree stumps which are used to house many of the brood chambers (North 1996).

The nest mounds are not just randomly accumulated piles of litter, but carefully constructed features, which are actively maintained (Brian 1977; Collins & Wells 1987). Noticeably, one of the first activities of a new season upon leaving hibernation, is to repair the damage caused to the nest over winter. This damage can be quite extensive, with large holes present in the surface, or in extreme cases, entire areas of the mound destroyed. Skinner (1980b) observed that ants returning to the nest in the first few weeks of activity were carrying nest material in almost the same frequency as items of food. Although the quantity of litter returned to the nest fell to smaller amounts in subsequent weeks, the supply was continuous throughout the season, highlighting the importance of nest construction and maintenance to the persistence of a colony (Adlung 1966; Brian 1977; Skinner & Allen 1996). For this reason, wood ant nests are protected from intentional damage by law in some European countries (Wells *et al.* 1983; Collins & Wells 1987).

The idea that these mound nests performed a thermoregulatory function was proposed several centuries ago. Although Reamur (1742) mentions this point, it is believed that Huber (1820) was the first to carry out detailed experimental work on internal nest temperatures (Scherba 1958, 1962). Considerable research has since been focused on the internal nest mound temperatures in a variety of species, most notably by Mayr (1855); Forel (1874); McCook (1877); Escherisch (1906); Steiner (1923, 1930); Andrews (1927); Wellenstein (1928); Dreyer (1932); Dreyer & Park (1932); Cole (1932); Weber (1935); Kato (1939); Ragnier (1947, 1948); Scherba (1958, 1962); Skinner (1976); Brandt (1980); Coenen-Stass *et al.* (1980); Martin (1980); Horstmann & Schmid (1986); Rosengren *et al.* (1987); and North (1991).

Mound nests maintain internal temperatures which are several degrees higher than the surrounding ambient air temperature (see Brian 1977; North 1996; Pontin 1996; and Skinner 1998 for more detailed reviews). A detailed analysis of the internal temperature of nests of *F. polyctena* was carried out by Coenen-Stass *et al.* (1980). They found that with an ambient air temperature of 13.6°C, the centre of the nest mound maintained temperatures up to 25°C.

However, exactly how these elevated temperatures are maintained has been a source of great debate over the years. According to Coenen-Stass *et al.* (1980), four key arguments have been proposed to explain elevated nest temperatures;

- i. The degradation of nest material causes nest temperatures to increase (Wasmann 1915; Coenen-Stass *et al.* 1980);
- ii. Direct absorption of solar radiation by the nest, and therefore nest construction is responsible (Forel 1920);
- iii. Spring massing – heat absorbed by the ants during the ‘spring mass’ is carried back inside the nest (Zahn 1958);
- iv. Combined explanation of direct solar radiation, together with the metabolic heat released by the ants themselves after the ‘spring mass’ (Kneitz 1964).

Despite extensive research no single argument has prevailed. In reality, there is probably no single factor which contributes solely to elevated internal nest temperatures, as all of the four key arguments are very much related. However, it is clear that nest location and orientation are key elements in all of these arguments, both of which are very much influenced by the processes of edge effects.

According to Adlung (1966), a key requirement of nest sites among the *F. rufa* group in general, is a canopy which admits sunlight to the forest floor. He describes how in Germany, introduced colonies of *F. polyctena*, moved their nests from beneath the canopy of spruce plantations and beech woods to the sunny edges, or to unshaded slopes. This account would appear to match a large portion of the work of other researchers throughout Europe and North America (Andrews 1926, 1927; Elton 1932b; Imms 1947; Finnegan 1975; Breen 1979a; Sudd *et al.* 1977). For example, according to Douglass & Sudd (1978), of the 326 *F. lugubris* nests found within a woodland in Northern England, 76% were located within 5m of the edge of the forest compartments. Further, only 4% were situated on the more shaded northern sides.

Due to the thermal qualities of their nests early in the season, *F. rufa* group colonies do not over-winter with brood. The queen(s) stop laying eggs in July and therefore by August, the last of the brood reach maturity (Skinner 1998). These new workers act as ‘temporary repletes’, storing much of the food gathered by the foragers until the last days of activity

(normally October or November throughout Europe, although in extreme northern latitudes activity may cease as early as September). At the onset of winter the queen(s), nurse workers and repletes move into the deepest chambers of the nest and form a dense cluster to conserve heat (Dumpert 1980). As the weather worsens, so the older outside foragers also move into the lower chambers and add to the cluster. If the winter is mild, some workers may be visible on the surface of the nest, but the active phase proper may not normally begin until February to April, depending on the latitude (Skinner 1998; Hölldobler & Wilson 1990).

As soon as the first warm days of spring arrive, many thousands of ants, workers and queens alike, leave the inner chambers and swarm (mass) on the surface of the nest, in many cases congregating on a particular area (Morley 1953; Brian 1977; Dumpert 1981; Skinner 1998) (Figure 2.4). The idea that this phenomenon was a mechanism to elevate internal nest temperatures (by the massing ants returning warmth to the depths of the nest), has been attributed to Forel (1874), although it had been a common explanation for this phenomena for many years (Reamur 1742; Huber 1820). However, according to Hölldobler & Wilson (1990), the important point is that the young repletes become activated in the sun and begin to convert their fat stores to high quality liquid food ready to be fed to the queen(s) and subsequent new larvae. The combined metabolic heat of the queens and the repletes warms a core area of the nest, the heat being maintained due to the thermoregulatory properties of the nest. In this core the temperature may reach around 25°C at a time when external soil surface temperature may remain close to freezing. These elevated temperatures allow the queen(s) to lay 'winter eggs' which, due to the elevated temperatures and high quality food reserves, may develop to adult reproductives in five to six weeks. After a break of a few weeks, the queens begin to lay 'summer eggs' which will develop into the new seasons workers. Therefore, the *F. rufa* group colonies, may avoid over-wintering with brood yet still be ready for the nuptial flight in May or June (Dumpert 1981; Hölldobler & Wilson 1990). The next challenge facing *F. rufa* group colonies is to ensure that newly inseminated queens are able to found new colonies during the short summer season of northern latitude regions. Rather than relying on solitary founding (haplometrosis), *F. rufa* group species employ different strategies.

The nuptial flight of *F. rufa* group species is a protracted affair, occurring over a period of a few weeks (Skinner 1998). In general, in nests producing both male and female reproductives, males are seen first on the nest surface, with the first virgin queens normally observed several days later (Breen 1979b). The workers appear to police the two sexes, ensuring that, at least on the surface, males and females from the same nest do not mate (termed intranidal mating). However, on rare occasions, the act of intranidal mating has been



a : Semi shaded nest (The trowel is 29cm long).¹

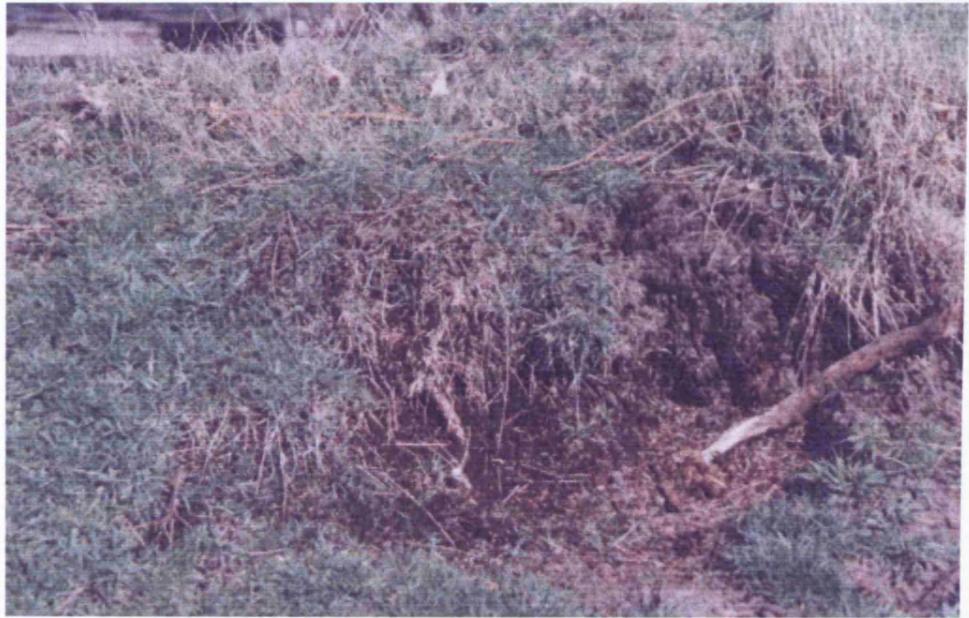


b : Nest in an open area of the forest edge.

¹ All photographs taken by the author unless otherwise stated.



c : Nest in full shade.



d: Nest built into a grassy south facing bank outside the woodland
(The branch is 32cm long).

Figure 2.3: Typical *Formica rufa* nest characteristics around Harlestone Firs.

A



B



Figure 2.4 : Spring Massing of *Formica rufa*.
A:- Massing workers on a nest built against a log; B:- workers on a small mound nest.

reported (Hölldobler & Wilson 1990), observed in the *F. rufa* group by Escherich (1906), Fortelius *et al.* (1990) and Pontin (1990), and has obvious implications for the genetic variation of local populations (Chapuisat 1998).

It is generally accepted that *F. rufa* group queens found colonies via three different strategies. Wheeler (1904) advanced the theory that *F. rufa* group females were incapable of founding colonies on their own, although Yarrow (1955) could find no physiological reason why they should not be able to do so. In accordance with that theory many researchers report that *F. rufa* queens found colonies via the temporary social parasitism of members of the sub-genus *Serviformica*, in Britain *Formica fusca* or *F. lemani* (Donisthorpe 1927; Yarrow 1955; Skinner 1976; Brian 1977; Dumpert 1981; Hofener *et al* 1996; Zahrádnik & Severá 1998).

The newly inseminated *F. rufa* queen locates a *Serviformica* nest, gains entry (forced entry or via mimicry of the colony scent, depending on the authority) and kills the *Serviformica* queen. At this point she is accepted by the parasitised colony (Brian 1977; North 1996; Skinner & Allen 1996) and begins laying eggs which are cared for by the *Serviformica* workers, giving rise to a mixed colony. After a year or two, the colony becomes pure *F. rufa*. This method of colony foundation is controversial, and although some accounts exist describing mixed colonies (Creighton 1950; Gosswald & Bier 1957; Skinner 1976), most researchers have never encountered this type of colony, suggesting that it is not the most common mechanism (North 1996; Pontin pers. comm.).

According to the literature the most common habit amongst inseminated wood ant queens is to return to their own maternal nest, and either remain there to take up egg laying duties, or for the colony to form a satellite nest nearby to which the new queen and group of workers will move. This is termed 'budding'. Alternatively, inseminated *F. rufa* queens may try to join an unrelated nest to begin their new lives. The *F. rufa* group, like all ants, tend to be highly territorial and therefore vast numbers of inseminated queens are lost to their own species, let alone to other species and predators (Yarrow 1955; Higashi 1976; Brian 1977; Welch 1978; Mabelis 1979, 1984; Dumpert 1981; Skinner 1987; Fortelius *et al* 1993; North 1996). However, observations have shown that workers in some wood ant colonies actively attempt to recruit foreign queens into their nest, suggesting that there is still much to learn about the reproductive strategies of the wood ants (Fortelius *et al* 1993; pers observation).

Therefore, these two successful groups of ants have developed quite different ways of founding colonies: *C. herculeanus*, without the benefit of nest mounds, relies on solitary

founding queens, which have over-wintered in the maternal nest; *F. rufa* group species, with the benefit of their mound nests, are able to rear brood from egg to adult in five to six weeks at the beginning of the season, and thus avoid the problems of over-wintering alone by parasitising an existing colony, or returning to their own maternal nest or the nest of another colony elsewhere.

In terms of the reproductive phase of colony life, edge effects may influence aspects of the biology and ecology of ant species in areas which have received little attention in previous studies. For example, in *C. herculeanus* and members of the *F. rufa* group, edge effects could realistically influence the timing of the nuptial flights around a forest. Boosma & Leusink (1981) have shown that the nuptial flights of four European species of ant correspond to specific weather conditions. This point has also been noted in wood ants, especially by Breen (1979b), and in their North American counterparts by Talbot (1959, 1971, 1972), who reported that wood ant 'take offs' occurred subject to a minimum surface air temperature of between 16-18°C. A reliance on these minimum temperatures for nuptial flights would make colonies very much subject to the altered microclimate associated with edge effects around the cardinal compass points of a fragmented woodland (Kannowski 1961). This could lead to some colonies flying in one area of a wood before colonies in other areas have suitable local conditions to begin their flights.

However, perhaps a more important factor for the *F. rufa* group is local climatic conditions early in the year. As reproductive brood development is so closely affected by early season temperatures, some colonies in more advantageous areas could theoretically begin brood development up to two to three weeks earlier than colonies living in exposed areas. This would confirm Scherba's (1958) general observation that northerly oriented nests lagged behind their south facing counterparts in the timing of activity phases (see also Klimetzek & Fass 1994). Although observations suggest that breeding times in species of the *F. rufa* group vary across their European range, apparently dependent on latitude, early observations suggest that there may be notable differences across a single wood (personal observation). This study therefore sets out to examine this impact in a natural environment and seeks to determine if edge effects allow colonies in warm, southern regions of a single wood to begin activity earlier than their more northerly counterparts. The results may have interesting implications for the conservation biology of the *F. rufa* group throughout its European range.

2.3:1 Nest Density and Persistence.

The density of wood ant nests within a given woodland may show great variation. Nests may be found rather sporadically around a wood, tending to occur in large numbers in some areas, whilst being absent from others (Breen 1979a; Welch 1978). Recent data from Pound Wood in Essex confirms this point (Cook 1998). Nest density calculated for the total area of the woodland gave a figure of 2.95 nests ha⁻¹. However, 65% of all nests occurred in an area of coppice covering 1.87 hectares producing an extremely high density of 22.45 nests ha⁻¹. *F. rufa* nest densities also show great variation across Europe. For example, in Germany, Buttner (1971) and Klimetzek (1972) report nest densities of between 1.50 ha⁻¹ and 3.33 ha⁻¹. In contrast, nest densities in England have been found to vary between 18 ha⁻¹ in Kent (Welch 1978), to 5 ha⁻¹ in the New Forest (Elton 1932a), and 1.33 ha⁻¹ in Bedford Purlieus, near Peterborough (Peterken & Welch 1975). It is likely that these figures are related to colony social structure, itself potentially influenced by processes of forest edge effects.

The persistence of an individual nest is apparently variable, with previous research showing a wide range of extremes (Breen 1979a). In many cases this is due to the habit of *F. rufa* group species of forming 'branch' or 'bud' nests close to the original nest during the early part of the season, normally before the nuptial flights take place (Andrews 1927; Higashi 1976; Vepsäläinen & Wuorenrinne 1978; Fortelius *et al.* 1990). These nests either become a fully functioning 'satellite' of the original nest, with reproductive females in residence, or after a short time, are reincorporated back into the original nest (Higashi 1976; Bourke & Franks 1995; Skinner 1998). Therefore, nest persistence can appear very tenuous, if 'short term' nests are included in the analysis at a particular site (Breen 1979a).

Nest splitting in mature, long lived nests by species of the *F. rufa* group has been studied in relation to human activities within a fragmented landscape. Working in Finland, Vepsäläinen and Wuorenrinne (1978) found that after severe habitat disturbance (clear cutting or timber felling), colonies quickly formed numerous smaller nests around the site of the original. This phenomenon has been noted on many occasions across Europe (Czechowski 1975; Brian 1977). Vepsäläinen & Wuorenrinne (1978) suggested that this splitting was due to either mechanical damage to the nest, mechanical and social hindrances to foraging, or due to the loss of food reserves. These factors, they felt, reduced the ability of a colony to sustain the energy needs of a large, long lived nest and as such, inner mound temperatures soon fell. Therefore, they theorised that colony adaptiveness would select for the foundation of many minor nest units, each with a subsequent reduction in food requirements and foraging area. This response would go some way to ensure that the colony could at least survive the

disturbance episode by the persistence of one or more of the smaller units, and that the colony may therefore expand as and when the environmental conditions allowed.

However, in the absence of disturbance nest persistence may be impressive. For example, although Klimetzek (1972) found that over a six year period new nests appeared at a rate of 15% per year (with 22% of all nests being abandoned), individual *F. rufa* group nests may survive for several decades. For example, Imms (1947) quotes a letter written by Charles Darwin to the Swiss myrmecologist A. Forel, reporting a *F. rufa* nest that had remained in the same location for 80 years. Indeed, according to King & Salee (1953), Forel himself studied a single *F. pratensis* nest for 56 years. North American studies tend to confirm these findings, with Andrews (1926) finding 21% of the 117 nests of *F. exsectoides* in his study still active after 15 years, and Dreyer (1942) and Haviland (1948) finding 75% and 63% respectively of their nests remaining after 10 years. With this in mind, King & Salee (1953) concluded that the duration of these nests was a good indication of the environmental conditions.

2.3:2 Colony Social Structure : Social Polymorphism in Ants.

The social structure of *F. rufa* colonies varies throughout its European range (Welch 1978; Rosengren & Pamilo 1983). Colonies may consist of a single queen occupying a single nest (a monogynous – monodomous colony), as found in most of Germany, Scandinavia and parts of England (Lange 1960; Otto 1968; Rosengren & Pamilo 1983; Rosengren *et al.* 1993) or multiple queens utilising multiple, socially connected nests (a polygynous – polydomous colony), a model that has been associated with warmer climates, for example France, Italy and parts of England (Yarrow 1955; Betrem 1960; Rosengren & Pamilo 1983; Hofener *et al.* 1996).

Optimum ecological conditions in a particular area may influence queen number in nests, thus leading to the development of different colony structures (Gyllenstrand *et al.* 2002). For example, in many wood ants (probably *F. rufa* included), polygyny develops secondarily via the adoption of new queens into originally monogynous colonies (Rosengren & Pamilo 1983; Fortelius *et al.* 1990; Goropashnaya *et al.* 2001). Monogynous (M-type) and polygynous–polydomous (P-type) colonies appear to form two distinct adaptive complexes. According to Goropashnaya *et al.* (2001) the P type tends to favour colonies living in stable, but patchily distributed habitats, where a single colony can monopolise the entire patch (Rosengren & Pamilo 1983; Puntilla 1996). It is suggested that this is caused by intraspecific competition for nest sites. As a patch becomes saturated, the only option for new queens, other than long

distance dispersal, is to enter an existing nest (Rosengren *et al.* 1993). Therefore, polygyny increases due to nest site saturation and the consequent competition for resources (Goropashnaya *et al.* 2001). However, the whole process is dependent upon a suitable microclimate to ensure that optimal ecological conditions prevail to support such large populations, once more linking edge effects as an influence on the ecology / population biology of wood ants.

2.4: Diet and Foraging in *F. rufa*.

F. rufa is omnivorous, deriving nutrition from two major sources; invertebrate prey and honeydew obtained from tended aphids (Hemiptera: sub-order Homoptera) (Brian 1977; Skinner 1980a; Skinner 1998). *F. rufa* utilises a wide variety of invertebrate prey, which it catches whilst foraging throughout the forest strata (Brian 1977; Cordella & Raffa 1996). A typical nest consumes a prodigious number of prey items in a season, with some researchers quoting figures of several million or more (Adlung 1966; Skinner 1980a&b, 1998; Wells *et al.* 1983; Fowles 1994). Table 2.2 lists the most common prey items recorded from studies of *F. rufa* diet. Many of these prey are defoliating insects and therefore woodland pests, and for this reason wood ants have been proposed as important components of woodland management (Adlung 1966; Brian 1977; Skinner 1980a; Skinner & Whittaker 1981; Wells *et al.* 1983; Way & Khoo 1992). However, it is the ant-tended organisms which are of most interest here from the view of *F. rufa* diet.

2.4:1. Ant-Aphid Relationships

The most common source of carbohydrate in the diet of *F. rufa* is honeydew, derived from aphids (Skinner & Allen 1996), which accounts for well over half of the food content that is returned to the nest (Skinner 1980a). According to Skinner (1980a) quantities of around 46kg dry weight honeydew per nest per year were recorded from woodlands in north west England. Whittaker (1991) calculated that honeydew always supplied more than two thirds of the energy brought to the nest, a point supported by Skinner (1980b) who observed that there were always more workers foraging for honeydew than for other food items or nest material.

As aphids are so important for the persistence of *F. rufa* colonies, it would be prudent to cover some aspects of their general ecology and their relationships with ants, many of which may be affected by edge effects.

2.4:2. British Tree Aphids

There are 140 species of tree aphid in Britain which spend all, or part of their lives in trees (Thacker & Hopkins 1998). They feed on plant sap, which is relatively poor in amino acids (Kyto *et al.* 1996; Skinner & Allen 1996), and therefore in order to obtain the proteins that they require, aphids extract large amounts of sap (Loehle 1996; Thacker & Hopkins 1998). Consequently, the aphids obtain much more sugar than they need, excreting the excess as 'honeydew' (Skinner & Allen 1996; Skinner 1998; Thacker & Hopkins 1998). Aphid reproduction is very rapid and with a generation time of around three weeks, they are quickly able to exploit favourable conditions. This is due to the production of live young and of the 'telescoping of generations', where nymphs begin to develop their own offspring before they themselves are born (Dixon 1973). The life cycles of aphids are complex, displaying several unusual traits of which host alternation is of particular interest from the view of ant-aphid mutualisms (Dixon 1985; Thacker & Hopkins 1998).

Table 2.2: Typical composition of the food items entering a *F. rufa* nest

Food Item	Source
Psocoptera	Skinner & Allen 1996; Skinner 1980a.
Coleoptera	Brian 1977; Skinner & Allen 1996; Hawes <i>et al.</i> 2002.
Isopoda	Skinner 1980a.
Hemiptera (not aphids)	Skinner & Allen 1996.
Aphids (both tended and non-tended)	Skinner & Whittaker 1981; Warrington & Whittaker 1985a.
Diptera	Brian 1977; Skinner 1980a.
Hymenoptera (ants and <i>Bombus</i> spp.)	Brian 1977; Skinner & Allen 1996.
Lepidoptera (adults and larvae)	Karhu & Neuvonen 1998; Skinner 1980a; Skinner & Whittaker 1981; Warrington & Whittaker 1985b.
Araneae	Brunning 1991; Kalay <i>et al.</i> 1997.
Dipronidae	Cordella & Raffa 1996.
Annelidae	Skinner & Allen 1996.

Host alternation involves the utilisation of the resources of two (or more) different hosts at different times of the year and is made possible by the fact that many species of aphid exhibit alary polymorphism; the production of winged and wingless forms in response to environmental conditions (Dixon 1973, 1985; Thacker & Hopkins 1998). According to Thacker & Hopkins (1998), many host alternating aphids overwinter as eggs on trees and on hatching, the first few generations are usually wingless. This is followed by a winged generation which disperses to the understorey vegetation to feed, completing several wingless generations before again producing a winged form to return to the host tree. In host alternation, the tree is referred to as the primary host and the summer plant, the secondary host (Dixon 1973; Thacker & Hopkins 1998).

It is believed that host alternation evolved as a strategy to avoid the summer period of lower quality tree sap (Thacker & Hopkins 1998). The growth of new leaf tissue in the spring tends to produce a more mobile and nutritious phloem sap than is available during the rest of the year (Dixon 1973; Nobel 1974). Therefore, aphids are able to take advantage of this mobilisation of nutrients to reproduce quickly (Thacker & Hopkins 1998). In autumn, to a lesser extent the reverse occurs, as trees withdraw nutrients from photosynthetic tissue prior to leaf drop, again mobilising a higher quality sap (Nobel 1974; Thacker & Hopkins 1998). Therefore, aphids that remain on the tree in summer must subsist on a poorer quality diet making reproduction difficult (Dixon 1985; Thacker & Hopkins 1998). It is common therefore, for aphids that utilise a single host to enter diapause, either as an egg or an adult (Dixon 1973,1985; Thacker & Hopkins 1998). Utilising a secondary host, which is usually a smaller, shorter lived plant, guarantees a more mobile and higher quality sap and allows metabolic activity to continue (Thacker & Hopkins 1998).

2.4:3. Aphid Habitat

Due to their size and vulnerability, tree aphids tend to be limited to particular locations on a tree, whether this be the trunk or more commonly the leaf area (Thacker & Hopkins 1998). They normally seek sheltered regions with a stable microclimate where wind or rain will not dislodge them (Dixon & Logan 1972; Oke 1987). Tree aphids tend to be specific in their choice of host and over half of Britain's tree aphids utilise only a single tree species during their life cycle. Of the rest, most are dependent on a single genus and the remainder, a single family (Thacker & Hopkins 1998). Therefore, the structure and density of a woodland is important for tree aphid survival and they have been found to seek areas where many trees of the same species are within easy reach. It is therefore likely that as aphids play such an important role in *F. rufa* feeding that they may greatly influence the location of their colonies throughout a woodland. This again links forest edge effects with important aspects of *F. rufa* ecology, the impacts of which are investigated here.

Chapter 3 :

Description of the Study Site and an Overview of the Study Sample Strategy.

3.1 Harlestone Firs, Northampton.

The research was carried out at Harlestone Firs, part of the Althorp Estate, situated 5 km to the north-west of central Northampton (Fig 3.1). The soil is composed of leached acidic sand overlying Northampton ironstone, which is part of the Oolite formation (Anon 1902; Laundon 1964). This area, once scrubby heathland with abundant stands of *Betula pendula* and *Quercus robur*, was planted as a coniferous plantation circa 1850 AD (Laundon 1964), and although some scrub remained in places until the beginning of World War1, the site became almost totally coniferous soon after (Laundon 1964; Hillsden 1975). The conifer plantations are today composed of *Pinus sylvestris*, *P. nigra*, *Picea abies* and *Larix decidua*, but also contain a good mix of broad-leaved species such as *Acer pseudoplatanus*, *B. pendula*, *Corylus avellana*, *Fraxinus excelsior* and *Q. robur* (See Appendix 3 for common names).

Harlestone Firs is home to a large *Formica rufa* population, supporting in excess of 500 nests. Local folklore suggests that the species was originally introduced to the wood to act as food for the Estate's game birds. This belief was prevalent as early as the late 1930s, being confirmed by Nelmes (1938). However, according to Satchell & Collingwood (1955) 'introduction' has been a common explanation for the presence of wood ants in particular woodlands throughout the country, in most cases in the absence of convincing evidence. Indeed, despite extensive research, no evidence has been found to support the claims of an anthropogenic origin for the ants at Harlestone Firs.

The number of colonies found in Harlestone Firs has increased steadily (Hillsden 1975). By 1998, the population had expanded out of the wood, having displaced other species of ants on the degraded Harlestone Heath. From here *F. rufa* continued to spread onto the nearby Northamptonshire County Golf Club, and north along the edge of the Northampton-Birmingham railway. By 2001, colonies had also spread southwards out of the main woodland along a network of hedgerows into the nearby Lodge Farm Industrial Estate, displacing colonies of the locally rare *Lasius fuliginosus* Latr. in their path.

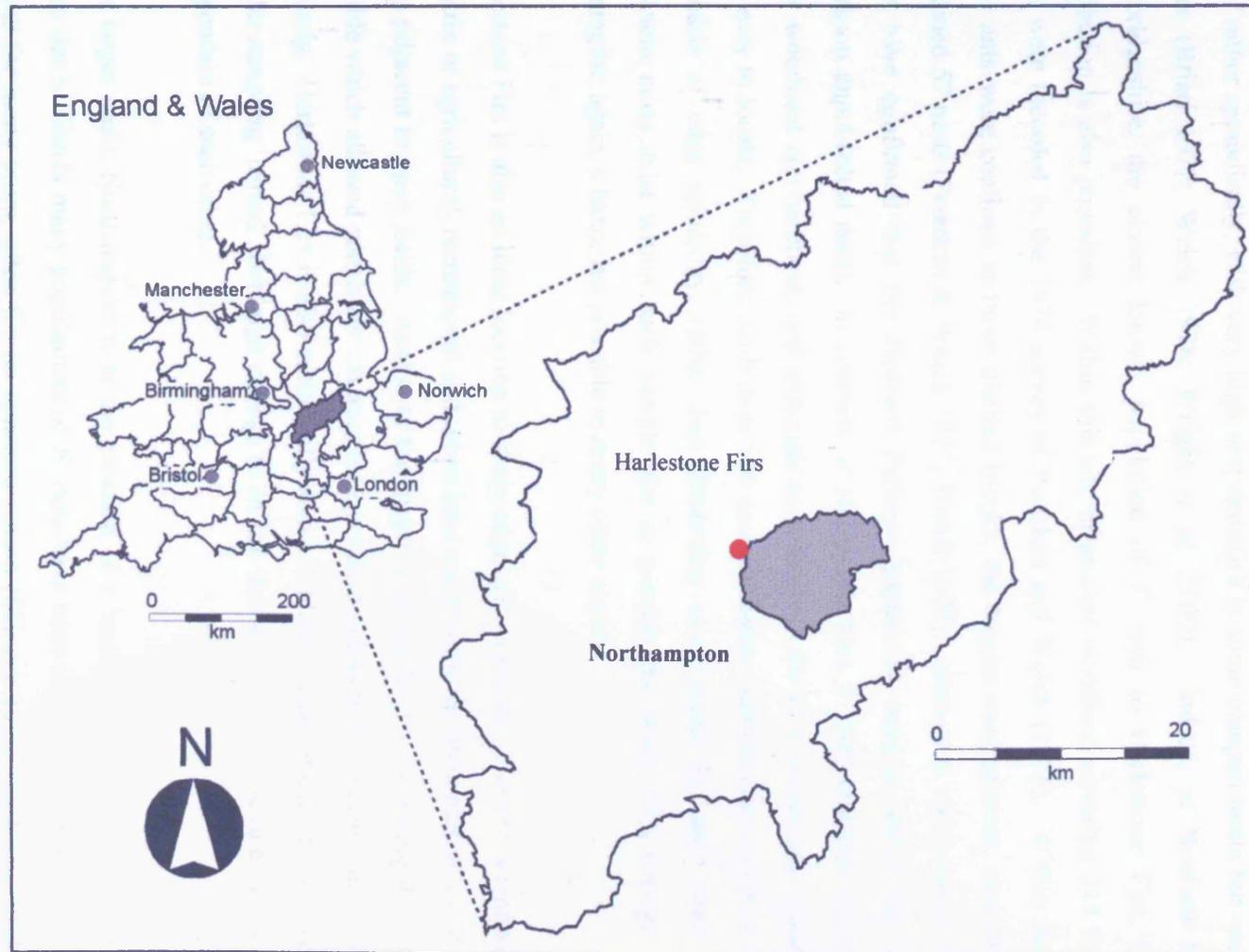


Figure 3.1 : Harlestone Firs in relation to the Borough of Northampton, UK. (Approximate location of Harlestone Firs is highlighted in red for guidance and is not to scale).

3.2. Justification of Selecting Harlestone Firs as the Primary Study Site.

Harlestone Firs provides a rare opportunity to study the impact of edge effects on the ecology of the wood ant, *F. rufa*. In many woodlands where wood ants thrive in England, the ants tend to occur rather sporadically, with very high nest densities in some compartments but none in many others (Brian 1977; Welch 1978; Wright *et al.* 2000). Indeed, at Bedford Purlieus in Cambridgeshire, the closest known population of *F. rufa* to Harlestone Firs, this patchy distribution is also prevalent. Within this site of ancient woodland covering 211 ha, only 155 nests were recorded in the 1974 survey of Peterken and Welch (1975). Within that area, the wood ants were confined to three distinct blocks, the largest compartment, covering 17.5 ha, contained 57 nests (Peterken & Welch 1975; Welch 1978). Numerous visits during the last few years have confirmed that the Bedford Purlieus population remains about the same today (Clarkson unpublished data). In contrast, at Harlestone Firs, *F. rufa* colonies can be found in every woodland compartment, and although nest densities do vary around the wood, nests are very easy to locate. Therefore, with over 500 nests available, sample sites could be selected on the basis of edge suitability, rather than depending upon where the ants could be found. Sufficient nests exist within each sample site to provide the study with enough data to be meaningful; again, a factor not possible in many other woods.

Harlestone Firs is also an ideal location to study edge effects *per se*. The site is embedded within a matrix of agricultural, recreational and urban land use and for the most part, has distinct, abrupt edges adjacent to open fields. Access to the majority of the land surrounding the wood is also possible which allowed consistent external measurement points to be selected for the duration of the study. Harlestone Firs is also sufficiently small to allow measurements to be taken during a regular sampling 'period', but large enough to ensure that all data from the sample sites remained independent of each other.

On a larger scale, Northampton is at the junction of a 'notional' boundary. To the north and across the Midlands many populations of *F. rufa* have been lost or have experienced a serious decline for many years, often for no apparent reason (Skinner 1998; Robinson 2001). This is especially true for smaller woodlands (Collingwood 1955 & 1964). To the south, with the exception of losses due to habitat destruction, *F. rufa* appears to be doing very well and indeed, in many cases, expanding within many of its strongholds (North 1993b).

All of these factors combined make Harlestone Firs an ideal location to study the influence of forest edge effects on the ecology of *F. rufa*. Thus, identifying the factors that make this site able to support an expanding population may shed light on issues for the conservation of *F. rufa* in the UK as a whole.

3.3 Study Sample Sites.

Rationale for the Selection of Appropriate Study Sites.

Data regarding the impact of forest edge effects in the UK are sparse (Moorecroft *et al.* 1998). It was therefore decided that this study would have a dual function; that it would not only generate data on the impact of aspect and distance related forest edge effects on a target species, but would also set out to provide comparable data with those studies that have contributed most to the current understanding of edge effects in temperate regions (Matlack 1993, 1994; Fraver 1994; Young & Mitchell 1994; Murcia 1995). Therefore the common approach in these type of studies was adopted and study sites were selected which were located on both the northern and southern edges of the wood. An attempt was also made to select two sites which faced more to the east and west. Unfortunately, the study sites chosen to represent the northern and western edges were quite similar in aspect due to restrictions related to the shape of the woodland boundaries and available access. However, each had a very different edge structure, a factor which could be expected to produce very different microclimate regimes immediately behind the forest edge. The sample site chosen to represent an eastern aspect in fact faced north-east, whilst the southern site faced in a more south easterly direction. Nevertheless, although sample aspects were not entirely orientated along the cardinal compass points (a goal also rarely achieved in any previous studies), the microclimatic differences between them are representative of the findings of previous key studies (Brothers & Spingarn 1992; Brothers 1993; Matlack 1993, 1994; Fraver 1994; Young & Mitchell 1994). Therefore this study is very valuable in the context of edge effect studies. Thus four forest edge sampling sites were selected so as to face as near as possible to the four cardinal compass points, whilst still retaining an abrupt forest edge of 200m in length and, where possible, bordered by open fields. The four locations were selected to ensure that they were also enclosed on three sides by woodland (Fig 3.2). The dimensions of the four sites ensured that sufficient colonies were present within each study aspect.



Figure 3.2: Aerial Photograph of Harlestone Firs with Approximate Location of Sample Sites. (Produced with permission from Overview Mapping Ltd. Aerial photograph taken in 1999. Young trees in open area to the east of North-West 2 were around 1.5 metres in height at the beginning of 2000).

3.3:1 Site Descriptions.

Southern Sample Site (SP 722 645)

The southern edge is bordered by a large field dividing Harlestone Firs from local housing estates and an industrial area (Fig 3.3). A major forest ride defines the western boundary and a small footpath the eastern. The sampling area extends back into the woodland until it meets the first forest ride, which is a distance of approximately 160m. The forest edge can be characterised as being 'closed' and is defined by a *Crataegus monogyna* boundary hedge and the adventitious limbs of mature edge trees.

The canopy is dominated by plantation trees such as, *P. sylvestris*, *L. decidua* and *P. nigra*. Many species of deciduous tree occupy the middle canopy, but the most common are *A. pseudoplatanus*, *Tilia platyphyllos* and *F. excelsior*. *Sambucus nigra* and *C. avellana* are very common understorey components and *P. aquilinum* and *Rubus fruticosus* agg. dominate the ground flora.

North Eastern Sampling Site (SP 723 645)

The north eastern edge faces Harlestone Heath Local Nature Reserve, a narrow strip of poor heathland between the woodland and railway, and is defined by an old *C. monogyna* boundary hedge (Fig 3.4). A major forest ride divides the south facing side of the site, but only a narrow path defines the northern side. The compartment stretches back for almost 200m, providing a large area of structurally similar woodland. The edge is defined as 'partly closed', being shielded by the boundary hedge and the adventitious limbs of the mature edge trees. *P. sylvestris* dominates the canopy. Many species of deciduous tree occupy the middle canopy, the most common of which are *A. pseudoplatanus*, *Q. robur*, *Sorbus aucuparia* and *B. pendula*. *S. nigra* is a very common understorey component, with *P. aquilinum* dominating the ground flora.

North West 1 Sampling Site. (SP 718 655).

The north west 1 edge borders an agricultural field which was fallow at the time of the research (Fig 3.5). The edge is defined by a line of *P. sylvestris* and invading *S. nigra* which offer some shelter, but is for the most part 'open' in nature. A major forest ride marks the western edge and



Figure 3.3 : The abrupt, closed edge of the southern sample site.



Figure 3.4 : Edge of the eastern sampling site viewed from Harlestone Heath



Figure 3.5 : Edge of the northern sampling site viewed from the adjacent field.



Figure 3.6 : The 'closed edge' of the western sampling site.

a well defined woodland trail the eastern boundary. The sampling area extends back approximately 160m into the interior, where it meets a major forest ride.

The canopy is dominated by planted *P. abies* and *P. sylvestris*. The broad-leaved middle canopy is composed of *A. pseudoplatanus*, *Q. robur* and *B. pendula*, but also has large numbers of *Castanea sativa* and *S. aucuparia* which are not found in the southern site. However, *S. nigra* and *P. aquilinum* dominate the understorey and ground flora respectively, as they also do on the southern edge.

North West 2 Sampling Site (SP 715 646).

The first 30m of this site is the oldest part of the wood, showing evidence of afforestation well before the remainder of the former heathland. The edge faces a large open field at the foot of a gentle slope. The edge is abrupt and is divided from the field by a small stream (Fig 3.6). The edge is characterized as 'closed', being sealed by a variety of understorey species, regenerating trees and shrubs and by the limbs of mature trees such as *Q. robur* and *F. excelsior*. The initial 30m of the woodland is flat and tends to be very damp. However, the ground begins to rise sharply soon after 30m; the gradient continuing to the end of the compartment at around 270m inside the woodland. The northern side of the site is embedded in woodland; the southern side by a major forest ride.

The first 30m of the site is characterised by the dominance of deciduous species, with several notably old *Q. robur* individuals. Other common species are *A. pseudoplatanus*, younger *Q. robur*, *F. excelsior*, *S. aucuparia* and *B. pendula*. *Alnus glutinosa* and *C. Monogyna* dominate the damper areas, as do *S. nigra* and *P. aquilinum* the understorey and ground flora respectively. The more sloping areas have extensive plantation of *P. abies*, *P. sylvestris* and *L. decidua*. Shading is severe and there is limited ground flora with *P. aquilinum* occurring in large clumps. In areas where the plantation thins, *A. pseudoplatanus* and *S. nigra* begin to dominate instead.

3.3:2 Limitations to Research Methods Imposed by Conditions at Harlestone Firs.

Harlestone Firs is a very popular location with the public and is used extensively for recreational activities. Much of the woodland is characterised by areas of human disturbance, and as wood ant nests are conspicuous features, they receive their share of the attention. Much of the damage

is caused by innocent investigation, but some no doubt is malicious. During the summer months when the ants are at the height of their activity, this 'anthropogenic' attention does not appear to adversely affect colonies, which quickly repair minor damage. However, although not overly serious for the ants, human disturbance does impact on the methods which are available to the researcher. The use of long term monitoring equipment was consequently not possible due to the likelihood of it being stolen or damaged. Therefore, the study had to rely on instantaneous measurements which at least did permit the collection of accurate long term monitoring data. However, despite some difficulties Harlestone Firs proved to be a valuable and justifiable study location.

Chapter 4:

Microclimatic Forest Edge Effects and the Consequent Responses of the Wood Ant, *Formica rufa* in Relation to Edge Width and Edge Aspect.

4.1 Introduction.

Microclimatic parameters, such as temperature, solar radiation and air and soil moisture, drive biological processes and determine the distribution of plants and insects within a forest environment (Geiger 1965; Wales 1967; Chapin *et al.* 1987; Chen *et al.* 1993). For that reason, understanding the impact and extent of the microclimatic conditions within edge environments is the key to predicting the biological responses which occur there (Geiger 1965; Chen *et al.* 1992, 1993, 1995). This chapter sets out to address the extent of the physical edge effects within the four study aspects, and seeks to determine if these processes influence aspects of the ecology of the wood ant, *Formica rufa* around Harlestone Firs.

4.2 Nest Characteristics and Location in the Wood Ant, *Formica rufa* L.

Mound nests are typically orientated to the sun, and thus have shallower slopes on the sides which receive the most light (Forel 1874; McCook 1877; Andrews 1927). This phenomenon is believed to ensure that nests provide a larger surface area with which to capture heat from the sun, a key factor in the thermoregulatory function of the nests (Scherba 1958, 1959, 1962; Collins & Wells 1987; Fowles 1994; North 1996). For example, Cook (1998) showed that 83% of the nests in her study received direct sunlight at some point during the day (52% of nests faced south). Indeed Huber (1820) reported the existence of 'compass' nest mounds on the open mountain slopes of Switzerland that had elongated slopes that faced the morning sun. Apparently this well known feature allowed natives of the Alps to navigate more effectively.

While it is accepted that wood ant species generally favour more open areas in which to place their nests, both Adlung (1966) and Robinson (2001) note that *F. rufa* can be considered a shade tolerant species often nesting beneath a dense canopy. In spite of this, Robinson (2001) indicates that although *F. rufa* colonies may thrive in these more 'harsh' conditions in the English Midlands, they cannot do so at the edge of their UK range in north-west England. This apparent 'relaxation' in nest site preference in response to a more favourable climate appears to be quite common amongst insects, and has implications for conservation strategies

throughout a species' range. For example, Thomas *et al.* (1998), looking at the habitats of the ant *Myrmica sabuleti* and its associated myrmecophilous butterfly *Maculinea arion*, found that at the northern edge of their range (or near their altitudinal limit), the two were confined to south facing slopes where the sward was less than 3cm in height. However, further south, in areas where the summer climate was 4°C warmer, they favoured habitats with any aspect other than south, and even survived in swards over 20cm tall. Although these findings show that species do respond to climatic variation over large geographical or altitudinal scales, one question remains: to what extent do small scale microclimatic changes influence aspects of habitat preference, such as nest location, across a single area of woodland in response to edge effects?

The specific questions addressed in this chapter are:

- 1) To what extent do physical edge effects modify the microclimate around the study aspects?
- 2) Is wood ant nest location influenced by edge effects?
 - a) What role does microclimate play in nest location?
 - b) Are nest characteristics (size, height, slope angle, orientation, distance from internal and external edges) influenced by edge effects?
 - c) Is nest density influenced by edge effects?

4.3 Methods

4.3:1 Microclimatic Edge Effect Measurements.

The sampling period extended from the beginning of the ants active period through to its close with the onset of the winter hibernation. Consequently, the measurement of microclimatic variables took place from February to November 2000 and February to December 2001. Sampling took place on a total of 177 days; 98 in 2000 and 79 in 2001. The shorter sampling period in 2001 was due to disruption by the nationwide 'Foot and Mouth' outbreak and by forest management operations which caused Harlestone Firs to close for a period of 31 days.

At each sample aspect, three edge to interior transects were set out to determine both the general forest microclimate and to calculate edge width. These extended from 20m outside the wood, through the ‘forest edge’, to 160m into the interior. As the characteristics of edge vegetation varied greatly around the woodland, it was important to define exactly where the ‘forest edge’ was deemed to exist so as to ensure that measurements were standardised. Thus, during this study the basic criteria described by Matlack (1993) were used, and the forest edge was defined as follows;

- The centre point of any boundary feature (fence or hedge) where it existed;
- Otherwise the centre of the trunks of the last row of trees.

Temperature ($^{\circ}\text{C}$), relative humidity (%), wind speed (ms^{-1}) and light intensity (lux) measurements were made at -20m, 0m, 10m, 20m, 40m, 80m and 160m into the woodland along these transects. Details of the equipment used during the study are provided in Table 4.1.

Table 4.1: Equipment used during the study.

Variable measured	Type of Equipment
Air Temperature ($^{\circ}\text{C}$)	Standard mercury thermometer
Relative Humidity (%)	Whirling Hygrometer, and Aspirated Psychrometer.
Wind Speed (ms^{-1})	Kestrel 1000 Digital Anemometer (accuracy \pm 1% - Richard Paul Russell Ltd);
Light Intensity (lux)	Hagner Digital Luxmeter (Model EC1 – accuracy \pm 3%).

Simultaneous measurements were made from 20m outside the wood to ensure that as far as possible, measurements inside corresponded to exterior conditions. Where this was not possible, five exterior measurements were made over a ten minute period, the mean of which formed the constant exterior value. Simultaneous measurements were achieved using a second operator with the same equipment taking readings at specified times. These methods are in keeping with previous work on edge effects (Brothers & Spingarn 1992; Brothers 1993; Chen *et al.* 1993; Matlack 1993, 1994; Fraver 1994; Young & Mitchell 1994).

All measurements were made at a height of 0.6m to incorporate the different conditions experienced throughout the year on both sides of the edge. This height ensured that measurements could be taken effectively, even where vegetation cover was dense. Where vegetation exceeded 0.6m, measurements were taken from the nearest location which was free

from vegetation, retaining the same distance from the woodland edge. A height of 0.6m reaches a suitable compromise between the requirements of edge effect studies and those centred upon ants, and is consistent with heights used in previous studies (Kapos 1989; Matlack 1993).

To ensure that conditions were as similar as possible at all four study sites on a given day, all measurements were obtained between two hours before solar noon and three hours afterwards. The extended period after solar noon is justified by the fact that the warmest part of the day generally occurs after solar noon (Ahrens 1994). This 'lag' depends on the time of year and the amount of vegetation cover, but the time period selected enabled the number of sample measurements required to be obtained. In order to standardise the data collection process, the order in which the sites were sampled was rotated constantly to ensure that measurements were not subjected to systematic errors related to sampling bias. Every sample point therefore had the same number of measurements before and after solar noon during the year.

Soil Analysis

Soil samples were taken on a single day in March, August and October, along the edge to interior transects from the four sample aspects in 2000 only. Samples were taken five days after the last recorded precipitation and processed on the same day to ensure more accurate results. From these, soil moisture and soil pH were determined. Soil moisture was determined using the method described by Allen *et al.* (1974). Soil pH was determined from the August samples only using a standard pH meter and calibration buffers.

4.3:2 Nest Microclimate Analysis

Within each of the four sample aspects, five nests and five control points were selected. Sample nests were selected, where possible, to provide a gradient from the edge to the interior of each sample aspect, but were at least 10m away from the edge to interior transect sampling points. Control points were also selected so as to ensure a 10m spacing from the edge to interior transect sampling points or the corresponding sample nest. They were the same distance away from the edge as the sample nests and in a location which showed no evidence of having supported a wood ant colony in the past.

Nests and control point measurements and edge to interior transect measurements were made on the same days to enable an accurate comparison of the data. All sample nest measurements were taken from 0.1m above the top of the nest mound or 0.6m above the forest floor, whichever was the lowest. Measurements at control points were made at 0.6m above the forest floor. The location of the transects, nests and control points within the four sites, together with their approximate distance from the forest edge are shown in Figures 4.1 - 4.4.

4.3:3 Nest Location and Characteristics.

In addition to the five sample nests within each sample aspect, numerous other nests were also used in this analysis to enhance the data set. The number of nests varied between the sampling sites due to the number of available nests, but overall a total of 82 nests were used during the analysis (Table 4.2). From each nest the following data were gathered;

- Nest height;
- Nest dimensions (length & breadth);
- Angle of the shallowest slope;
- Orientation of the shallowest slope;
- Distance from the nearest external edge;
- Distance from the nearest internal edge;
- The number and density of nests at each study aspect around the wood.

Table 4.2: Additional Sample Nests used during the Study
(does not include original 20 nests).

South	25
North East	12
North West 1	8
North West 2	17

Nest height was measured in centimetres to the highest part of the nest above the surrounding soil surface and nest dimensions by measuring the length and breadth of the area of forest surface covered by nesting material. Nest orientation was determined by taking a compass bearing at the centre of the shallowest slope of each nest. This method builds on the long established view that wood ants tend to construct their nests so as to ensure that a shallow slope faces the most important source of light, thus increasing its surface area to trap more

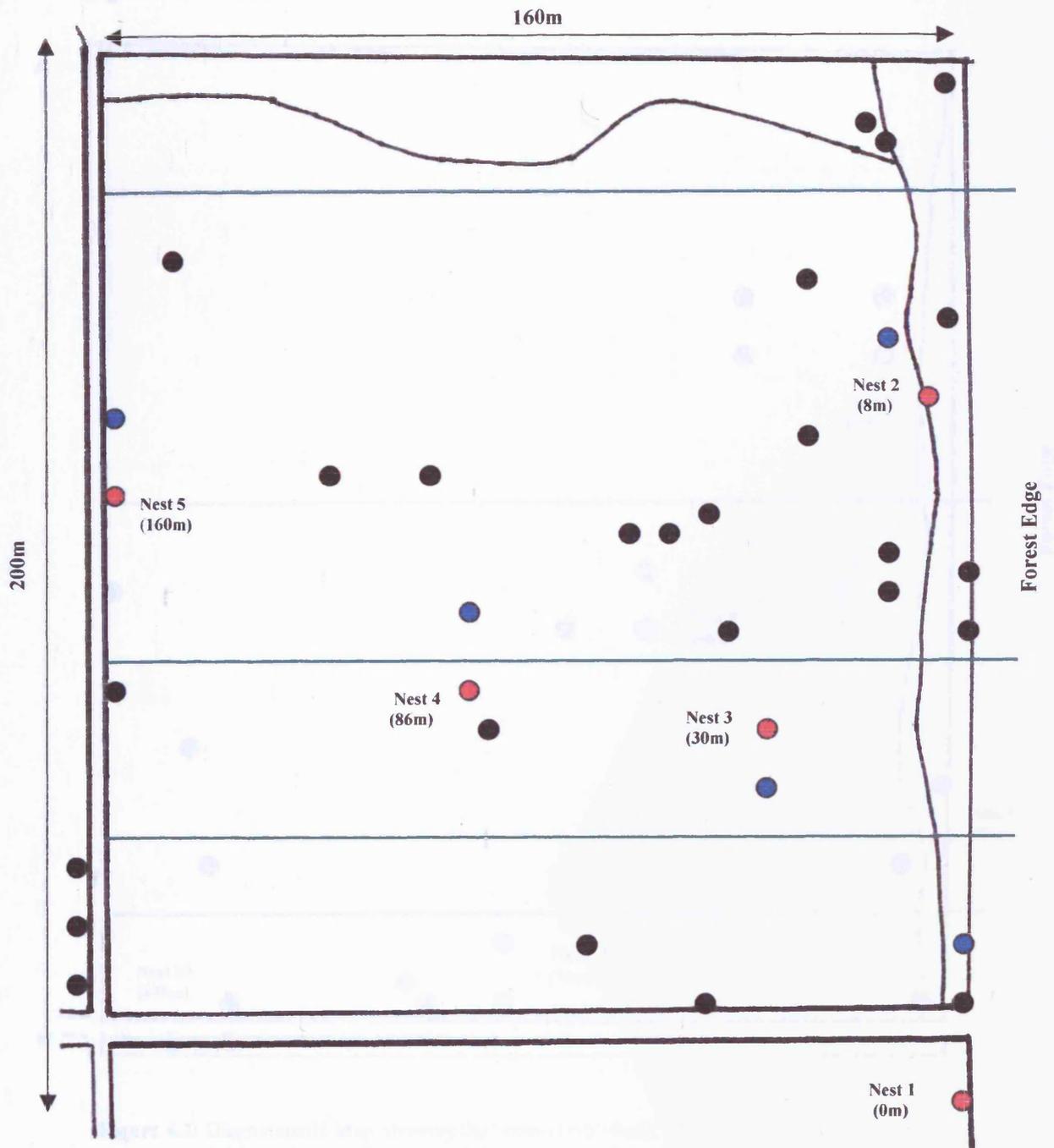


Figure 4.1: Diagrammatic Map Showing the Study Nests (Red); Control Points (Blue); Additional Nests (Black) and Edge to Interior Transects (Green) for the Southern Aspect. Distances measured to +/- 3m.

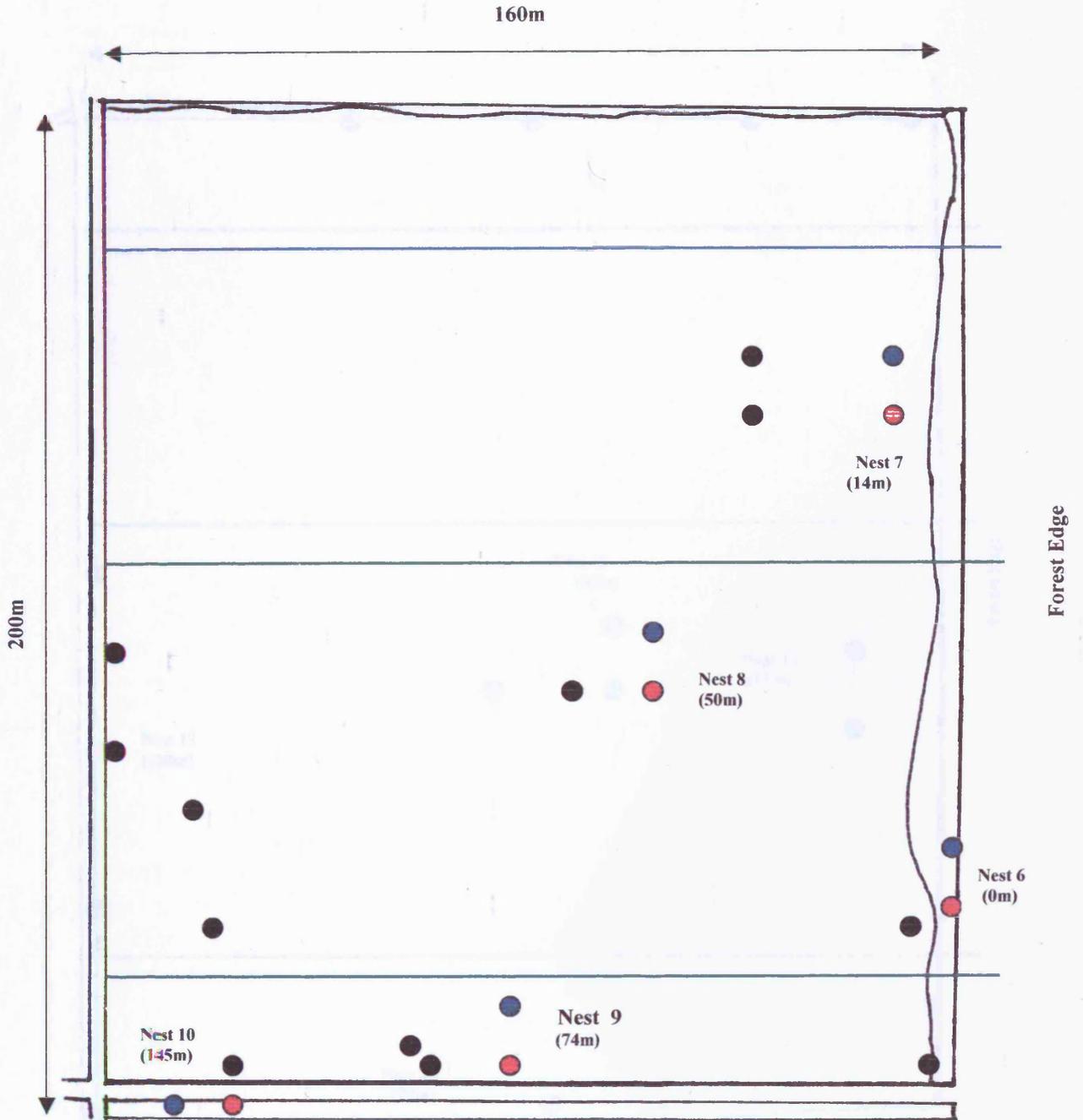


Figure 4.2: Diagrammatic Map Showing the Study Nests (Red); Control Points (Blue); Additional Nests (Black) and Edge to Interior Transects (Green) for the North Eastern Aspect. Distances measured to +/- 3m.

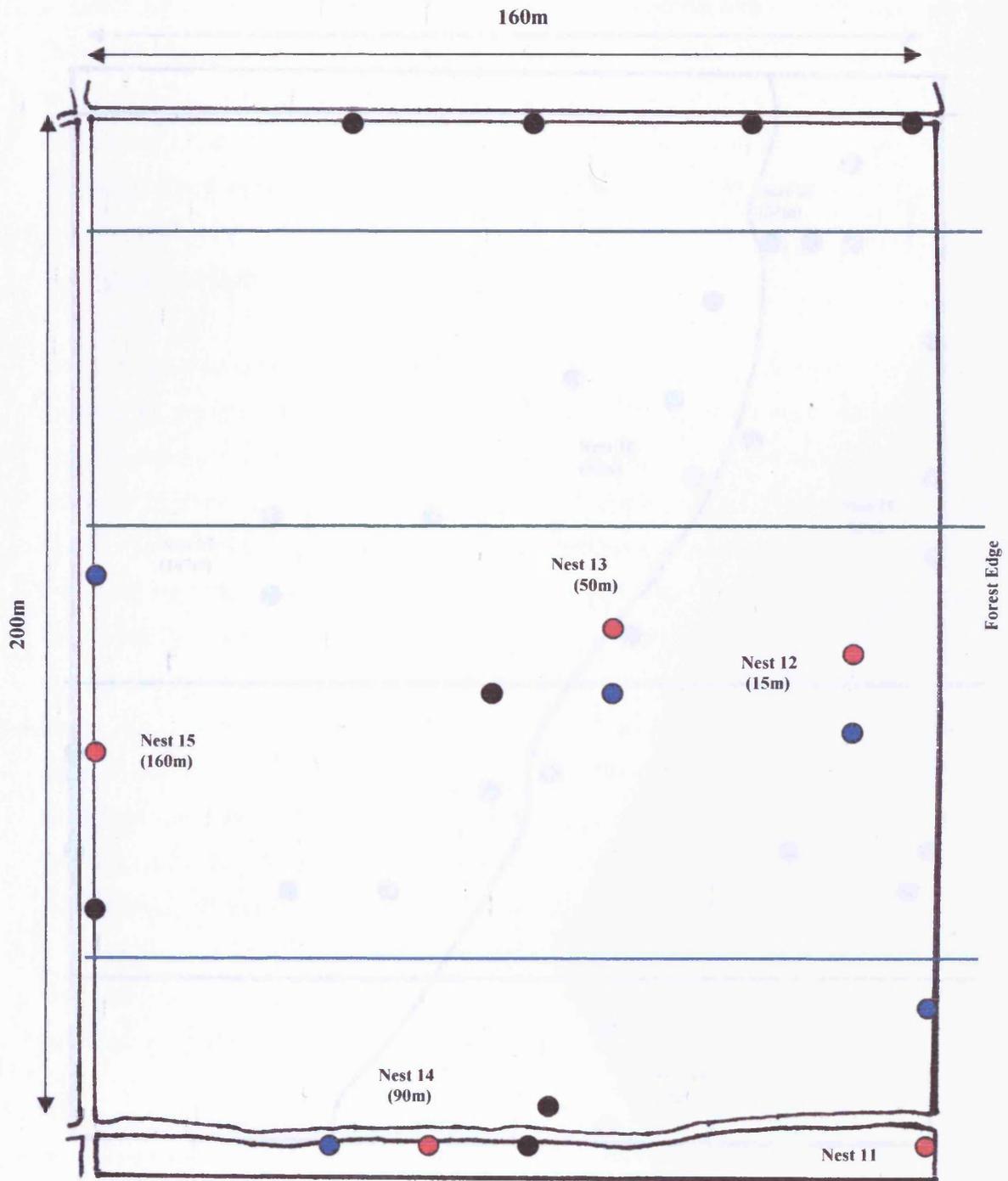


Figure 4.3: Diagrammatic Map Showing the Study Nests (Red); Control Points (Blue); Additional Nests (Black) and Edge to Interior Transects (Green) for the North Western Aspect. Distances measured to +/- 3m.

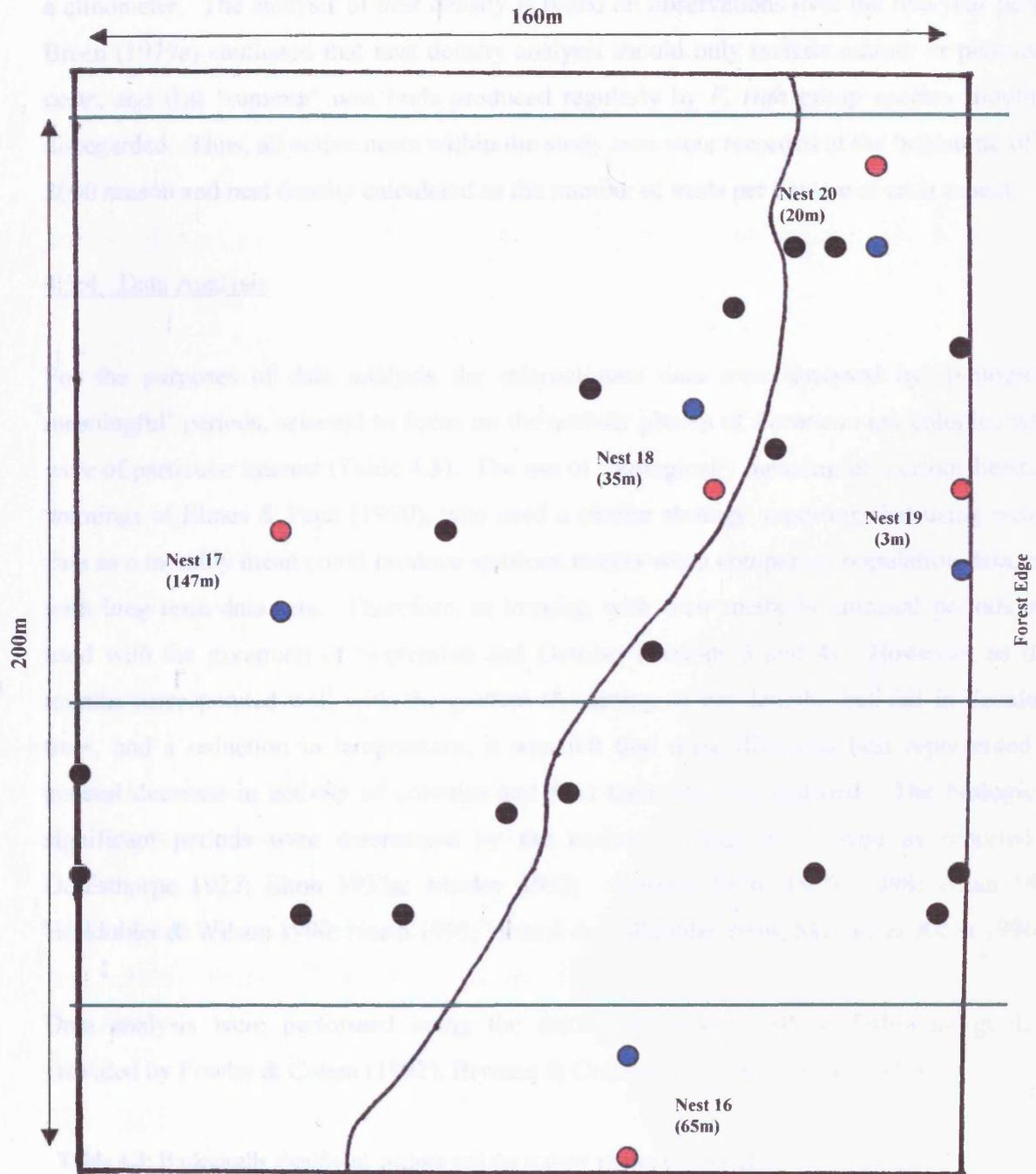


Figure 4.4: Diagrammatic Map Showing the Study Nests (Red); Control Points (Blue); Additional Nests (Black) and Edge to Interior Transects (Green) for the North Western 2 Aspect. Distances measured to +/- 3m.

heat (see Chapter 2, Section 2.3). The angle of this shallowest slope was also measured using a clinometer. The analysis of nest density is based on observations over the two year period. Breen (1979a) cautioned that nest density analysis should only include mature or permanent nests, and that ‘summer’ nest buds produced regularly by *F. rufa* group species should be disregarded. Thus, all active nests within the study area were recorded at the beginning of the 2000 season and nest density calculated as the number of nests per hectare at each aspect.

4.3:4 Data Analysis

For the purposes of data analysis the microclimate data were analysed by ‘biologically meaningful’ periods, selected to focus on the activity phases of *Formica rufa* colonies which were of particular interest (Table 4.3). The use of ‘biologically meaningful’ periods heeds the warnings of Elmes & Petal (1990), who used a similar strategy, reporting that using weather data as a monthly mean could produce spurious results when comparing population data, even with long term data sets. Therefore, in keeping with their methods, unequal periods were used with the exception of September and October (Periods 3 and 4). However, as these months corresponded well with the gradual shortening of day length, leaf fall in deciduous trees, and a reduction in temperature, it was felt that these divisions best represented the general decrease in activity of colonies and thus their use was justified. The biologically significant periods were determined by the known ecology of *F. rufa* as reported by Donisthorpe 1927; Elton 1932a; Morley 1953; Skinner 1976, 1989, 1998; Brian 1977; Hölldobler & Wilson 1990; North 1993; Heinze & Hölldobler 1994; Skinner & Allen 1996.

Data analysis were performed using the statistical package SPSS, following guidance provided by Fowler & Cohen (1992), Bryman & Cramer (1996) and Waite (2000).

Table 4.3: Biologically significant periods and the activity phases of interest.

Division	Duration	Activity of Interest
Period 1	Feb-Mar	Dates of first activity, foraging and spring ‘mass’
Period 2	Apr-June	Emergence of reproductive forms and the timing of the nuptial flights
Period 3	Sept	Decrease of activity after summer maximum
Period 4	Oct	Onset of the gradual reduction in activity
Period 5	Nov-Dec	Dates of last activity.

Physical Edge Effects and Nest Microclimate Analysis.

The initial step was to determine if there were differences between the four variables with aspect around the wood. Therefore, microclimate data from the three edge to interior transects were analysed using One-Way ANOVA tests with finer scale interpretation of the results achieved by the use of Tukey HSD *post-hoc* tests. Where data were not normally distributed \log_{10} or square-root transformations were applied and the data re-tested for normality.

Analysis of the microclimate at the five sample nests and control points at each sample aspect were conducted in the same manner to initially determine if *F. rufa* colonies appeared to select nest locations in response to microclimate.

In all cases, ANOVA results are reported in the text, whilst levels of significance for *post hoc* analysis are presented in the Appendices (see App 3).

Soil Analysis.

Soil moisture data sets were normally distributed and were therefore compared using One-way ANOVA tests with *post hoc* analysis achieved via the Tukey HSD test. Soil pH values were transformed to their real values by way of the antilog function. The transformed data were not normally distributed and could not be transformed further to conform to this requirement. Therefore data were compared by way of the non-parametric Kruskal-Wallis test.

Edge Width.

The extent of the microclimatic edge effects along the transects were determined by the use of Kruskal-Wallis tests. A non-parametric test was chosen to avoid the need to normalise the data sets and thus 'compress' the data. The results represent all four aspects together during each biologically significant period for the two years. This method gave an indication of the extent of the edge effects whilst ensuring that the number of statistical tests carried out could limit the potential for both 'type 1' and 'type 2' statistical errors. The actual mean edge gradient for each statistically significant variable at the different aspects during the biologically significant periods is presented graphically in Appendix 4.

The Responses of Colonies via Nest Characteristics to Edge Effects.

Initially the nest characteristics data were tested for differences between nests found within the different sample aspects. Nest orientation, height, dimensions and slope angle and distance to the nearest edge were therefore analysed using One-Way ANOVA tests with *post hoc* analysis achieved by way of the Tukey HSD test.

Data were then analysed to determine if relationships existed between nest height and size, nest orientation and the angle of the shallowest slope with distance to the nearest internal and external edge. This was achieved by using standard linear regression with built in ANOVA tests.

4.4 Results.

4.4:1 Aspect Related Microclimate Edge Effects.

Summary of the Overall Trends

In 2000 the mean temperature and light intensity values in the southern aspect were higher than in the three other aspects during Periods 1, 2, 4 and 5. In Period 3, temperature and light intensity in both the north-eastern and north-west 1 sites were higher than the south or north-west 2 (Appendix 1). The southern aspect also recorded the highest mean relative humidity values in Periods 1, 2 and 4, the north-eastern aspect having the highest mean values in Periods 3 and 5. Mean wind speed was highest in north-west 1 in all Periods.

Patterns in 2001 were slightly different. The south was on average warmer in Periods 1 to 4, with the north-east being the warmest in Period 5 (Appendix 1). Light intensity was also different, with mean values in the south being highest in Periods 1, 4 and 5. The north-west 1 aspect had the highest mean light intensity values in Period 2 and north-west 2 in Period 3. Mean relative humidity was highest in the south during Periods 1, 2, 3 and 5, with the north-east having the highest mean values in Period 4. Mean wind speed remained highest in north-west 1 (Appendix 1).

Results of Data Analysis during 2000.

In Period 1, the results showed that significant differences existed in light intensity (One-Way ANOVA $F=20.145$; d.f.3; $p<0.001$), wind speed ($F= 4.124$; $p=0.007$) and relative humidity ($F=10.125$; $p<0.001$). *Post hoc* analysis showed that the southern aspect received significantly higher light intensities than all other aspects, and that the north-eastern aspect received higher light levels than north-west 2. North-west 1 received significantly higher wind speeds and lower relative humidity values than all other aspects.

Similar trends were maintained during Period 2, with significant differences once again being found in light intensity (One-Way ANOVA $F=3.675$; d.f.3; $p=0.012$), wind speed ($F=37.730$; $p<0.001$) and relative humidity ($F=19.759$; $p<0.001$). *Post hoc* analysis showed that the southern and north-eastern aspects received significantly higher light intensities than north-west 2. North-west 1 again received significantly higher wind speeds, but lower relative humidity values than all other aspects.

In Period 3, again light intensity (One-Way ANOVA $F=10.842$; d.f.3; $p<0.001$), wind speed ($F=15.061$; $p<0.001$) and relative humidity values ($F=3.543$; $p=0.015$) showed significant differences. *Post hoc* analysis showed that north-west 2 received higher light levels than either the south or north-west 1 and that the north-east received higher light levels than north-west 1. Once again, wind speeds at north-west 1 were significantly higher than at all other aspects, but on this occasion relative humidity values were significantly lower than only the south.

During Period 4, only light intensity (One-Way ANOVA $F=3.747$; d.f.3; $p=0.011$) and wind speed ($F= 23.183$; $p<0.001$) showed significant differences. *Post hoc* analysis confirmed that light intensity values were higher in the south than at all other aspects. Once again, wind speeds were significantly higher in north-west 1 than at all other aspects, but on this occasion wind speeds were higher in the north-east than at north-west 2.

In Period 5, significant differences existed in all four variables (temperature One-Way ANOVA $F=19.756$; d.f.3; $p<0.001$: light intensity $F=6.565$; $p<0.001$: wind speed $F= 14.966$; $p=0.002$: relative humidity $F= 5.014$; $p<0.001$). *Post hoc* analysis confirmed that both temperature and light intensity values were significantly higher in the south than at all other aspects. Wind speed was higher at north-west 1 than at all other aspects, and relative humidity lower than the south and north-east. Results are summarised in Table 4.4.

Table 4.4: Summary of the Analysis of Microclimate by Aspect (> statistically significant).

Variable	Period 1	Period 2	Period 3	Period 4	Period 5
2000					
Temperature	N/S	N/S	N/S	N/S	South > All Aspects
Light	South > All Aspects North East > North West 2	South > North West 2 North East > North West 2	North West 2 > South North West 2 > North West 1 North East > North West 1	South > All Aspects	South > All Aspects
Wind Speed	North West 1 > All Aspects	North West 1 > All Aspects	North West 1 > All Aspects	North West 1 > All Aspects North East > North West 2	North West 1 > All Aspects
Relative Humidity	South > North West 1 North East > North West 1 North West 2 > North West 1	South > North West 1 North East > North West 1 North West 2 > North West 1	South > North West 1	N/S	South > North West 1 North East > North West 1
2001					
Temperature	N/S	N/S	South > North West 2	South > All Aspects	N/S
Light	South > North East South > North West 2 North West 1 > North East North West 1 > North West 2	North West 1 > North East	N/S	South > North West 2	South > North West 2
Wind Speed	North West 1 > All Aspects	North West 1 > All Aspects	North West 1 > All Aspects	North West 1 > South North West 1 > North West 2	North West 1 > All Aspects
Relative Humidity	N/S	South > North West 1	N/S	N/S	N/S

Results of Data Analysis during 2001.

In Period 1 of 2001, ANOVA results showed that significant differences occurred within the light intensity (One-Way ANOVA $F= 10.730$; d.f.3; $p<0.001$) and wind speed data ($F= 13.622$; $p<0.001$). *Post hoc* analysis showed that light intensity in the south and north-west 1 was significantly higher than either the north-east or north-west 2. Wind speed at north-west 1 was significantly higher than at all other aspects.

During Period 2 significant differences existed in the light intensity (One-Way ANOVA $F= 4.274$; d.f.3; $p=0.005$), wind speed ($F=34.023$; $p<0.001$), and relative humidity ($F= 4017$; $p=0.008$) data. *Post hoc* analysis confirmed that north-west 1 received significantly higher light levels than the north-eastern aspect. Wind speeds were significantly higher at north-west 1 than at all other aspects. However, relative humidity was significantly lower in north-west 1 only than in the southern aspect.

In Period 3 significant differences existed in only the temperature (One-Way ANOVA $F=2.865$; d.f.3; $p=0.038$) and wind speed data ($F= 17.000$; $p<0.001$). *Post hoc* analysis showed that the southern aspect was significantly warmer than north-west 2, but that north-west 1 received significantly higher wind speeds than all other aspects. In addition the north-east received higher wind speeds than the south. During Period 4 significant differences existed in the temperature (One-Way ANOVA $F= 9.852$; d.f.3; $p<0.001$), light intensity ($F=3.963$; $p=0.009$) and wind speed ($F=15.076$; $p<0.001$) data. *Post hoc* analysis showed that temperature in the south was significantly higher than all other aspects, and that light intensity was significantly higher than north-west 2 only. Wind speed was significantly higher at north-west 1 than along the south or north-west 2 transects.

Finally, in Period 5 significant differences existed in the light intensity (One-Way ANOVA $F=3.600$; d.f.3; $p=0.14$), and wind speed ($F=16.826$; $p<0.001$) data. *Post hoc* analysis showed that light intensity in the south was significantly higher than in north-west 2, and wind speed significantly higher at north-west 1 than at all other aspects. A summary of the results is shown in Table 4.4.

Soil Moisture.

Annual Pattern.

There were significant differences between the percentage soil moisture along the transects of the four study aspects (One-Way ANOVA $F= 10.979$; d.f 3; $p= <0.002$). Along both the southern and north-west 1 transects, soil moisture was significantly less than along those within north-west 2 (Tukey HSD $p<0.001$).

Soil moisture profiles along the edge to interior transects showed differences between the sites. The southern and north-west 1 transects followed the expected trend with moisture generally increasing with distance into the wood. However, increases were small and consequently edge width was negligible. Soil moisture along the north-eastern transects showed no real trend, with values remaining generally stable with distance into the wood. However, the north-west 2 transects followed the reverse trend with comparatively high values recorded until 10m inside the edge. From this point values fell sharply with distance into the interior (Fig 4.5).

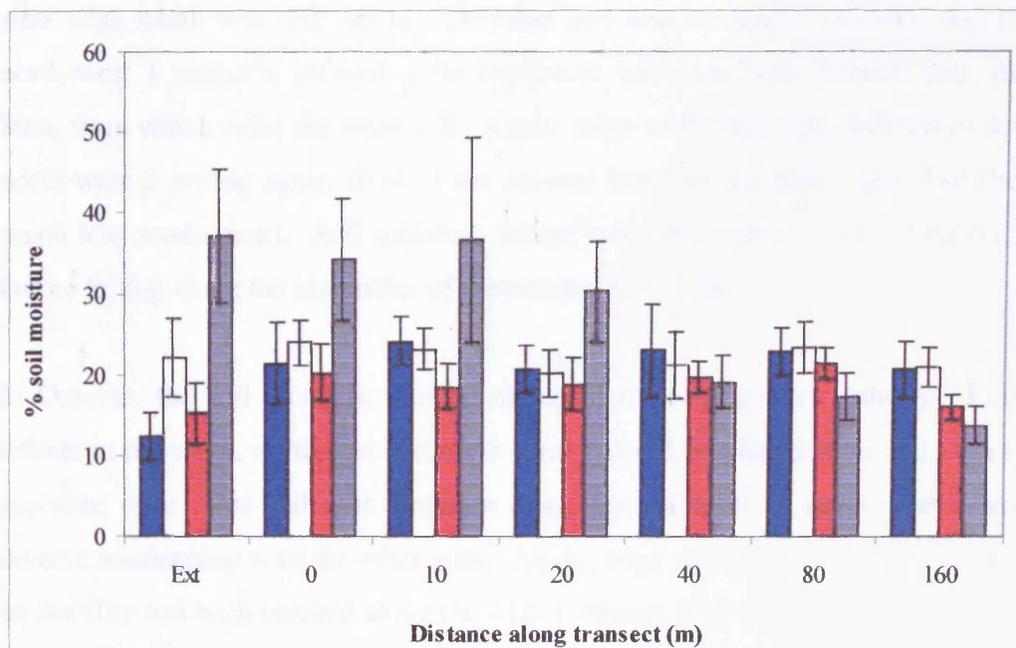


Figure 4.5: Overall mean percentage soil moisture along the edge to interior transects at the four study Aspects during 2000. Key: Blue – South; White – North-East; Red – North-West 1; Grey – North-West 2.

Seasonal Differences.

Significant differences in soil moisture between the sites were found in March 2000 (one-Way ANOVA $F= 14.996$; d.f.3; $p<0.001$). Once again, soil moisture in north-west 2 was much higher than within the other aspects (Tukey HSD $p<0.001$). The edge to interior soil moisture profile remained similar to the annual profile and no discernible edge effects were noted in the south, north-east and north-west 1. The north-west 2 transect retained the basic annual trend, apart from the decrease in values from 10m into the interior, which became more pronounced (Fig 4.6).

There were no significant differences between the sites with respect to soil moisture in either August or October (One Way ANOVA – August $F= 2.371$; d.f.3; $p= 0.077$: October $F=2.054$; $p=0.113$). However, the edge to interior soil moisture profiles were very different (Fig 4.6).

In August 2000 the southern transect showed greater fluctuation, moisture values increasing initially, before falling back at 40m. A similar pattern occurred in the north-east. In both sites edge width was difficult to determine and thus no useful estimate was possible. The north-west 1 transects showed quite consistent increases with distance into the wood until 80m, from which point the value fell. Again, edge width was very difficult to determine. The north-west 2 profile again showed the reverse trend to the other sites, but the pattern was much less pronounced. Soil moisture values remained constant until 20m on this occasion before falling along the remainder of the transect (Fig 4.6).

In October, the soil moisture profiles appeared to show greater stability. Edge influenced habitat in the south, north-east and north-west 2 could be placed at around 10m to 20m. Soil moisture once more fell with distance along the transects in north-west 2 maintaining an inverse relationship with the other sites. Again, edge width was very difficult to determine as no stability had been reached along the whole transect (Fig 4.6).

Soil pH around Harlestone Firs.

There were no significant differences between the soil pH values within the four study sites (Kruskal-Wallis $\chi^2 - 5.264$; d.f.3; $p= 0.153$). Median soil pH was lower in all sites than the exterior, however, the profile along the transects did not follow well-defined trends (Fig 4.7).

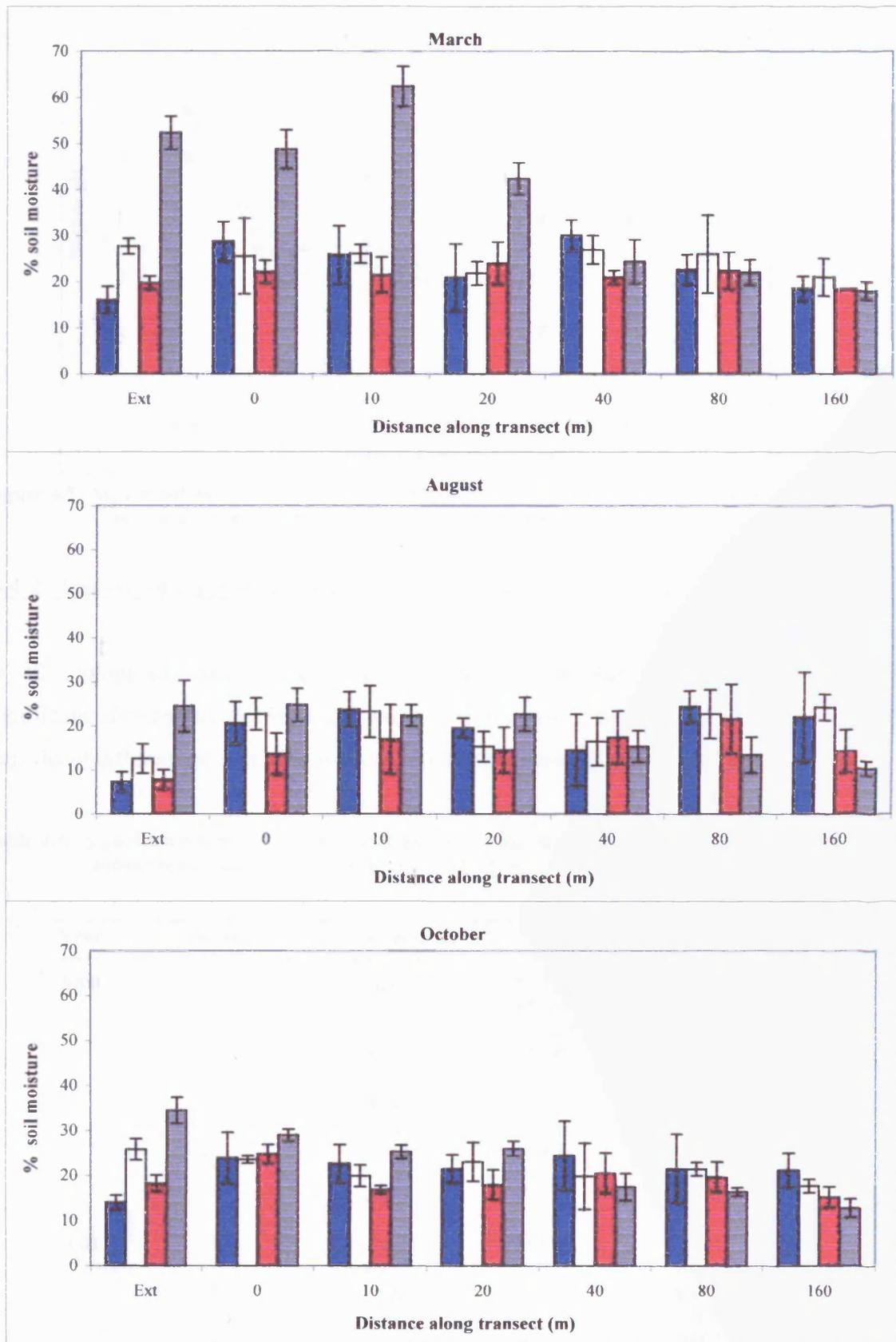


Figure 4.6: Seasonal mean percentage soil moisture along the edge to interior transects.
 Key: Blue - South; White - North-East; Red - North-West 1; Grey - North-West 2

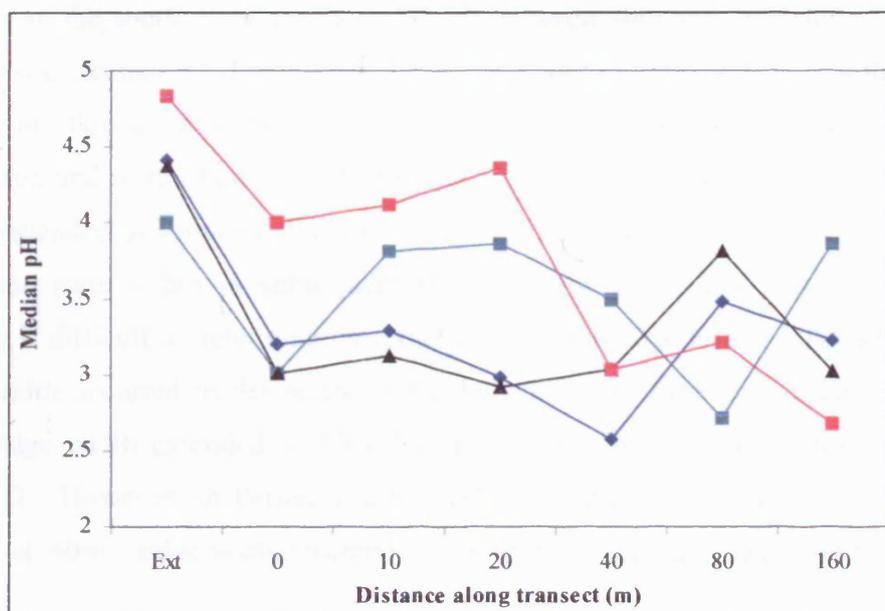


Figure 4.7 : Median pH along the edge to interior transects within the four study sites. (Key: blue – south; green – east; black – north; red – west – Quartiles not shown for clarity).

4.4:2 Analysis of Edge Width Around Harlestone Firs.

In all biologically significant Periods, light intensity and wind speed values showed significant differences between the edge and interior. However, in Period 4 of 2001, significant differences were also found in the temperature data (Table 4.5).

Table 4.5: Significant results of Kruskal-Wallis tests to compare the microclimate along the transects within the four study aspects (5 degrees of freedom).

Year	Period	Variable	χ^2	p
2000	1	Light	57.115	<0.001
	1	Wind	15.932	0.007
	2	Light	132.114	<0.001
	2	Wind	69.787	<0.001
	3	Light	84.868	<0.001
	3	Wind	25.639	<0.001
	4	Light	82.979	<0.001
	4	Wind	17.426	0.004
	5	Light	56.119	<0.001
	5	Wind	17.334	0.004
2001	1	Light	84.653	<0.001
	1	Wind	25.825	<0.001
	2	Light	152.737	<0.001
	2	Wind	140.851	<0.001
	3	Light	66.306	<0.001
	3	Wind	32.579	<0.001
	4	Temperature	14.552	0.012
	4	Light	46.163	<0.001
	4	Wind	47.064	<0.001
	5	Light	74.783	<0.001
5	Wind	73.147	<0.001	

In 2000 in the south, light values stabilised between 10m and 20m during all Periods. This pattern was maintained during Period 1 in 2001, but in Periods 2 to 5, light values tended to 'spike' at 40m and 80m before falling once more at 160m (Fig 4.8 & Appendix 4). The north-east and north-west 1 light intensity gradients were more stable. During 2000, edge width extended to between 10m and 20m in all Periods. In 2001, the Period 1 data followed the same pattern, but in subsequent Periods, light values fell steadily along the transect making it difficult to determine the exact influence of edge effects. The greatest variation in edge width occurred in the north-west 2 light intensity data set. In Periods 1 to 3 of both years edge width extended to 20m during Period 1, 80m during Period 2 and 40m during Period 3. However, in Period 4, edge width was difficult to calculate due to a noticeable 'spike' at 40m. Edge width returned to 10m in both years during Period 5.

Edge width related to wind speed values differed from the light climate. At all aspects during Period 1 in 2000, edge width extended to 10m. In 2001 there was greater variation, especially within the spread of the data at the two north-west facing sites. Edge width again extended to 10m in the south and north-west 2, but extended to 20m in the north-east and 40m at north-west 1. During Period 2, again edge width in the south and north-west 2 extended to only 10m. In the north-east the distance varied between the two years, 10m in 2000 and 40m in 2001. However, in north-west 1 edge width remained at 40m in both years.

During Period 3 in the south in both years and in the north-east in 2001 no discernable edge effects were identified with regards to the wind speed data. Edge width in north-west 1 and north-west 2 remained the same in both years, at 40m and 10m respectively. In the north-east in 2001, edge width extended to 40m. During Period 4, the south, north-west 1 and north-west 2 maintained the same edge width during the two years (20m, 40m, 10m). No discernable edge width occurred in the north-east in 2000 and in 2001 values fell steadily from edge to interior making the exact determination of edge width impractical. During Period 5, edge width remained largely similar across the two years. Edge width in the south extended to 20m, in north-west 1 to 40m and in north-west 2 to 10m. A steady decrease in values was found in the north-east again making the determination of edge width problematical.

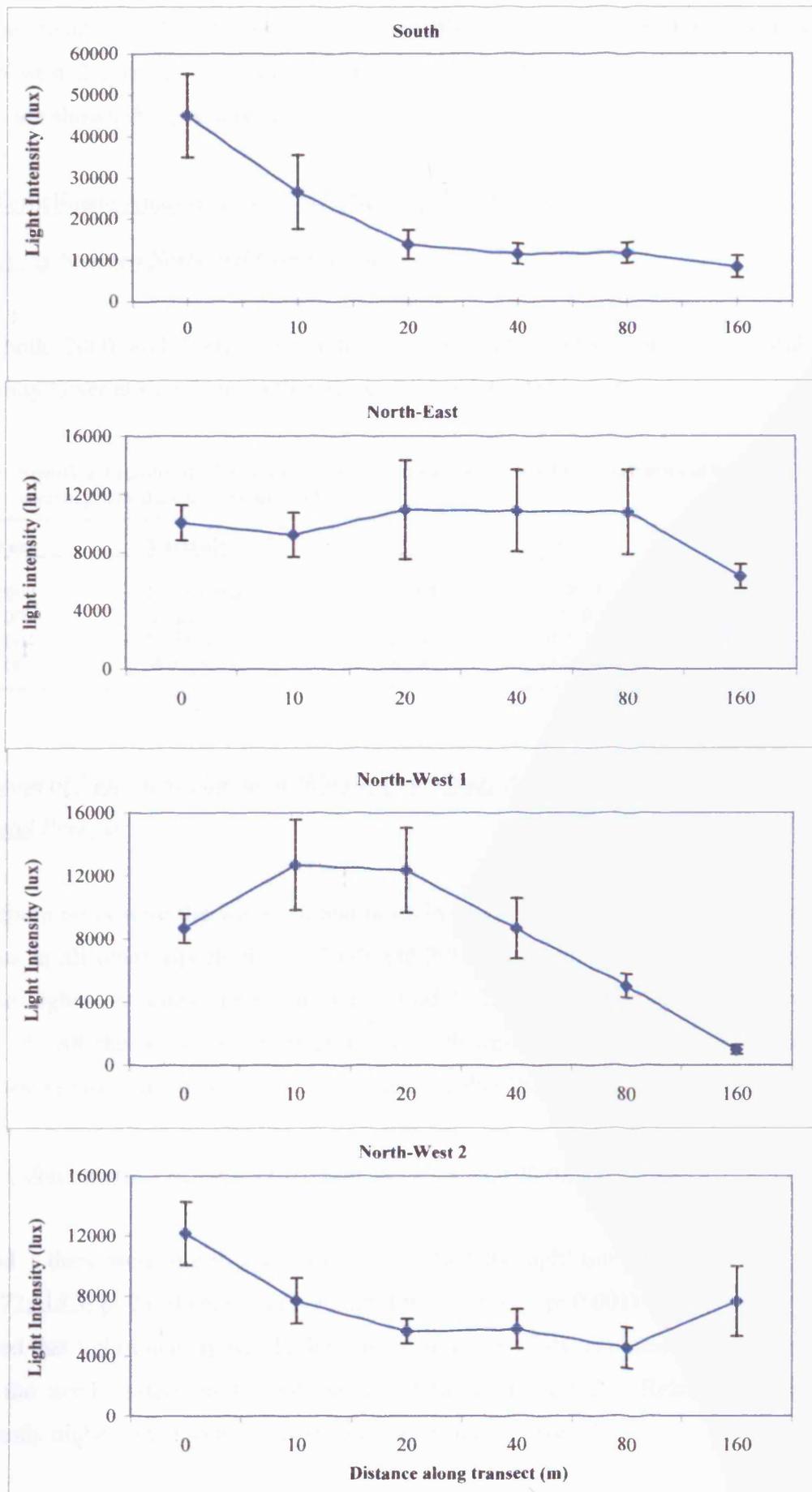


Figure 4.8 : Mean light intensity transect gradients during Period 1 of 2000.

In Period 4 of 2001, thermal edge effects were identified. Edge width extended to 80m in both the south and north-west 1 and 20m in the north-east. No distance could be estimated for the north-west 2 transects as values fell steadily from edge to interior. All mean transect gradients are shown in Appendix 4.

4.4:3 Microclimate Analysis at the Study Nests and Control Points.

Comparisons between Nests and Control Points.

During both 2000 and 2001, light intensity was significantly higher, but wind speeds significantly lower at sample nests than the control points (Table 4.6).

Table 4.6: Significant results of ANOVA comparisons of the four microclimate variables at nests and control points during 2000 and 2001.

Year	Variable	F	p
2000	Light Intensity	34.964	<0.001
2000	Wind Speed	6.601	0.010
2001	Light Intensity	18.085	<0.001
2001	Wind Speed	18.993	<0.001

Comparison of Nest Microclimate within the Four Study Aspects during the Biologically Meaningful Periods.

The southern nests were the warmest, and nests in north-west 1 received higher wind speeds than nests in all other aspects during 2000 and 2001 (Appendix 1). Light intensity values were also highest at southern nests during Period 1, 2, 4 and 5 in both years. However, in Period 3 of 2000 the north-east and in 2001 the north-west 2 nests received the highest values. The highest relative humidity values were found at either the southern or north-eastern nests.

Results of data analysis of the microclimate at the nests with aspect – 2000.

In Period 1 there were significant differences within the light intensity (One-Way ANOVA $F= 16.172$; $d.f.3$; $p<0.001$) and relative humidity ($F= 6.645$; $p<0.001$) data. *Post hoc* analysis confirmed that light intensity was highest at the southern nests than nests in all other aspects, and at the north-eastern nests and nests within north-west 2. Relative humidity was significantly higher at the southern nests than nests in north-west 1.

The ANOVA tests showed that significant differences existed in the light intensity (One-Way ANOVA $F= 11.379$; d.f.3; $p<0.001$), wind speed ($F= 19.692$; $p<0.001$) and relative humidity ($F= 21.751$; $p<0.001$) data in Period 2. *Post hoc* tests confirmed that nests within north-west 2 received significantly lower light levels than those at all other aspects. Nests in north-west 1 received higher wind speeds, but lower relative humidity values than nests in all other aspects.

In Period 3, significant differences existed in the light intensity (One-Way ANOVA $F= 11.693$; d.f.3; $p<0.001$), wind speed ($F= 5.333$; $p=0.001$) and relative humidity ($F= 3.447$; $p=0.017$) data. *Post hoc* tests confirmed that the north-eastern nests received significantly higher light levels than nests in all other aspects. Nests in north-west 1 received higher wind speeds than nests in either the south or the north-east. The nests in north-west 1 received lower relative humidity values than the southern nests.

During Period 4 significant differences within the light intensity (One-Way ANOVA $F= 6.615$; $p<0.001$) and wind speed ($F=13.000$; $p<0.001$) data. *Post hoc* tests confirmed that nests in the south received significantly more light, and nests in north-west 1 higher wind speeds than those in all other aspects.

In Period 5, significant differences were found in the temperature (One-Way ANOVA $F= 15.012$; d.f 3; $p<0.001$), light intensity ($F= 9.033$; $p<0.001$), wind speed ($F= 11.203$; $p<0.001$), and relative humidity ($F= 4.063$; $p=0.008$) data. *Post hoc* tests confirmed that nests in the south were significantly warmer and received higher light levels than nests in all other aspects. Nests in north-west 1 received higher wind speeds and lower relative humidity values than nests in all other aspects. Results are summarised in table 4.7.

Results of data analysis of the microclimate at the nests with aspect – 2001.

In Period 1 there were significant differences in the light intensity (One-Way ANOVA $F= 9.643$; d.f 3; $p<0.001$) and wind speed ($F= 7.430$; $p<0.001$) data. *Post hoc* tests confirmed that the southern nests received significantly higher light levels than nests in all other aspects. Nests in north-west 1 received higher wind speeds than those in the south or north-east, and nests in north-west 2 received higher wind speeds than nests in the north-east.

During Period 2, significant differences existed in the light intensity (One-Way ANOVA $F= 4.444$; d.f.3; $p=0.004$), wind speed ($F= 18.592$; $p<0.001$) and relative humidity data ($F=$

3.502; $p=0.016$). *Post hoc* tests confirmed that nests in the south received higher light levels than nests in all other aspects. Nests in the north-east received higher light levels than those in north-west 1. Nests in north-west 1 received higher wind speeds than nests in all other aspects, and lower relative humidity values than nests in the south.

In Period 3 significant differences existed in both the light intensity (One-Way ANOVA $F=6.309$; d.f. 3; $p<0.001$) and wind speed data ($F=5.635$; $p=0.001$). *Post hoc* tests confirmed that nests in north-west 1 received higher light levels than nests in the south and north-west 2. Wind speeds were higher at nests in north-west 1 than those at all other aspects.

During Period 4, significant differences existed in the temperature (One-Way ANOVA $F=6.423$; d.f.3; $p<0.001$), light intensity ($F=16.931$; $p<0.001$) and wind speed ($F=9.092$; $p<0.001$) data. *Post hoc* tests confirmed that the southern nests were significantly warmer and received higher light levels than nests in all other aspects. Wind speeds were significantly higher at north-west 1 nests than those within all other aspects.

In Period 5, significant differences existed in the light intensity (One-Way ANOVA $F=9.538$; d.f.3; $p<0.001$) and wind speed ($F=7.004$; $p<0.001$) data. *Post hoc* tests confirmed that the southern nests received significantly higher light levels than nests in all other aspects. In addition, the nests in north-west 1 received higher wind speeds than nests in all other aspects. Results are summarised in table 4.7.

4.4:4 Analysis of Nest Characteristics.

Differences in Nest Characteristics between the Four Sample Aspects.

Nests in north-west 1 were significantly lower in height than nests within the south (One-Way ANOVA $F=3.178$; d.f.3; $p=0.029$ – Tukey HSD $p=0.016$), but overall nest dimensions did not differ significantly with aspect (Fig 4.9 & Appendices 5).

No significant differences were found between the angle of the shallowest slope between the various aspects. However, nests in the south and north-east were orientated significantly closer to the south than nests within the two north-western facing sample sites (One-Way ANOVA $F=12.942$; d.f. 3; $p<0.001$) (Fig 4.10).

Table 4.7: Summary of Nest Analysis of Microclimate by Aspect (> statistically significant).

Variable	Period 1	Period 2	Period 3	Period 4	Period 5
2000					
Temperature	N/S	N/S	N/S	N/S	South > All Aspects
Light	South > All Aspects North East > North West 2	South > North West 2 North East > North West 2 North West 1 > North West 2	North East > All Aspects	South > All Aspects	South All Aspects
Wind Speed	N/S	North West 1 > All Aspects	North West 1 > South North West 1 > North East	North West 1 > All Aspects	North West 1 > All Aspects
Relative Humidity	South > North West 1	South > North West 1 North East > North West 1 North West 2 > North West 1	South > North West 1	N/S	South > North West 1 North East > North West 1 North West 2 > North West 1
2001					
Temperature	N/S	N/S	N/S	South > All Aspects	South > All Aspects
Light	South > All Aspects	South > All Aspects North East > North West 1	North West 1 > South North West 1 > North West 2	South > All Aspects	South > All Aspects
Wind Speed	North West 1 > South North West 1 > North East North West 2 > North East	North West 1 > All Aspects	North West 1 > All Aspects	North West 1 > All Aspects	North West 1 > All Aspects
Relative Humidity	N/S	South > North West 1	N/S	N/S	N/S

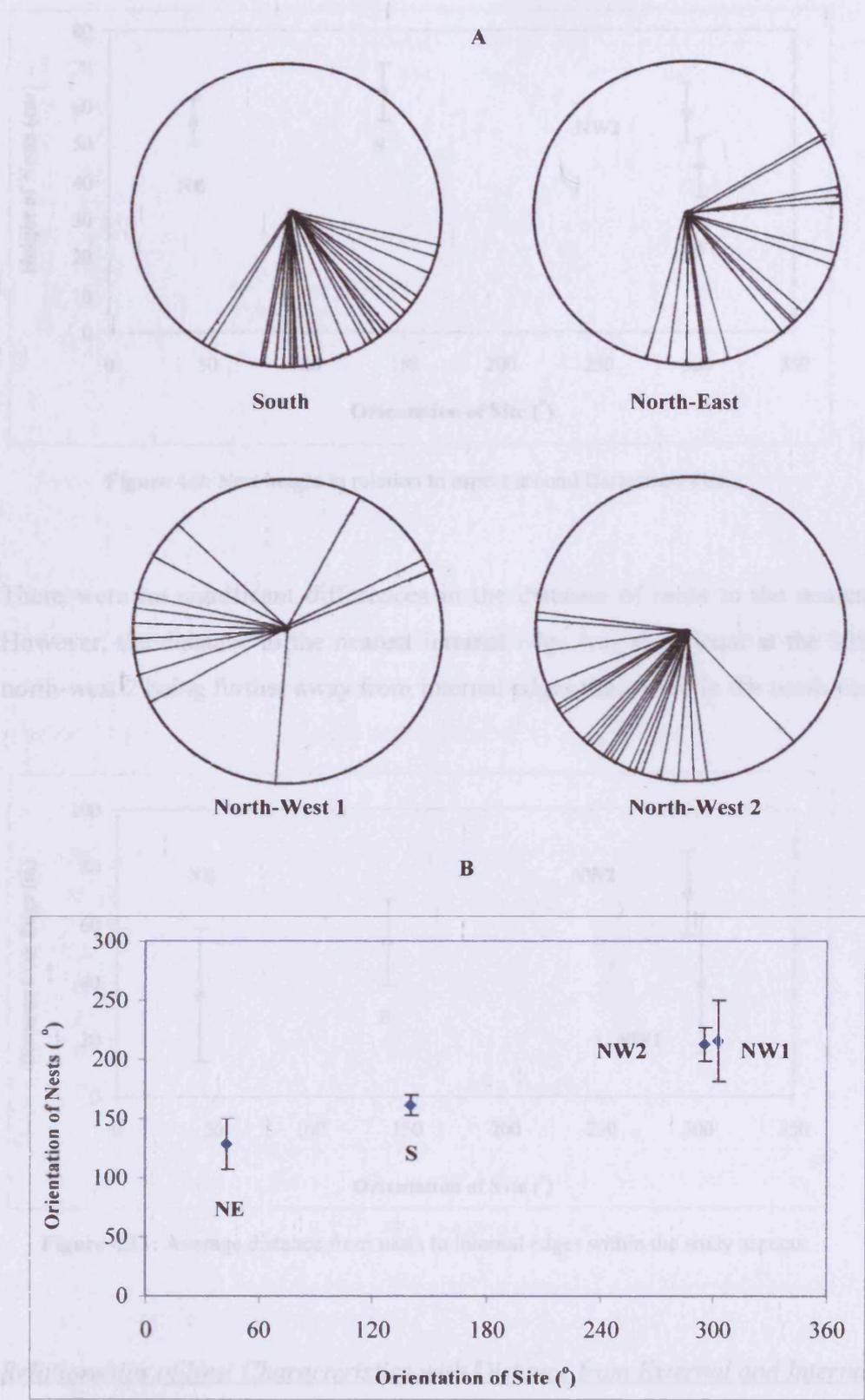


Figure 4.10: Nest orientation in relation to aspect around Harlestone Firs.
 A- Orientation by sample aspect in relation to the cardinal compass points.
 B- Diagrammatic representation showing mean orientation and 95% confidence levels.

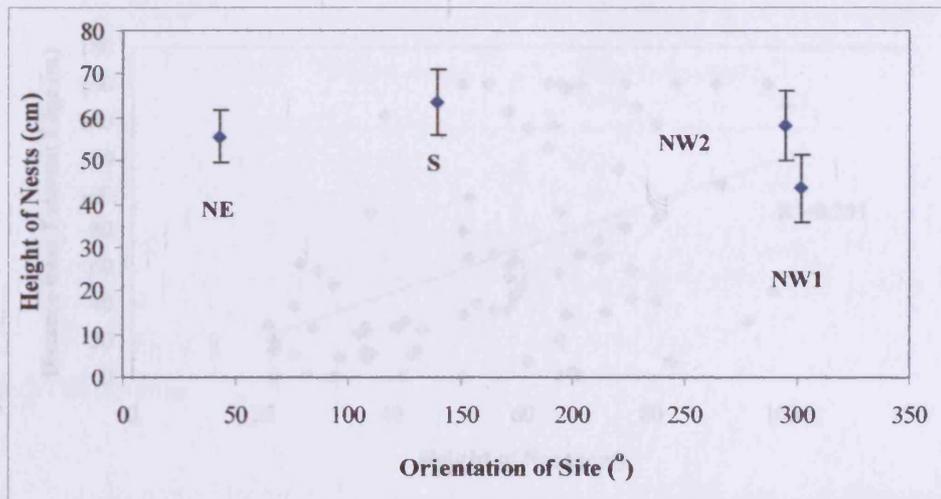


Figure 4.9: Nest height in relation to aspect around Harlestone Firs.

There were no significant differences in the distance of nests to the nearest external edge. However, the distance to the nearest internal edge was significant at the 93% level, nests in north-west 2 being further away from internal edges than those in the north-east (Fig 4.11).

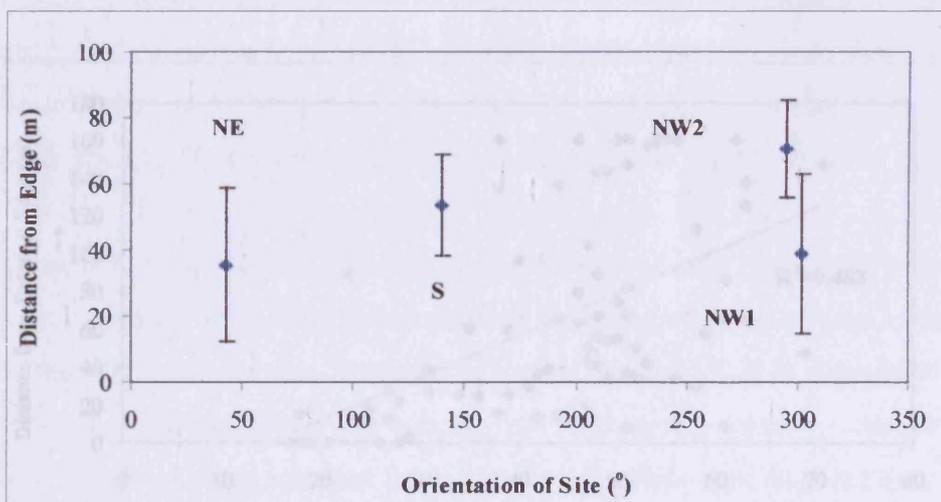


Figure 4.11: Average distance from nests to internal edges within the study aspects.

Relationships of Nest Characteristics with Distance from External and Internal Edges.

There was a significant relationship between nest height and distance to the nearest external edge (ANOVA $F= 10.790$; $d.f.2$; $p<0.001$), but no similar relationship existed within nest height and nest dimension data and distance to the nearest internal edge (Fig 4.12).

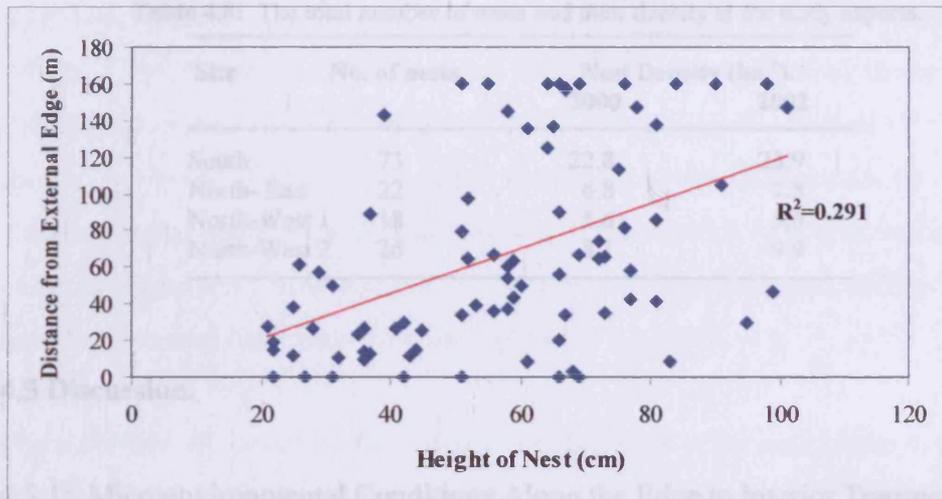


Figure 4.12: Regression analysis of the relationship between nest height and distance from the nearest external edge.

A significant relationship also existed between the angle of the shallowest slope and the distance to the nearest external edge (ANOVA $F= 36.828$; $d.f.2;p<0.001$), but no similar relationship existed in the internal edge data (Fig 4.13). There was also no significant relationship with nest orientation and distance to the nearest edge.

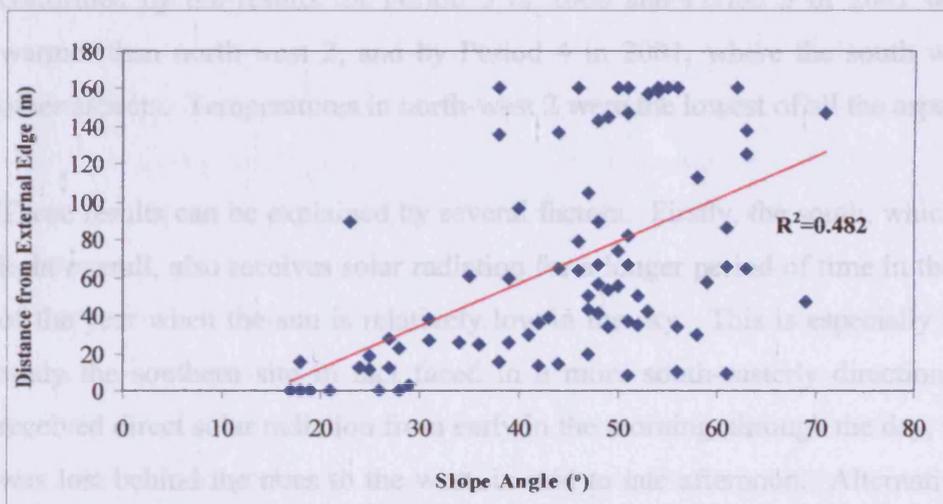


Figure 4.13: Regression analysis of the relationship between nest slope angle and distance from the nearest external edge.

Nest Density.

The total number of nests within the four study aspects showed great differences, the southern site supporting more nests than the other sites combined. This was thus reflected in the nest densities (Table 4.8).

Table 4.8: The total number of nests and their density at the study aspects.

Site	No. of nests	Nest Density (ha ⁻¹).	
		2000	2002
South	73	22.8	23.9
North- East	22	6.8	7.8
North-West 1	18	5.6	5.6
North-West 2	26	8.1	9.9

4.5 Discussion.

4.5:1: Microenvironmental Conditions Along the Edge to Interior Transects of the Four Study Sites.

The southern site was the warmest of the four, although only statistically significantly warmer in three biologically significant periods. This general trend is consistent with other northern hemisphere studies (Matlack 1993; Fraver 1994), which have found that southern and eastern facing edges, referred to by Murcia (1995) as ‘warmer’ edges, receive more solar radiation than their north and west facing (cooler) counterparts. This significant thermal relationship is confirmed by the results for Period 5 of 2000 and Period 3 of 2001 where the south was warmer than north-west 2, and by Period 4 in 2001, where the south was warmer than all other aspects. Temperatures in north-west 2 were the lowest of all the aspects in both years.

These results can be explained by several factors. Firstly, the south, which received the most light overall, also receives solar radiation for a longer period of time in the early and late part of the year when the sun is relatively low in the sky. This is especially true here, as in this study the southern site in fact faced in a more south-easterly direction. Thus the south received direct solar radiation from early in the morning, through the day, until the setting sun was lost behind the trees to the west, in mid to late afternoon. Alternatively, north-west 2, because it is situated at the bottom of a slope, tended not to receive direct sunlight at the extreme edge for much of the day. North-west 2 thus received much more diffuse and diagonal beam radiation at these times of the year (Malcolm 1998; Moorecroft *et al.* 1998). Alternatively, the north-eastern aspect received the early morning sun, and north-west 1, being more open in nature, received direct sunshine in the early and late parts of the year during the period surrounding solar noon, hence temperatures remained higher.

The conclusion that the thermal conditions within the sites were related to solar radiation in relation to aspect is entirely consistent with established theory (Barry & Chorley 1992; Ahrens 1994; Murcia 1995), and was identified as the principal factor in determining the forest microenvironment by Matlack (1993) and Young & Mitchell (1994). Nevertheless it should be noted that these results may have been influenced by the timing of the measurements, many of which on the sampling rotation would have been taken before or close to solar noon, before direct sunlight had reached this part of the woodland, and thus lower values may have been inevitable (Chen *et al.* 1995).

The influence of aspect on the modification of edge microenvironments is confirmed by the analysis of the light intensity data. These showed that the south received significantly more light than all aspects in Periods 1, 4 and 5, and than either/or north-west 1 and 2 in Periods 2 (2000) and 4 and 5 in 2001, thus confirming the explanation for the temperature results. However, in Period 2 of 2001, and Period 3 of 2001, other aspects received more light or the relationship became non-significant. This is simply linked to the closure of the crown and/or side canopy, which caused observed light intensity values to fall and variation between the study aspects to be diminished (Appendix 1). Matlack (1993), after finding similar results commented that after crown and side canopy closure, light, temperature and air moisture gradients could become non-significant around a woodland.

During all periods north-west 1 received significantly higher wind speeds than the other sites. This is a direct result of aspect and the characteristics of the four sample aspect edges (Sigmon *et al.* 1984; Young & Mitchell 1994; Murcia 1995)

The north-west 1 aspect, is bordered by a very large open field system which is exposed from the north west to north north east. This allows winds driven by weather systems approaching from these quadrants, to move across the immediate landscape without impediment and to strike the abrupt open north-west 1 edge (Barry & Chorley 1992; Sigmon *et al.* 1984). Wind speeds therefore tended to be higher further inside the edge in north-west 1 than at the other aspects, where during the summer, the development of side canopies provided varying degrees of shelter (Gysell 1951; Wales 1967; Matlack 1993; Murcia 1995; Didham & Lawton 1999).

The north-west 2 edge, situated at the bottom of a slope, tended to escape the impact of the most severe winds due to two main factors. Firstly, the edge itself was 'closed' hence winds could not easily penetrate far into the sample site during the summer months. Secondly, the

main thrust of the wind tended not to reach the lower portions of the edge, being pushed into and over the canopy because of the slope (Fritschen *et al.* 1971; Sigmon *et al.* 1984; Oke 1987; McNaughton 1989; Quine *et al.* 1995; Gardiner & Stacey 1996; Moorecroft *et al.* 1998; Quine *et al.* 1999).

The north-eastern edge faces the embankment of the Northampton-Birmingham railway line, which itself borders another forest compartment. This tends to hinder the passage of easterly winds, which again tend to strike the top of the canopy only. Some of that wind is pushed down inside the edge, but most continues its journey across the landscape, passing over the canopy to fall into the open area at the centre of Harlestone Firs (Fritschen *et al.* 1971; Sigmon *et al.* 1984; Oke 1987; McNaughton 1989; Chen *et al.* 1992; Quine *et al.* 1995; Gardiner & Stacey 1996; Veen *et al.* 1996; Moorecroft *et al.* 1998). However, the forest management operations in early 2001 did expose this site to winds from the northern edge some three hundred metres away. The lack of a developed understorey in this area allowed northern winds to push deep into the forest, elevating wind speeds which were reflected in the results.

Comparatively, the southern edge is sheltered from the west by a shelterbelt which extends for several hundred metres along the edge of the nearby industrial estate. This, combined with the 'closed' edge, meant that wind speed remained low, and consequently had little effect on this aspect. This was especially clear as soon as the crown and side canopies were fully developed (Wales 1967).

Relative humidity was consistently higher in the south than in the north-western aspects, north-west 1 having the lowest values of the four (Appendices 1). This in itself is entirely consistent with the findings of previous research (Geiger 1965; Oke 1987; Kapos 1987; Barry & Chorley 1992; Matlack 1993; Fraver 1994; Camargo & Kapos 1995; Murcia 1995). However, although these relationships were statistically significant during most of 2000, they were significant on only a single occasion in 2001. These results confirm previous research, that relative humidity is more complex than simply a relationship between the temperature/light and wind speed, and that rates of evapotranspiration of the extant vegetation are also likely to have an influence (Oke 1987; Chen *et al.* 1992, 1993, 1995; Murcia 1995; Gehlhausen *et al.* 2000). The lack of statistical relationships in 2001, may be due to the effects of forest management activities, the removal of individual trees in certain areas of each site allowing greater mixing in the air column immediately above the ground, which would explain the lower values.

Of the study aspects, the south received the most light, experienced the lowest wind speeds and the highest relative humidity. Although, not statistically so, the south was also the warmest. The south therefore may represent a very stable and equitable microclimate.

4.5:2 Analysis of Edge Width along the Study Aspect Transects.

The only variables which were significantly different from edge to interior in all Periods were light intensity and wind speed. The temperature gradient however was significant in Period 4 of 2001.

These results confirm that the light intensity and wind speed followed the expected trend. Period 1 and the first month of Period 2 covered the period where the crown and side canopy were not fully developed. Thus at these times, light intensity and wind speeds were much higher, as there was little shelter within the sites to mitigate their impacts (Young & Mitchell 1994; Murcia 1995; McCollin 1998). Further, any periods of higher winds during this period would ensure that the air column close to the ground along the transects was 'mixed', depressing both temperature and relative humidity values (Oke 1987; Barry & Chorley 1992). Therefore, light intensity and wind speed values would be at their most extreme, but the differences between the temperature and relative humidity values along the transects would be reduced, explaining the statistical significance of only light intensity and wind speed (Sigmon *et al.* 1984; Matlack 1993; Moorecroft *et al.* 1998).

In Periods 4 and 5 (covering October, November and December), the study sites were once again exposed to the full force of unimpeded wind speeds, able to penetrate into the sites and again, ensuring that the distance relationship was statistically significant. Light intensity values increased with the onset of leaf fall in deciduous species allowing light to pass through the now more open canopy. It should be noted that the onset of more overcast weather conditions during the autumn and winter period would have acted to lower light intensity values, which although remaining significant with distance, would not have been expected to reach Period 1 values (Marquis 1965; Barry & Chorley 1992; Murcia 1995; McCollin 1998; Moorecroft *et al.* 1998).

The actual width of the edge influenced habitat showed some variation between the years. The light intensity gradients extended only to 10-20m in the south during both years. However, noticeable 'spikes' appeared in the trend lines during Periods 2 to 5 of 2001. Here values fluctuated, falling to 20m, before rising at 40m and 80m. This is simply a response to

forest management activity. Early in the year the removal of some plantation trees ‘opened’ the canopy in the central part of the site.

The north-east and north-west 1 gradients remained stable over the two years with edge width extending to around 10m to 20m in all Periods of 2000 and Period 1 of 2001. The gradient did not show well defined edge effects during the remainder of 2001, with values falling steadily from edge to interior. This pattern is difficult to explain, although it should be noted that no forest management activity directly influenced either aspect.

The north-west 2 gradient showed the greatest variation through the year, edge width moving between 10m and 80m in both years. The ‘spike’ at 40m in Period 4 of 2001 was again due to the influence of forest management activities, which thinned some plantation trees between 35m and 70m behind the edge. The remainder of the variation is probably best explained by the wax and wane of the crown and side canopies through the year and its influence on the light environment beneath the canopy.

Edge width in relation to wind speed data again showed variation. In the south during both years the maximum extent of the wind driven edge effects was 20m. This is due to the development of the side canopy and the fact that this aspect is sheltered from the prevailing winds. In the north-east, for the most part, edge width was no more than 10m. However, during Period 3 of 2000 and Period 2 of 2001, edge width was extended to 40m. This may simply have been due to the prevalent weather systems during the two sampling periods as no other phenomenon was likely to have affected the results. North-west 2 gradients showed the least variation with edge width extending to 10m in all Periods of both years. These results are likely to have been linked to the closed nature of the edge and the shelter offered by the topography of the sample aspect. North-west 1 experienced the largest area of wind derived edge effects, extending to 40m. This is a product of the structure of the edge which remains open throughout the year allowing winds to penetrate deep into the edge.

The significant thermal edge effects identified in Period 4 of 2001 are probably a product of the particularly warm run of weather during October 2001 (measured at the University College Northampton weather station). The subsequent movement of warm air inside the edges would explain the significant differences between the edge and interior.

It is thus concluded that these results and their interpretation are very much intuitive given the findings of long term previous research and that edge effects related to distance do influence

the four study aspects (Gysell 1951; Geiger 1965; Wales 1967; Hutchison & Matt 1977; Sigmon *et al.* 1984; Young & Mitchell 1994; Murcia 1995; Malcolm 1998; Moorecroft *et al.* 1998).

4.5:3 Soil Analysis.

Overall during the year, soil moisture values were significantly higher in north-west 2 than either north-west 1 or the south. Due to the characteristics of north-west 2 (section 3.31) and the area of very wet, boggy ground just inside the edge these results are very much as expected. The slope which begins at 30m inside the compartment allows moisture from the higher ground to move 'down slope' into the edge region, where it collects during the wetter periods of the year.

The edge to interior gradient profiles were therefore consistent with expected results. Moisture levels in the south and north-west 1 increased with distance into the wood (Kapos 1989; Camargo & Kapos 1995). The north-east followed a roughly similar profile, but remained more stable. However, in north-west 2, values started very high, falling from 20m into the wood to produce the reverse trend, confirming the influence of the topography of this study site as the cause of the results (Fig 4.5).

In March 2000, north-west 2 once again recorded significantly higher soil moisture values than the other aspects; the edge width profiles remaining similar to the annual pattern. This is entirely as expected, the initial part of north-west 2 remaining 'boggy' after the winter period (Fig 4.6).

However, there were no significant differences between the aspects in either August or October. In both months, edge width profiles also showed much greater fluctuation in the south, north-east and north-west 1 (Fig 4.6). This follows the findings of Kapos (1989), who reported that observed soil moisture changes within a woodland were more complex than a simple linear relationship between distance into the wood and increasing values. A number of factors may influence soil moisture, from gaps in the canopy to species composition and density (Matlack 1993; Camargo & Kapos 1995).

The reduction in water in north-west 2 could be explained by the usual reduction in precipitation during the summer / early autumn, the impact of evaporation due to the warmer air temperatures and most importantly, by the work of the dense vegetation removing vast

amounts of water from the soil via the process of photosynthesis via the transpiration pump. Higher moisture levels in the south and north-west 2 are probably due to the overall higher humidity values, moisture levels being maintained inside the edge by the calmer conditions. In all sites, elevated soil moisture values could also have been due to the insulating effect of surface leaf litter. In all cases, this litter was removed immediately prior to taking the samples, which were themselves taken from the immediate surface. Perhaps, different results would have been found if soil had been taken from greater depths.

Soil pH did not provide significant results and the edge to interior profiles did not provide clear trends. However, north-west 2 did have the highest pH values in the initial part of the site. This may be due to the area of boggy ground just inside the edge which allows deciduous leaf litter to remain in this zone and to be broken down more readily by decomposer organisms. This increase in organic matter may therefore give rise to a slightly different soil composition (Chapman & Reiss 1992). Alternatively, it could simply be due to the age of this area of the wood. However, it can be concluded that in general, soil type and composition for the most part remains consistent around Harlestone Firs.

4.5:4. The Comparison of Nest and Control Points Microclimate.

Analysis of nest and control microclimates showed that nests received significantly more light and lower wind speeds than the controls during 2000 and 2001. These results confirmed that nest location was strongly influenced by available light, *F. rufa* selecting nest sites which receive more light than the normal background woodland environment. These results are thus consistent with the findings of previous research (Forel 1874, 1920; McCook 1877; Andrews 1926, 1927; Elton 1932b; Scherba 1958, 1959, 1962; Kneitz 1964; Finnegan 1975; Breen 1979a; Sudd *et al.* 1977; Douglas & Sudd 1978; Rosengren & Pamilo 1986; Adams 1991; Klimetzek & Fass 1994; North 1996; Pontin 1996; Cook 1998; Skinner 1998).

Higher light levels certainly do facilitate the commencement of colony activity thus confirming the overall ecological strategy of the *F. rufa* group species, the emphasis on elevating nest mound temperatures beyond ambient to facilitate the rapid development of the reproductive brood early in the active season being vital for colony success (Hölldobler & Wilson 1990; Heinze & Hölldobler 1994).

The link with temperature and light intensity has not been established statistically during this study. This may be due to two factors. Certainly, *F. rufa* is selecting nest sites which, by

receiving higher light intensities, should be generally warmer. However, this relationship may not have been identified statistically due to the sampling height chosen. Surface temperatures would be much higher than those within the air column above, which is mixed by the movement of air (Oke 1987; Barry & Chorley 1992; Ahrens 1994). Therefore, it is likely that although 0.6m is a suitable height to measure variables for the purpose of edge effects, for the ants the measurement of surface conditions would have been better (Bernstein 1979). However, the more stringent conditions imposed by the measurement of air column climate does at least alleviate the chances of making a false association between ant activity and the observed microclimatic conditions.

That high wind speeds hinder foraging activity has been confirmed by Holt (1955) and Adlung (1966). It would appear that the temperature threshold at which wood ants are active is severely reduced by exposure to high winds. Hence, many studies have suggested that *F. rufa* group species locate nests so as to obtain shelter from the north (Adlung 1966; Sudd *et al.* 1977; Skinner 1998; Robinson 2001). The selection of nest sites which are less exposed would be a mechanism to ensure that surface temperature remains high early in the year, nest zones tending to act as sun traps (Pontin 1996). However, with the development of the surrounding vegetation

colonies do become sheltered from the extreme temperatures which have been shown to endanger colonies, whilst ensuring that relative humidity increases due to evapotranspiration, again, important for colony survival (Adlung 1966; North 1991, 1993; Skinner & Allen 1996; Skinner 1998).

Thus it is concluded that colonies living within the four aspects at Harlestone Firs are selecting nest locations in response to the microclimatic conditions as a result of edge effects. Nest sites are selected on the basis of the light regime and are situated in areas which offer shelter from high winds.

4.5:5 Microclimate Variation at the Nests within the Four Study Sites.

Nest microclimate during the biologically significant 'periods' showed important differences between the study sites. In Period 1, nests in the south received significantly more light than those at all the other aspects and nests in the north-east had higher light levels than nests in north-west 2. These results suggest that southern nests have a distinct advantage over nests in the other sites, receiving more light and shelter, and thus probably higher nest surface temperatures to enhance a colony's ability to make an early start to the active season.

Although nests in other aspects received more light than the control points, they still clearly lagged well behind the southern nests (Table 4.6). North-west 1 received the highest wind speeds in all but Period 1 of 2000 and thus consequently, where relative humidity was significant, values here were also the lowest.

In Period 2, covering the period after hibernation and the lead up to reproduction, the results showed slight differences. Although in 2001, the Period 1 trends were maintained, in 2000, the north-west 2 nests received significantly less light than nests in all other aspects. Again, the southern nests appear to have had the most equitable microclimate, maintaining their advantage over nests in the other sites. The light intensity values in north-west 2 during 2000, were probably due to the developing crown and side canopies and to the topography of the site (Table 4.6).

During Period 3, light intensity patterns changed. At this time, ambient temperature is sufficient to support colony activity throughout the wood, and therefore the light resource is less important. However, in Period 4, with the breakdown of the crown and side canopies, aspect once again conferred an advantage to southern colonies. The southern nests received significantly more light than the nests in the other aspects in Period 4 and 5 of both years and higher temperatures than in Period 4 of 2001. These results reinforce the findings that southern nests have an aspect-related advantage at the end of the active season, conditions remaining more favourable than those nests within the north-western aspects.

4.5:6 Nest Characteristics.

Differences in Nest Characteristics between the Four Sample Aspects.

The height of the north-west 1 nests was significantly lower than nests in the south. This is probably a response to a number of factors. Firstly, most nests in this aspect are located in rather open areas, or close to internal edges, where direct sunlight strikes the nest at some point during the day. Many previous researchers have found that nests in open areas tend to be flatter and lack the characteristic dome (Brian 1977; Skinner & Allen 1996). A further cause may be the link with the higher average wind speeds within north-west 1. The fact that nests tend to remain lower to the ground in these more open areas may be a response to disturbance as high winds move over the surface. It is likely that higher wind speeds would lead to lower temperatures, and most importantly, lower humidity values which can be very dangerous to ant colonies. It should be noted that the tallest nests within north-west 1 were

all situated towards the interior of the site in shaded areas away from the influence of high winds. These results certainly suggested that both aspect and distance edge effects are influencing wood ant behaviour.

There was no evidence that the size of nests or the angle of the shallowest slope was influenced by aspect. It is likely that nest basal dimensions are not reacting to microclimate but rather to the age and size of the colony as suggested by Adlung (1966) and Breen (1977a). Slope angle is generally influenced by the amount of sunlight which strikes the nest (Forel 1874). It is thus not surprising that no significant differences were found around the four aspects because the same processes would be at work in all.

However, the orientation of the nests was significantly different with aspect; the southern and north-eastern nests tending to face more towards the south than the north-western nests (Fig 4.10). That southern nests faced more noticeably towards due south than nests in all other aspects highlights that the southern aspect is providing optimal microclimatic conditions for the ant colonies, the number of nests is a response to the large number of suitable nest sites. Within the other aspects colonies are having to select nest sites on the basis of available sunlight, and tend to locate nests only where direct sunlight will be received for at least some part of the day.

This is perhaps confirmed by the analysis of distance to the nearest edge. Although no significant differences existed in the distance of nests to the nearest external edge with aspect, a relationship did exist with internal edges. Nests in north-west 2 tended to be further away from internal edges than those in the north-east. This is a product of the characteristics of the two different sites. The north-east aspect had two internal edges available to the colonies whereas the north-west 2 study site had only one. Colonies here have to rely instead on locating nests in any available open area rather than placing them close to internal edge as they do in the north-east.

Relationships of Nest Characteristics with Distance from External and Internal Edges.

The relationship between nest height and distance to the nearest edge could be somewhat misleading if treated as 'fact'. Nest height is believed to reflect the amount of solar insulation which a nest receives, and thus nests in shade are taller than those exposed to direct sunlight (Brian 1977; Skinner & Allen 1987). It is generally true in this study that the further away from an edge a nest is located the less light it is likely to receive. This would then lead to the

pattern which is found here, where nest height increases with distance from the edge as the level of available sunlight falls. However, several anomalies exist around the four aspects. Clearly, nests in north-west 1 do not entirely follow this relationship, nests located in the open some distance from the edge being amongst the smallest nests. Alternatively, Nest 2 in the south, although only 8m from the nearest external edge was in deep shade and was thus one of the tallest of the sample nests at 85cm. Therefore, the general 'rule of thumb' of nest height being linked to available light proposed by several researchers appears to hold true while the distance relationship could give spurious results (Andrews 1927; Elton 1932b; Adlung 1966; Skinner 1998).

The relationship between the angle of the shallowest slope and distance from the nearest external edge was also significant. Again, it has long been proposed that the angle of the shallowest slope will increase as the amount of available sunlight decreases (Forel 1874). This relationship was confirmed here, where in general, slope angles increased with distance into the wood. Although, several exceptions were found in all study aspects, this significant relationship does confirm that *F. rufa* nests are influenced by distance and aspect related edge effects and that colonies react differently in the different parts of the wood.

Nest Density.

Nest density within the four study sites showed wide variation (Table 4.8). In the south nest densities equalled those reported by Cook (1998) in Essex, which themselves were very high compared to the estimates proposed by Welch (1978) (see below). This highlights that conditions in the south are close to the optimum for the ants, with colonies responding to the more favourable microclimate which is available. These results also appear to show that in the absence of interspecific competition from other members of the group, *F. rufa* colonies may produce strikingly dense aggregations of nests (Adlung 1966), and at these densities, may have some use in pest management within forest plantations.

The density of nests in the other aspects are themselves slightly higher than those reported in mainland Europe (Adlung 1966; Buttner 1971; Klimetzek 1972), and are probably once again a product of reduced interspecific competition (Table 4.8). In terms of nest densities in England, they fall within the range described by Welch (1978), being higher than those in the New Forest (Elton 1932) and at Bedford Purlieus (Peterken & Welch 1975), but lower than the maximum of 18 ha⁻¹, found at Blean Woods NNR in Kent (Welch 1978). These data indicate that conditions throughout Harlestone Firs are favourable for wood ant populations.

4.6 Conclusion.

The four study aspects of Harlestone Firs are clearly influenced by abiotic edge effects. The edge to interior transects showed such effects with respect to light intensity and wind speed throughout the two years. The aspect of each site was very important in determining the magnitude of the edge effects and their impact on wood ant ecology. In relation to this, the southern edge had the most favourable microclimate of the four aspects.

F. rufa colonies are selecting nest locations which receive more solar input and are therefore warmer than the normal background woodland microclimate. Nest sites sheltered from high winds also appear to be favoured. Again, the southern site is providing the most advantageous conditions for wood ant colonies. In addition, the height and orientation of nests showed significant differences with aspect. Nests in north-west 1 were smaller than nests in the south and both the southern nests and north-eastern nests were more likely to be orientated towards the south. A relationship was also found between nest height and the angle of the shallowest slope with distance into the wood; nests became generally taller and the slope angle increased with distance into the wood.

Chapter 5

The Phenology of *Acer pseudoplatanus* and *Formica rufa* with Respect to Edge Effects.

5.1 Introduction

In the last chapter it was established that physical edge effects related to both aspect and distance were in operation within the four study aspects at Harlestone Firs. This chapter sets out to determine how ant phenology and also bud-burst in a common tree, the sycamore (*Acer pseudoplatanus*) are influenced by edge effects.

There is great variation in the timing of *F. rufa* activity across Europe. Species of the *F. rufa* group may leave hibernation as late as April in many northern parts of Fennoscandia, typically during March in central Europe, and as early as February in parts of southern England (Adlung 1966; Rosengren 1970; North 1993; Clarkson unpublished data). These differences lead to the active season being shorter in some areas than others. For example, Adlung (1966) reports that in Germany, *F. rufa* group species are active for no more than 180 days per year, which in contrast to UK observations of around 250 days, appears to be rather short (North 1996; Cook 1998; Skinner 1998). However, apart from Scherba's (1958) observation (re-iterated by Breen in 1979a), that colonies inhabiting nests which were in heavy shade lagged behind in terms of activity, no actual data appears to exist on the timing of events over small spatial scales. This is important, because according to Kaspari *et al.* (2001), the timing of activity phases in ants is determined by abiotic, biotic and historical factors. Therefore, understanding how the populations within the four study sites are affected by edge effects here, may contribute to the formulation of coherent conservation strategies for the future.

It has been experimentally determined that physical edge effects may influence the timing of various activity phases in edge vegetation, such as leafing, flowering and fruiting on different sides of a fragmented wood. According to Hunter & Lechowicz (1992) three key factors influence bud burst; spring warming, winter chilling and photoperiod (length of day).

Spring warming has received the most attention of the three factors and was originally singled out as the major determinant for the timing of bud burst (Wang 1960). Subsequent studies, especially those concerned with fruit trees, concluded that in many species spring warming works in association with winter chilling (Hickin & Vittum 1976; Thompson & Moncrief

1982; Couvillon & Erez 1985). Most dormant trees will not respond to warm temperatures and break bud unless they have been exposed to temperatures of below 10°C for varying periods of time (Perry 1971; Cannell & Smith 1983). Therefore, those individuals exposed to extremes of temperature during the year will react differently than those in sheltered areas, at least with respect to bud dormancy (Hickin & Vittum 1976; Lechowicz 1984).

In experimental work, reactions to photoperiod have brought mixed results. Wareing (1953) found that *F. sylvatica* relied solely on photoperiod to trigger bud burst. Research shows that other species rely on both photoperiod and temperature; in most cases the longer the photoperiod the cooler the temperatures that are required to initiate bud burst (Campbell & Sugano 1975; Nizinski & Saugier 1988). However, under natural conditions for most species it seems that photoperiod is unimportant, as increasing temperatures tend to bring about bud burst before the length of day has any effect (Perry 1971; Campbell & Sugano 1975; Hunter & Lechowicz 1992). For that reason, Campbell & Sugano (1975) and Lechowicz (1984) concluded that spring warming is the principal determinant of bud burst, although in reality this situation is far from simplistic. An analysis of the impact on edge effects on the observed timing of bud burst in relation to these factors will prove of great interest.

The questions addressed in this chapter are;

1. Is bud-burst in *A. pseudoplatanus* influenced by edge effects around the wood?
2. How are activity phases in *F. rufa* affected by aspect and edge effects?

5.2 Methods

5.2:1. Bud-burst in *A. pseudoplatanus* in relation to Edge Effects.

To determine the timing of bud burst of a tree species in relation to the impact of edge effects, *A. pseudoplatanus* was selected. This species was selected because it tends to produce leaves very early in the season, and along with *S. nigra*, had been the first deciduous species upon which *F. rufa* had been seen tending aphids for the previous few years.

Ten individual trees were selected within the following bands from each of the four sample aspects;

- 0 to 10m
- 11 to 30m
- 31 to 80m
- 81 to 160m.

Five buds were selected on each tree, marked and their growth development recorded and ranked as;

- <1cm (bud less than 1cm)
- >1cm (bud over 1cm)
- LO (as soon as the bud burst)
- FO (as soon as the leaflets were fully open and thus clearly visible).

5.2:2 Phenology of Key Activity Phases of the Sample *Formica rufa* Colonies.

The key activities chosen for observation and classification of *F. rufa* colonies were as follows;

- The date of first worker activity (>25 workers moving with some purpose on the nest for 5 consecutive days);
- The date of the first 'spring massing' (first mass covering an area of 10cm²);
- Date of the appearance of the first alates (single or multiple);
- The last activity of each colony (date when <25 workers were visible on 5 consecutive days);
- The total length of the activity season.

Observations were made during the normal sampling period around solar noon (see Chapter 4 for details). Although it is acknowledged that activity may have occurred outside of this arbitrary 'window', this approach acted to standardise the analyses. In addition, as the chosen activities are considered to be temperature dependent, it followed that classifying activity during the warmest part of the day was the most appropriate method.

The survey of the season's nuptial flights was based on the findings of research by Breen (1979b), Talbot (1959, 1971, 1972) and from personal observations in 1999. Many of the previous studies have reported that flights of the *F. rufa* group species generally take place during the early morning at air temperatures of over 16°C. However, as Donisthorpe (1927)

reported a late afternoon flight of *F. rufa* group species in Scotland, observations were made on the basis of weather conditions and temperature.

These surveys required at least two observers to ensure that, as far as possible, flights were recorded accurately. However, even with the greatest dedication to the task, it is inevitable that flights were missed, a common problem in previous studies also. As the survey of nuptial flights in wood ants is an 'inexact' art at the best of times, it is considered that the data obtained here represent only a 'fair' indication of flight behaviour. Activity is categorised as 'flights' when workers actively encouraged alates to fly, or 'take-offs' when alates flew away from the nest individually of their own volition, usually being discouraged by the colony's workers.

Nest light intensity and temperature data were then used to determine if physical edge effects related to aspect and distance from the edge were influencing the activity phases within the *F. rufa* colonies around Harlestone Firs. Light intensity data were selected in Periods 1 and 2 due to the positive relationship between light and temperature and the previous assumption that available light triggers wood ant activity phases (Scherba 1958; Breen 1977). The end of season activity was compared using the temperature data which had already shown to be statistically significant during Periods 4 and 5 in the previous chapter. The differences between the two years were linked also to the weather data from the nearby weather station situated at Park Campus, University College Northampton (UCN), approximately two miles away. Although the microclimate probably varies between Harlestone Firs and UCN, both locations are influenced by the same general air masses and thus conditions would be sufficiently similar for reasonable comparisons to be made.

5.2:3. Statistical Analysis.

Colony activity and nest microclimate data were all normally distributed and were compared for differences between the study sites using One-Way ANOVA tests with finer scale *post hoc* analysis using the Tukey HSD test. In 2001, comparisons of the first date of spring massing were excluded, due to incomplete data sets brought about by forest closure. Otherwise, where values were missing, the date of the latest observed activity plus 1 was inserted to balance the data sets for the purposes of ANOVA.

To determine if the *F. rufa* phenological data showed a relationship with the light intensity or temperature data from the sample nests, linear regression analysis with its related ANOVA

tests was used. Light intensity and temperature data from the relevant period leading up to the activity of interest were used in all analyses. In addition, the relationships between nest characteristics and the onset of activity phases were also explored in the same way.

5.3 Results

5.3:1 *A. pseudoplatanus* Bud Development Analysis

Bud development on sample trees around Harlestone Firs showed marked variation. By the 1st March 2000, buds on sample trees in all sites were classified as <1cm. However, early spring conditions brought about rapid development with over 50% of buds in the south and 20% in north-west 1 reaching >1cm by the 7th. The first three buds to fully open did so by the 14th. Two were located in the south, at 18m and 30m and one in north-west 1 at 30m.

On the 19th March a further bud had fully opened in the south, this time at 89m and 80% of buds had begun the transition between >1cm and LO. In the north-east and north-west 2, bud development was split between <1cm and >1cm. The north-west 1 buds had developed well with around 80% reaching >1cm.

Despite a run of colder weather, by the 25th March growth in the south had progressed, 50% of buds being classified as >1cm, 40% in the transition towards LO, and around 10% being fully open. The first bud to be fully open in the north-east was at 160m, the general trend showing a progression towards LO. Development in north-west 1& 2 had been retarded.

The 5th April saw the south continue its rapid development despite continued poor weather. All buds had moved into the transitional phase between >1cm and LO and 20% overall were fully open at this point. In the north-east, three buds could be classified as fully open, the rest developing well towards LO. Buds in north-west 1& 2 still lagged behind the other sites, but those on the edge were further advanced.

On the 18th April, in the south 50% of sample buds were fully open, the rest already classified as LO. In the north-east, 80% of buds could be classified as LO, 15% >1cm and 5% fully open. In north-west 1, although a single bud on a tree at 160m was fully open, development behind the edge was noticeably behind. Buds on edge trees were for the most part progressing from LO to fully open. Buds in north-west 2 followed a similar pattern.

By the 23rd April, all buds in the south and north-east, and those and the edge of north-west 1&2 were fully open (Table 5.1 & Fig 5.1). At 11m to 30m in both north-west sites bud development had progressed to the stage of LO, the majority of buds between 81m and 160m remaining at >1cm. On the 30th April, all buds on sample trees from 11m to 81m had fully opened. In north-west 2 almost 90% of remaining buds between 81m and 160m were fully open, compared to 70% in north-west 1. However, all sample buds were fully open by the 3rd May.

In 2001, the Foot and Mouth outbreak hindered a full investigation of bud development and therefore only the dates when buds were fully open are listed. The overall pattern was remarkably similar, buds being fully open along the edges of the sites only two days later than in 2000. However, bud development did vary with distance into the wood. In the south and north-east, buds on selected trees inside the wood were a day behind those on the edge. Again, in both north-west 1&2 buds on trees selected at 160m inside the wood were fully open eleven and twelve days respectively, behind those on the edge (Table 5.2).

5.3:2 Phenology of Key *F. rufa* Activity Phases.

There was great variation in the dates of the first observed worker activity on sample nests between the four study sites, the southern sample colonies leaving hibernation much earlier than those in the other sites (Fig 5.2 and 5.3; see Appendix 6 for actual dates). These relationships were highly statistically significant in both years (One-Way ANOVA 2000 - $F=26.266$; d.f.3; $p<0.001$; 2001- $F=21.882$; d.f.3; $p<0.001$), *post hoc* tests confirming that the southern colonies commenced activity significantly earlier than colonies in all other sites ($p<0.001$).

Once again, there was variation in the first dates of observed 'massing', the southern colonies massing earlier in 2000 and appearing to follow the same trend before the closure of the wood in 2001 (Fig 5.2 and 5.3). The relationship in 2000 was statistically significant (One-Way ANOVA $F=3.786$; d.f.3; $p=0.32$), *post hoc* tests confirming that southern colonies began their 'massing' before those in north-west 2 ($p=0.031$).

The first alates were observed earlier on southern sample nests in both years (Fig 5.2 and 5.3). This relationship was statistically significant (One-Way ANOVA 2000- $F=18.676$; d.f. 3; $p<0.001$: 2001- $F=8.807$; d.f. 3; $p=0.001$). *Post hoc* analysis showed that alates appeared on southern nests significantly earlier than nests in all other sites (2000 - $p<0.001$: 2001 north-

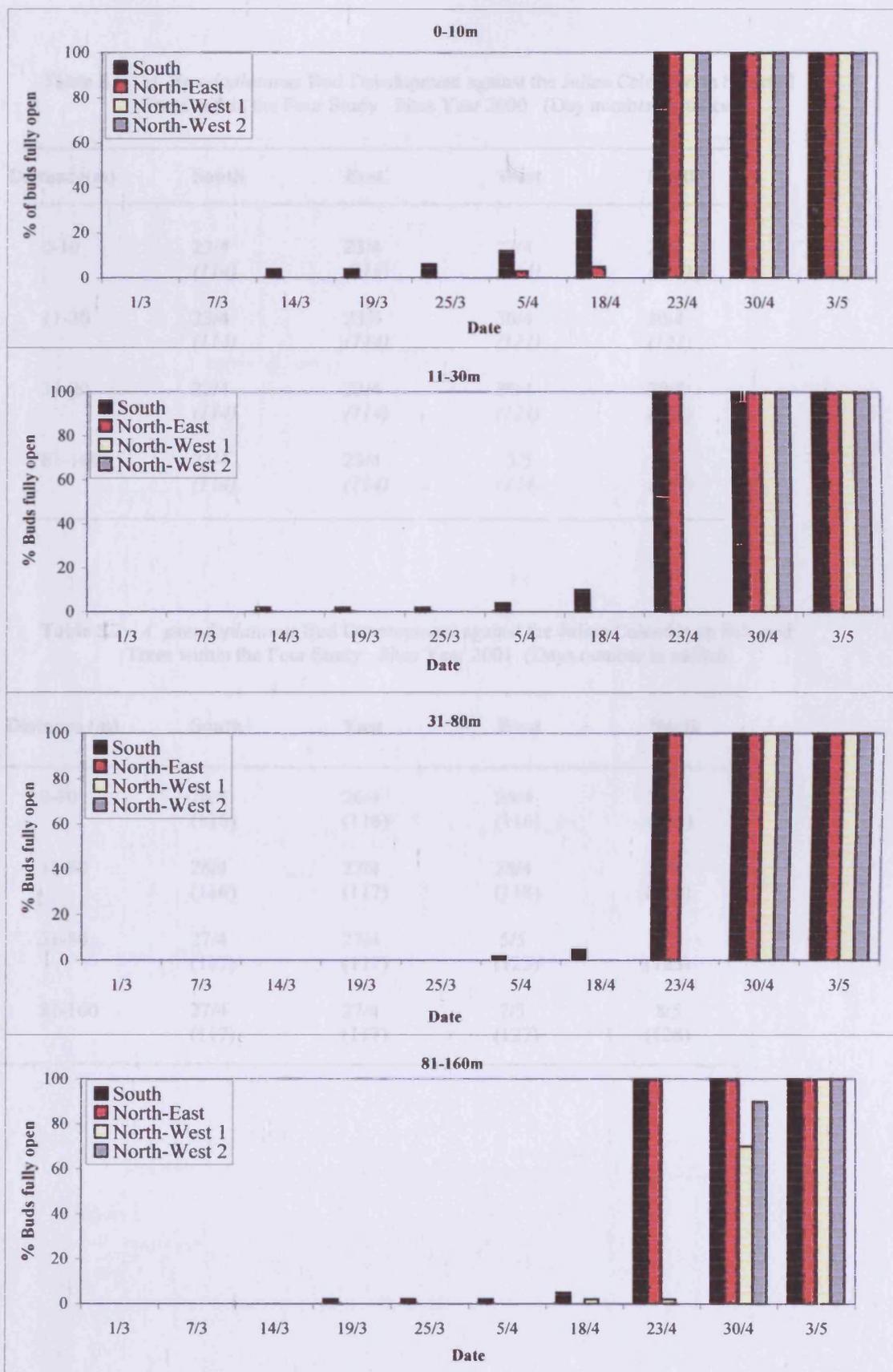


Fig 5.1: Percentage of buds on sample *Acer pseudoplatanus* trees classified as 'fully open' by date within the four study aspects.

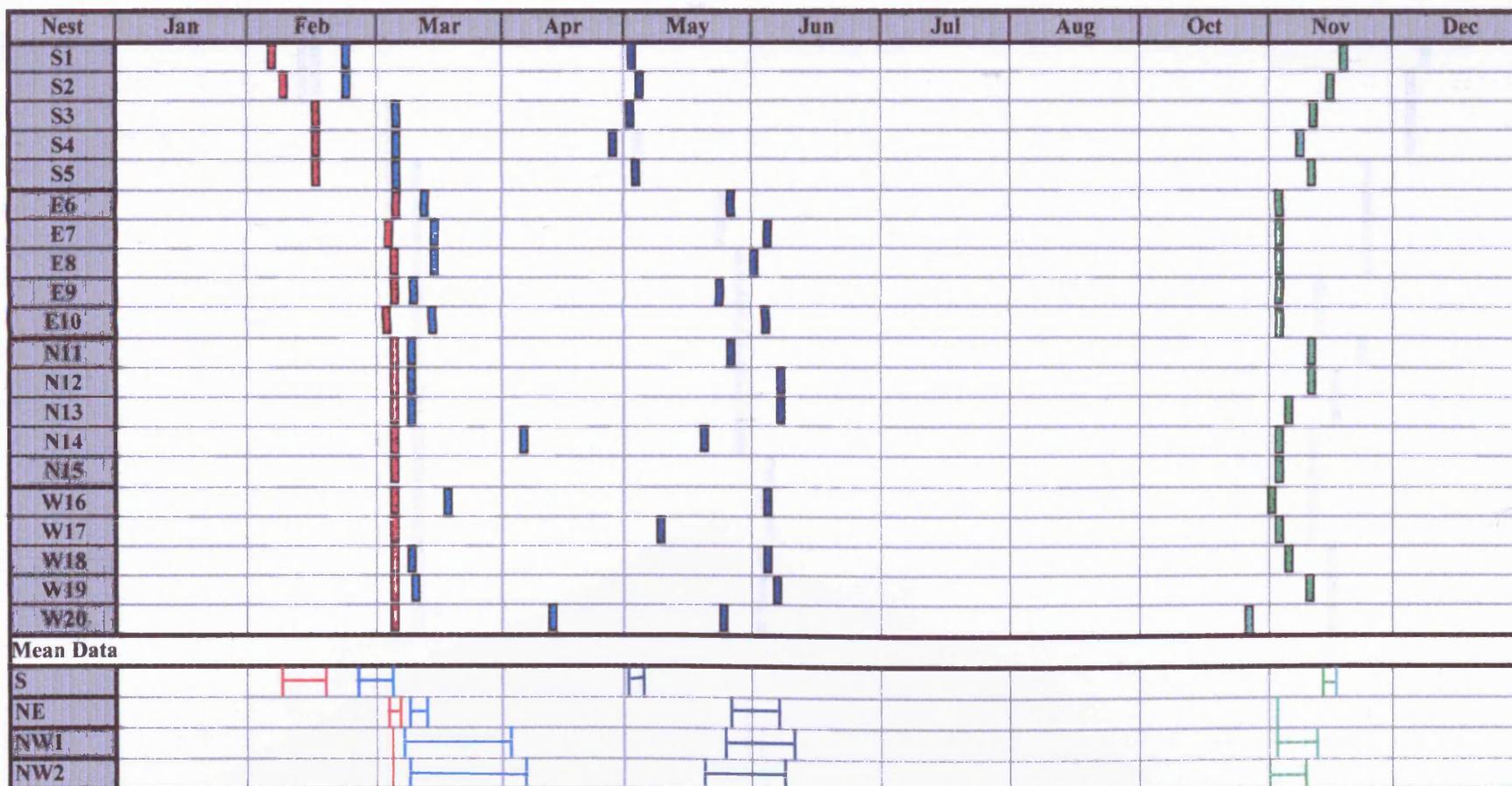
Table 5.1 : *A. pseudoplatanus* Bud Development against the Julian Calendar on Selected Trees within the Four Study Sites Year 2000 (Day number in italics).

Distance(m)	South	East	West	North
0-10	23/4 <i>(114)</i>	23/4 <i>(114)</i>	23/4 <i>(114)</i>	23/4 <i>(114)</i>
11-30	23/4 <i>(114)</i>	23/4 <i>(114)</i>	30/4 <i>(121)</i>	30/4 <i>(121)</i>
31-80	23/4 <i>(114)</i>	23/4 <i>(114)</i>	30/4 <i>(121)</i>	30/4 <i>(121)</i>
81-160	23/4 <i>(114)</i>	23/4 <i>(114)</i>	3/5 <i>(124)</i>	3/5 <i>(124)</i>

Table 5.2: *A. pseudoplatanus* Bud Development against the Julian Calendar on Selected Trees within the Four Study Sites Year 2001 (Days number in italics).

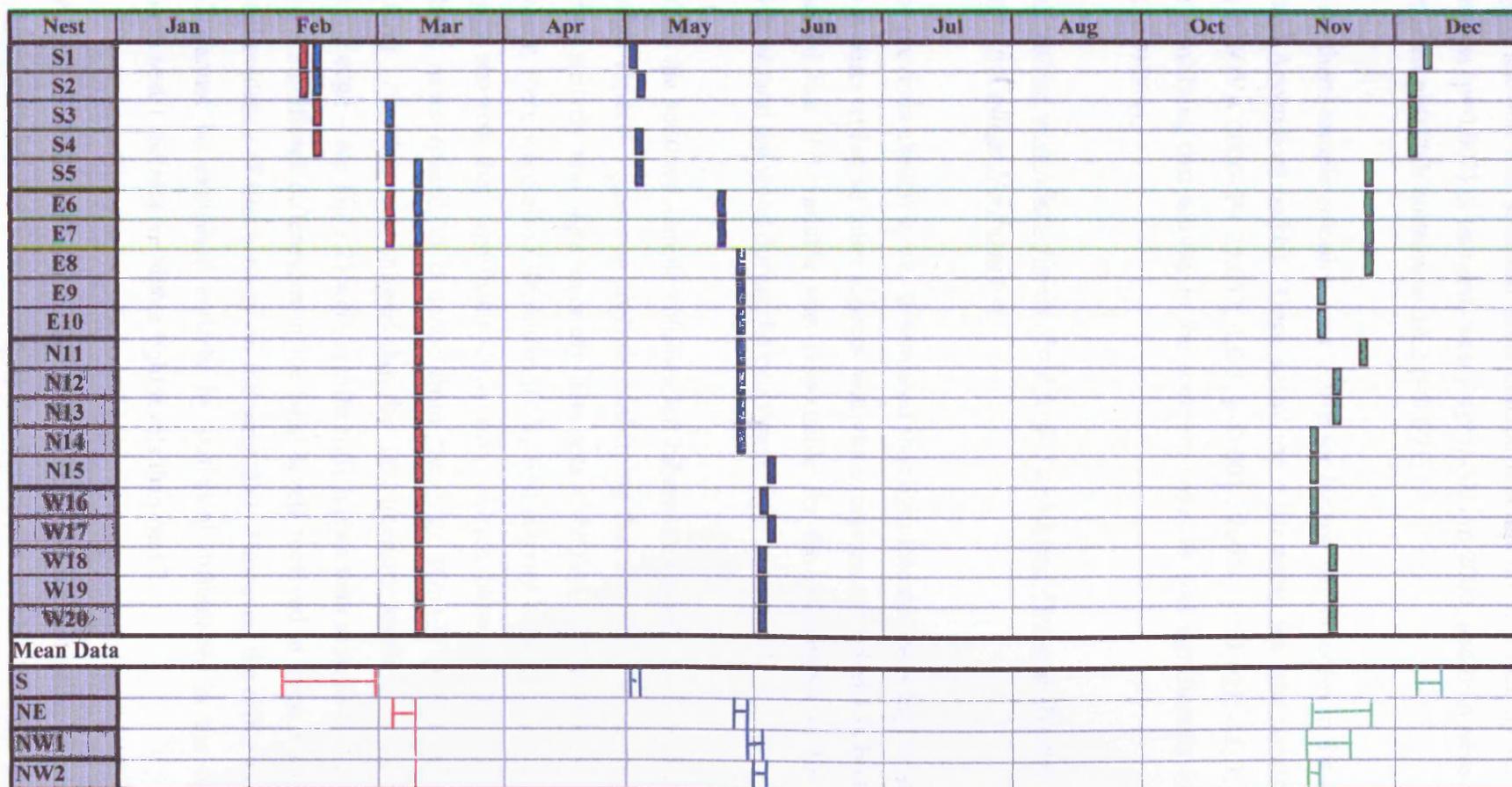
Distance (m)	South	East	West	North
0-10	26/4 <i>(116)</i>	26/4 <i>(116)</i>	26/4 <i>(116)</i>	26/4 <i>(116)</i>
11-30	26/4 <i>(116)</i>	27/4 <i>(117)</i>	28/4 <i>(118)</i>	28/4 <i>(118)</i>
31-80	27/4 <i>(117)</i>	27/4 <i>(117)</i>	5/5 <i>(125)</i>	5/5 <i>(125)</i>
81-160	27/4 <i>(117)</i>	27/4 <i>(117)</i>	7/5 <i>(127)</i>	8/5 <i>(128)</i>

Fig. 5.2 : Phenology of key activity phases in sample *Formica rufa* colonies around Harlestone Firs - 2000



Key: ■ First Worker Activity; ■ First Spring Massing; ■ First Alate Activity; ■ Last Activity; — 95% confidence limits.

Fig. 5.3 : Phenology of key activity phases in sample *Formica rufa* colonies around Harlestone Firs - 2001



Key: ■ First Worker Activity; ■ First Spring Massing*; ■ First Alate Activity; ■ Last Activity; —|— 95% confidence limits.

* Excluded from the mean data section due to the small sample size.

east $p=0.019$, north-west 1 $p=0.004$, north-west 2 $p=0.001$). The southern colonies were the last to become inactive (Fig 5.1 and 5.2), the relationship being statistically significant (One-Way ANOVA 2000- $F= 8.987$; d.f. 3; $p=0.001$; 2001- $F= 14.928$; d.f. 3; $p<0.001$). *Post hoc* analysis showed that southern nests entered hibernation significantly later than those in the north-east ($p=0.002$) or in north-west 2 ($p=0.002$) in 2000, and than nests in all sites in 2001 (north-east $p=0.002$; north-west 1&2 $p<0.001$).

The southern sample colonies were active for longer than colonies in the other sites (Fig 5.2, 5.3 and Appendices 6a&b). Once again, the relationship was statistically significant (One-Way ANOVA 2000- $F= 29.657$; d.f. 3; $p<0.001$; 2001- $F= 21.931$; d.f. 3; $p<0.001$), *post hoc* tests identifying that activity in the southern colonies was significantly longer than all other sites ($p<0.001$).

Relationships with Microclimate Data from Harlestone Firs and Weather Station Data from University College Northampton.

In the previous chapter it was determined that light intensity was higher at the southern nests than at nests within all other aspects, with the exception of Period 3 in both years. It was thus suspected that this variable was responsible for the differences in first observed worker activity around the wood during the two years.

In 2000, the southern sample colonies left hibernation significantly earlier than nests within the other aspects, regression analysis confirming that a positive relationship existed between the first activity and light intensity data sets (ANOVA $F= 8.040$; $p=0.003$; $R^2= 0.486$). However, there were also differences in the first activity between nests in the south. Again, analysis showed that significant differences existed between the light levels within the southern nests related to distance from the edge (One-Way ANOVA $F= 7.119$; d.f.4; $p<0.001$). *Post hoc* tests showed that the light intensity levels at nest 1 and 2 (0m and 8m from the edge – see Fig 3.2) were significantly higher than at nests 3, 4 and 5. Indeed, there were no significant differences in the light levels received at these interior nests which all showed evidence of first activity on the same day. However, the differences between nests 1 and 2 cannot be explained entirely by statistical differences in the light intensity data, although nest 1 did receive higher light levels than nest 2.

Once again in 2001, nests in the southern aspect (with the exception of nest 5, situated 160m into the woodland) left hibernation earlier than nests within the other aspects. Regression

analysis showed that a significant relationship existed between the first worker activity and light intensity data (ANOVA $F= 8.959$; $p=0.008$; $R^2 = 0.332$). Analysis showed that significant differences existed once more between nests in the southern aspect (One-Way ANOVA $F= 6.934$; d.f.4; $p<0.001$). *Post hoc* tests confirmed that nest 1 and 2 received significantly higher light levels than nests 3, 4 or 5. Nest 5 in the south had light intensity levels similar to nests 6, 7 and 8 in the north-east which all recorded first worker activity on the same day.

The differences between the first worker activity between the two years may be a product of the climate during February. Mean temperature was 1.34°C higher in February overall and 1.3°C higher in the seven days before the first recorded activity in 2000 than in 2001 (Table 5.3). Rainfall patterns seven days prior to first activity were also different, with 11.9mm falling in early February 2000 as opposed to 39mm in 2001. First worker activity occurred on the warmest day of February (12.7°C) in 2000, but only on the 5th warmest day (10.5°C) in 2001.

Table 5.3: Weather data prior to first activity in 2000 and 2001.

Year	Mean February Temp ($^{\circ}\text{C}$)		Mean Temp($^{\circ}\text{C}$) 7 days before activity.	
	Max	Min	Max	Min
2000	9.23	2.43	10.2	5.04
2001	7.89	1.09	8.9	2.71

First massing dates did show a significant relationship with light intensity data in 2000 (ANOVA $F= 3.919$; d.f.2; $p=0.040$; $R^2= 0.301$). The early massing date at nests 1 and 2 on 21st February 2000 occurring on a day with 7.6 hours of sunshine, well above the monthly average.

There were no significant relationships between light intensity and the first appearance of alates on nests (2000 ANOVA $F= 0.019$; d.f.3; $p=0.895$; $R^2= 0.001$: 2001 $F= 1.323$; $p=0.438$; $R^2= 0.098$). In 2000, reproductives first appeared on nests where the minimum daytime temperature was 14°C or over in all but two nests (Nest 6 on the north-eastern edge and Nest 11 on the north-west 1 edge). On these two nests alates were first seen on the 27th May which had a maximum daytime temperature of 13.4°C (measured at the UCN weather station), but which experienced 11.3 hours of sunshine.

There was a significant relationship between temperature and the date of last worker activity in 2000 (ANOVA $F= 7.308$; d.f.3; $p=0.015$; $R^2= 0.289$). The One-Way ANOVA analysis of differences between the temperatures at the sample nests showed significant differences existed in the data sets ($F= 4.498$; $p<0.001$). *Post hoc* analysis confirmed that nests 1 and 2 were significantly warmer than the other nests. However, no such relationships were found during 2001.

There was a difference of 22 days between the last recorded activity in 2000 and 2001 (Table 5.1 and 5.2). Data from the UCN weather station showed that there were differences in average temperatures in October and November of both years which may account for this disparity (Table 5.4).

Table 5.4: Average temperature ($^{\circ}\text{C}$) recorded at the UCN Weather Station in 2000 and 2001.

Year	October	November
2000	13.58	9.76
2001	16.61	10.42

Relationships between Nest Characteristics and the Onset of Activity Phases.

Testing for relationships between the onset of activity after the winter hibernation and aspect, distances from the nearest external edge and internal edge and nest orientation did provide a very highly significant result (ANOVA $F= 30.091$; d.f. 5; $p< 0.001$; $R^2= 0.984$). This highlights that the connection is not solely intuitive. However, within this model only the relationship between the commencement of activity and aspect was significant ($p<0.001$).

No significant relationships were found between the onset of activity and the slope angle of nests, their orientation and height, or distance from the nearest external or internal edge (ANOVA $F= 1.933$; d.f 5; $p=0.152$; $R^2= 0.197$).

Nuptial Flights

Nuptial flights or swarms proved to be lengthy affairs, in both years lasting up to 6 weeks (Fig 5.4 actual dates Appendices 7). It should be noted, however, that flights did not occur every day, and none were observed from Nest 15 in 2000. There appeared to be no overlap in flights in the south with those from the other sites in 2000, and only limited overlap in 2001 (Fig 5.4). Most flights did occur during the morning, between 08.00 and 11.00 hours. Within

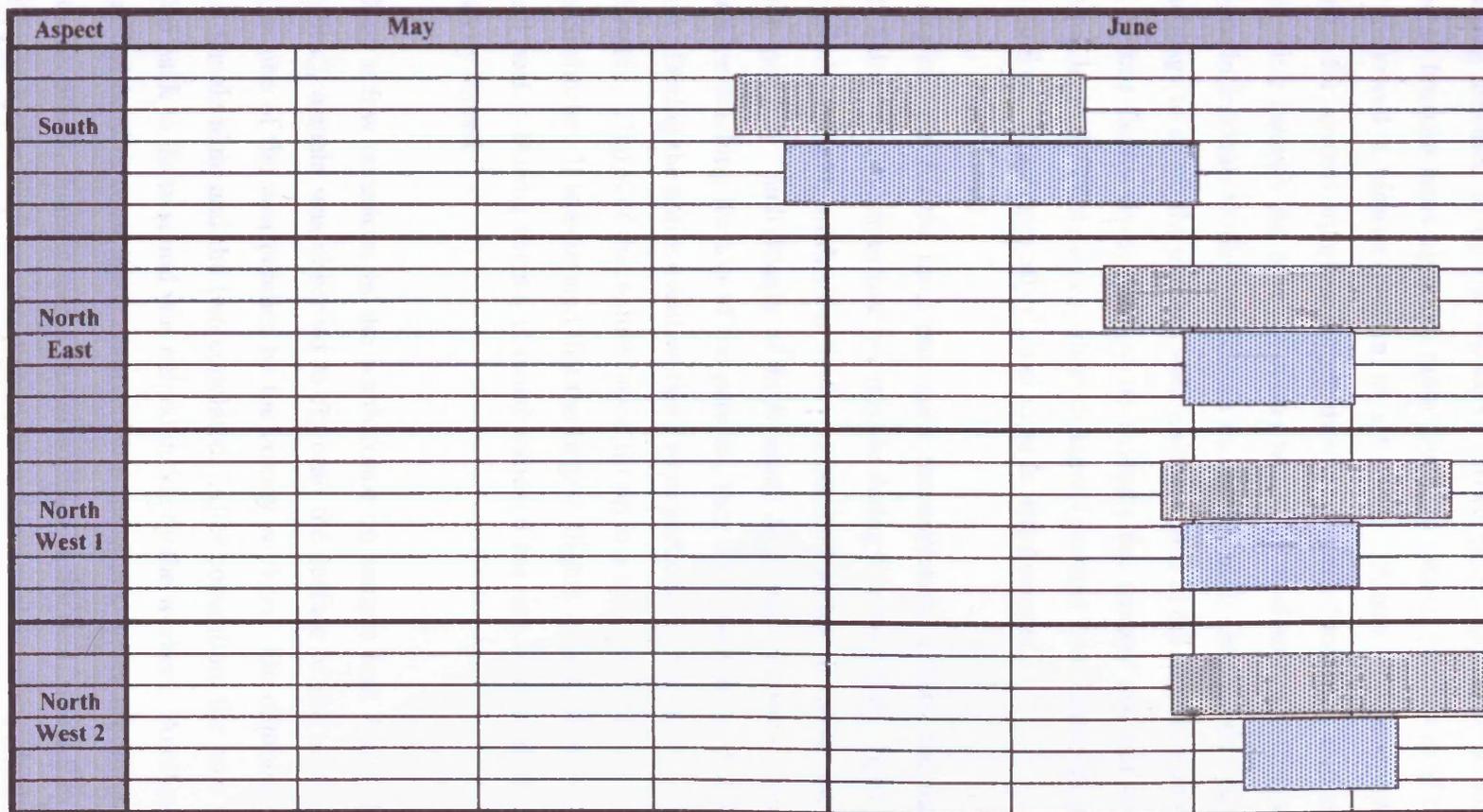


Fig 5.4: Breeding times in *F. rufa* colonies within the four study sites. Key- Black = 2000; Blue = 2001.

that time, flights most commonly took place between 09.00 and 10.30 hours. Some afternoon flights did take place, but these tended to be on days when morning conditions were not suitable (for example rain or low temperatures), and took place as late as 18.00 hours.

Alates appeared a few weeks before the actual flights. During the first few weeks alates of both sexes made no effort to leave the nests, spending most of their time sunning themselves whilst being attended to by the workers. However, as the flight period drew closer they appeared to become more agitated, many trying to ascend perches as if to fly. At this time activity followed a similar pattern at all nests. Alates appeared on the nest sunning themselves for several minutes before moving toward 'perches', normally small twigs or stems growing through the nest. Workers would try to discourage their ascent, and in most cases these individuals would soon return inside the nest. On the odd occasion however, they would manage to climb the perches unhindered. Once at the top, they would beat their wings rapidly, before finally flying straight up towards the canopy and out of sight. Unusually, some individuals flew only a very short distance (perhaps 2 to 5 metres), and then returned to the nest on foot. These take offs tended to be isolated events.

Actual flights were for the most part quite inconspicuous affairs, the maximum number of take offs being no more than five per minute during the most busy flight period. During the major period of flight, workers actively encouraged alates to move out of the nest and to climb the perches. Individuals of both sexes followed the same pattern, and on these occasions, on reaching the top of the perches, they flew away immediately without apparent hesitation. During the entire event workers were particularly aggressive, making observations uncomfortable. Flights of this nature lasted for up to a maximum of two hours, although most were much shorter. It is estimated that the largest flights consisted of <40 alates from each individual nest. During flights, if clouds blocked the sun or a local gust of wind blew up, alate activity ceased.

In 2000 on a few occasions in the south (once on sample nest 4 and the other on a non-specific nest), a male was observed to fly onto the surface of the nest. Once there, it was ushered to one of the nest perches by the colony workers. On climbing the perch the male located a female alate and the two copulated. After copulation, the now inseminated female descended back to the nest and was helped inside by the workers. Another unusual event was also observed in both years, most commonly in the south, where the initial impression was of an aggressive attack. Female alates would walk on to the nest, where they would be instantly pounced upon by the workers who pinned them down to the surface. In the frantic movement

that ensued, the wings of these individuals were torn off and they were forced inside the nest by the workers. Nests 3 in 2000, and 4 in both years appeared to produce a male biased reproductive brood.

5.4 Discussion.

5.4:1. Phenology of Bud Burst in *Acer pseudoplatanus*.

The timing of bud burst in *A. pseudoplatanus* within the four sites showed variation in both years (Fig 1, Tables 5.1 & 5.2). In 2000, although all buds were ‘fully open’ on the same day at 0m in the four sites, variation occurred in bud development with distance into the wood in the north-western aspects. In the south and north-east, buds were fully open by the 23rd April, some thirteen days earlier than the buds at 160m in north-west 1 and north-west 2. These results are most probably explained by the higher spring temperatures which were recorded in the south and north-east. Although the differences were not statistically significant, there may be some underlying ‘biological significance’ which is not being identified due to the sampling regime adopted. Certainly in the south, the significantly higher light intensity values would have contributed to these results. In the north-east, although mean light intensity values at and around solar noon were the lowest of the four sites in 2000 here the rising sun would have provided the north-eastern trees with much greater ‘biologically significant’ light intensity values than either of the north-western sites, which may have prompted early bud burst.

Bud development on sample trees in the north-west 1 and north-west 2, with the lowest temperatures (App 1), would have been expected to have been behind those in the south and north-east, and although mean solar noon light intensity values were higher in north-west 1 than either the north-east or north-west 2, it is likely that these values would not have been maintained for as long a period as in the south, due to the lower angle of the sun in the sky. However, the question of why buds on edge trees were fully open on the same day as their southern and eastern counterparts is less easy to explain. Certainly in the very early spring, the north-western edges would have received little direct sunlight, and in fact, those areas further back, would have been likely to have received more direct sunlight through the developing crown canopy than the extreme edges. However, edge regions would have received warmer air by the process of advection from the surrounding landscape (Hutchison & Matt 1977; Moorecroft *et al.* 1998). Also, in the absence of direct radiation, the early

season overcast skies would have allowed greater diffuse radiation to penetrate into the edge, a process which according to Moorecroft *et al.* (1998) means that forest edge areas may experience very similar conditions to the surrounding landscape.

In 2001, results were very similar. Once again, buds on sample trees were open in all sites at 0m on the same day. In the south and north-east, sample buds were fully open at 160m, only a day after those sample buds at the edge. In 2001, again the south was the warmest of the sites, which although not statistically significant, probably had some 'biological significance'. The south also received significantly more light than north-west 2 and the north-east. In the north-east, although spring temperatures were about the same as north-west 2, and 'solar noon' light intensity values were lower than north-west 1, once more, the rising sun would have provided much greater sunlight early in the day, than would have been received by either north-western aspect. Again, this increased light availability was probably biologically significant and prompted early bud burst. Results in the north-western sites were very similar to 2000 and it is most likely that the same explanations apply.

These results are consistent with the published literature. Certainly, winter chilling was not a major influence on the results, as in all sample aspects temperatures would have fallen below 10°C for a large portion of the deep winter period. It is most likely that spring warming, as suggested by Wang (1980) in the USA, is the key to bud burst in *A. pseudoplatanus* in Harlestone Firs. Initial analysis of the results would suggest that spring warming did initiate bud burst before photoperiod had any effect, in agreement with Perry (1971), Campbell & Sugano (1975) and Hunter & Lechowicz (1984). However, it would certainly appear that light intensity values did play an important role also, most obviously in the south. In the north-east, direct sunlight would have been received for longer during the morning due to the orientation of the edge. Therefore, it should be noted that the processes that 'trigger' bud burst are far from simplistic (Campbell & Sugano 1975; Lechowicz 1984), although the results do confirm that trees do respond to forest edge effects differently in different parts of a woodland.

5.4:2 Phenology of Key *F. rufa* Activity Phases.

There were striking differences in the phenology of the selected activity phases between colonies inhabiting the south and the other three sample aspects, all of which were statistically significant. This is clearly a response to the more favourable microclimatic conditions in the south, which tends to support the view that in the early part of the year light intensity was the

most important factor. This is confirmed by the positive relationship between the light intensity and nest characteristics data, the date of the first observed worker activity and also by the analysis on the southern sample nests only. Workers on nest 1 at the woodland edge, which was warmer and received significantly more light than nests 3, 4 and 5, left hibernation earlier than workers on the interior nests. The difference between activity on nests 1 and 2 occurred in spite of there being no significant difference between the two nests with respect to temperature and light intensity, although nest 1 was warmer and received higher light levels. It may be the case that extremely small differences in these variables are sufficient to trigger activity, and that the arbitrary selection of 95% confidence limits is not sufficiently sensitive to identify this relationship. It is also likely that the moisture levels within the nests have influenced the observed results. Nest 1 on the edge and in the open tends to be notably drier than nest 2, which is constructed around the trunks of three trees and tends to be wetter, especially at the beginning and end of the year. This would lead to the interior temperature being lower in nest 2 than nest 1 and thus may have contributed to the differences in the observed activity.

This relationship with early season moisture is further supported by the comparison of the first dates of activity between the two study years. Activity began earlier in 2000 due to the higher maximum and minimum mean temperature (Table 5.3) and the lower rainfall values. Again, damper nests in the woodland interior and within the three more northern aspects (which also recorded lower light intensity values than the first four southern nests, but did not differ significantly within these aspects), caused interior nest conditions to be cooler and thus wood ant activity to be retarded. The same factors are likely to have been responsible for the first spring massing data, early massing being associated with higher light intensities in the south. The particularly early massing on nests 1 and 2 is again probably a response to the bright sunshine received on that day (7.6 hours of sunshine) which was able to strike both nests for longer than was possible at the other sample nests.

The appearance of the first alates on the nest again occurred significantly earlier on the southern nests than on those at the other study aspects. The earlier massing in the south, and generally more favourable microclimatic conditions enabled these colonies to begin the production of the reproductive brood earlier. These results are thus very much as expected. It is also notable that alates appeared on the nest on warm spring days, and on days which were particularly sunny, again confirming the outline of the known ecology of the *F. rufa* group species provided by Hölldobler & Wilson (1990).

Therefore, *F. rufa* colonies are responding directly to higher surface temperatures in the south and leaving hibernation very early. This is further confirmed by the different responses of southern colonies to differences in light intensity values with distance from the edge. This head-start then helps colonies living in the south to maintain their advantage through the year, with colonies massing earlier, thus enabling the development of the reproductive brood to occur earlier, which in turn appear on the nests earlier. The active season is also longer, thus enabling colonies in the south to build up greater nutritional stores which help to start brood development early the next year, as well as ensuring that the colony can survive until abundant food resources are once again available.

However, a number of questions come to mind when reviewing these results. Firstly, how can colonies be classified as active almost a month before the date of the first foraging activity? (see Chapter 6). Workers from colonies which become active very early in the season do not immediately leave the nest. The reason for this behaviour is unclear, but is probably linked to the importance of ensuring that the mound is repaired as soon as possible, so that its thermoregulatory properties are restored. Without this, the colony would be unable to raise their reproductive brood in time for the season's flights and thus this habit confirms the evolutionary strategy of *F. rufa* groups species described by Hölldobler & Wilson (1990) and Heinze & Hölldobler (1994). Skinner (1976, 1980a) also observed similar behaviour, and even when workers began foraging for food, they still collected nest material at a similar rate, confirming the importance of nest maintenance and internal temperatures.

The first massing activity highlighted notable behaviour. Major masses tended to form on the portion of the nest which was in direct sunlight, consistent with the theory of Forel (1874). However, after a few days of this massing period, smaller 'masses' began on damaged parts of the nest, and it was noticeable that nest material was carried from areas immediately surrounding the mound into these dense aggregations. Once these masses had dispersed, it was obvious that damage to the nest surface had begun to be repaired, perhaps suggesting that there may be a dual function to this phenomenon, although it is clear that much greater observation is required to confirm this view. However, what is clear, is that colonies invested a great deal of time and effort at the beginning of the active season to restore the nest surface, before the first tended aphid populations left diapause.

The question of why alates appear on the nest several weeks before the commencement of the season's flights is difficult to explain, but this phenomenon has been observed by most researchers working with the *F. rufa* group (Scherba 1958; Breen 1979a; Fortelius *et al.*

1993). In the south, the particularly lengthy period before flight is probably related to microclimate, alate development occurring rapidly before conditions for flights and their synchronisation with other nearby nests, are optimal. Nevertheless, how *F. rufa* colonies synchronise their flights is difficult to explain, as the entire process lasts for several weeks, and actual copulation has been witnessed on few occasions (Talbot 1945; Breen 1979b; Fortelius *et al.* 1993). This is certainly an area which requires further investigation.

Finally, the active season at Harlestone Firs appears to be abnormally long compared to the figure of 180 days given by Adlung (1966); activity in the south was over one hundred days longer in both years. This may be due to two factors. Firstly, Adlung (1966) was reporting on observations made in central Germany, where the climate tends to be more continental than the mild weather prevalent in the UK, and thus a shorter season would have been inevitable (Barry & Chorley 1992). The other important factor is the impact of climate change. As winter temperatures have become more mild in recent years, especially in central England, colonies would certainly be able to extend their period of activity, responding in the same way as a number of other organisms (Sparks & Yates 1997; Sparks *et al.* 1997; Sparks 1999; Roy & Sparks 2000; Sparks *et al.* 2000; Burton & Sparks 2002). This is certainly confirmed by the 2001 season, where southern colonies were active until December. The average monthly temperature in October was 3°C higher in 2001 than in 2000, and 0.6°C warmer in November. These warmer conditions meant that the active season was 22 days longer in 2001.

It should also be noted that differences between this and other studies may also be due to the recording protocol, perhaps the activity thresholds used in the other studies were more stringent than those used here. However, as in 2001 the mild conditions allowed small numbers of workers to continue foraging on nearby trees into early December, whilst foragers were still moving up trees in search of food, it was considered justified to classify the colony as 'active'.

Following the normal pattern, reproductive activity began much earlier in the south, there being evidence that flights did not overlap with those from other sites, which seems to suggest that some degree of reproductive isolation exists. However, whether this pattern of reproductive activity is rare cannot be determined by these results. It may be that this apparent isolation is a direct result of climate change, higher early season temperatures conferring a greater advantage to southern colonies due to the process of aspect and distance related edge effects allowing them to begin the nuptial flight very early. For the most part,

alates from colonies in the other sites flew at the same time, this synchronisation probably in response to favourable weather conditions around these more northerly edges. The reason why flights from certain study nests lasted longer than others in the same sites is unknown and the fact that most of these latter flights consisted of males may be significant. It would therefore appear that gene flow between these populations and the south are limited, but a more detailed analysis of the genetic structure of populations is needed before more solid conclusions can be made.

5.5 Conclusion.

Colonies in the south are responding to the favourable microclimate which led to the onset of activity phases occurring significantly earlier in the south, and continuing later into the season. This early development in the south has led to earlier breeding, leading to the apparent reproductive isolation of southern colonies. Southern colonies therefore have an advantage over colonies in the other study aspects which they maintain throughout the year.

Although the most significant difference in colony behaviour was related to ‘aspect’ driven edge effects, distance relationships also proved significant. In the south, the two sample nests closest to the edge received significantly more light than the nests situated from 30m or more from the edge, and thus began activity earlier. This highlights that distance related edge effects are having an important impact on *F. rufa* activity.

The differences between the aspects is also confirmed by sycamore bud development. Buds on trees at all distances within the south and north-east were fully developed 10 to 12 days earlier than those on trees between 31 and 160m in north-west 1 and north-west 2. These results again confirm the presence of both aspect and distance related edge effects within Harlestone Firs.

Chapter 6:

Biological Edge Effects and their Impact on the Ecology of the Wood Ant, *Formica rufa*.

6.1 Introduction.

The presence of certain species of aphid-supporting trees are important determinants of nest location (Barrett 1968; Hughes 1975; Breen 1979a; Sudd *et al.* 1977; Welch 1978; Skinner 1980 a&b, 1998; Sudd 1983; Warrington & Whittaker 1985 a&b; Adams 1991). For example, Sudd *et al.* (1977) found that all of their study nests had at least one tree over two metres high within six metres of the nest. Breen (1979a) found similar results in Ireland. However, it remains to be seen at which point colonies switch from a dependence on a favourable microclimate to a preference for proximity to trees which support favoured aphids, a factor which may be determined by forest edge effects.

Preliminary investigations during 1998 and 1999 indicated that the number of nests varied considerably between areas close to the southern and northern edges of the wood, the southern edge sites supporting considerably more nests than the north (Clarkson unpublished data). It also appeared that nests in the north were further away from the nearest tree (and thus a possible food resource) than those nests in the south, a factor which may have been due to microclimate. These observations raised questions about the factor which most determined the selection of a nest site and many behavioural responses in *F. rufa*; is it microclimate or proximity to and the quality of food resources, and is there a threshold beyond which one was more important than the other?

The specific questions addressed in this chapter are thus:

1. Does edge vegetation show variation in response to edge effects?
2. Are there specific associations between species of tree and ground flora at nest locations?
3. Is there a pattern of foraging dependence on a particular species of tree(s) at nest locations and do these patterns change with location around the wood?
4. How stable are nest sites in time? Do colonies move nests due to edge effects?
5. Is colony structure determined by edge effects?

6.2 Methods.

6.2:1. Overall Vegetation Survey

From each sampling point along the three transects in each sample site, and from each nest and control point, the identities of the ground flora and tree species within a 5m radius were recorded. The trunk circumference of all trees within this zone was also measured at a height of one metre. In addition, all of the trees within a 5m radius of the additional study nests (to give a total of 82 nests – see section 4.3:3 chapter 4) were also identified. From these data sets, analyses of species composition and tree density were made. The distance of the nearest tree to each nest was also recorded to provide an indication of whether colonies were selecting nest locations solely on microclimate or proximity to food resource. The analysis was divided into three parts for easier comparison – Part 1 covers the vegetation survey along the transects within the four aspects; Part 2, the survey of vegetation within nests and controls; Part 3 compares the tree species composition and location for all 82 study nests to provide greater definition to the results.

6.2:2 Foraging Activity of the Sample Colonies.

All foraging trails were followed to the individual trees which the colonies favoured in 2000. On each tree, the number of ascending foragers crossing a fixed point were counted using a ‘click counter’ over a one minute period. This was repeated on a weekly basis for every sample colony within the four study sites. Data for March and May were excluded due to anomalies caused by illness which led to the under recording of some species. Where it was necessary to highlight the utilisation of a particular species of tree or the differences between sites, total counts were used. In these cases mean values did not reflect colony preferences when several individuals of the same species were utilised. However, mean foraging values for each month on each species of tree were calculated to highlight foraging preference for particular species at certain times of the year.

6.2:3 Nest Persistence & Colony Structure

The analysis of nest density and persistence is based on observations over the two year period. Breen (1979a) cautioned that nest density analysis should only include mature or permanent nests, and that ‘summer’ nest buds produced regularly by *F. rufa* group species should be disregarded. Thus, all active nests within the study area were recorded at the beginning of the

2000 season. After the forest management activities in 2001, numerous bud nests were formed, but only those still in use at the start of the 2002 season were recorded. Finally, nests listed in the original 2000 survey which had been permanently abandoned were also recorded to enable a comparison of nest persistence within each site.

As this study was based on a ‘non-intervention’ approach due to conditions set by the landowner, excavating nests to determine the exact numbers of queens, and thus the social structure of the colonies, was not possible. However, as colonies of *F. rufa* tend to be highly territorial other techniques were available. These were adapted from research by Rosengren & Pamilo (1983), and included the following;

- single and group graft experiments;
- mass marking of workers on nest mounds.

Where workers from one nest were accepted by those of other nests a relationship was considered to exist. Although colonies utilising more than a single nest, in most cases, also possess multiple queens (Pamilo & Rosengren 1984), colonies were classified only as monodomous or polydomous in this study.

6.2:4. Data Analysis

Biological Edge Effects and Nest Vegetation Survey.

The data concerning the total, mean number and density of plant species along the edge to interior transects, and from around the sample nests and control points, were normally distributed and were compared using either one-way or two-way ANOVA tests. *Post hoc* analysis was done using the Tukey HSD test.

Principal component analysis (PCA), a reduction technique that attempts to identify the underlying variables which explain the pattern of correlation within a set of observed variables, was used to identify a small number of factors (or principal components), which explain most of the variation within the much larger original data set. Unique scores can then be calculated from the principal components, which may be plotted on an ordination diagram (Waite 2000). Clusters of points represent similarities, or in this case, species associations. Conversely, points which are more widely scattered show less similarity with one another.

The data concerning the frequency of tree species found within the nest and control zones and the distance from the nests to the nearest tree were not normally distributed and were therefore compared for differences using the non-parametric Kruskal-Wallis test.

The comparison of the presence or absence of tree species in nest zones of all study nest in relation to aspect and the distance to the nearest tree data were compared by way of the Kruskal-Wallis test. The General Linear Model (GLM) was used to compare the differences in the tree species found within the nest zones of the study nests in relation to distance to the nearest internal and external edges. The GLM retains the benefits of using standard analysis of variance (ANOVA) tests, but enables two or more variables to be examined in one test. Thus, Type 1 errors are avoided, as the number of statistical tests required is reduced to acceptable standards (Hebrant 1981). The output of GLM is an overall F-Test for all dependent variables together. If this test is statistically significant, then it is justifiable to report the univariate F-tests for each dependent variable individually. Finer scale interpretation of the results are made possible by the use of a 'Post hoc' analysis, in this case, the Tukey HSD test.

Foraging Activity

The foraging activity on the various tree species through the year and the distance of the longest forage trail at each nest was compared using One-way ANOVA with Tukey HSD *post hoc* tests. To determine if the onset of activity phases (see Chapter 5) was influenced by the availability of food resource, the activity data were retested using the General Linear Model test in SPSS, with the tree species *A. pseudoplatanus* and *S. nigra* added as covariates. These were the only two species which were found in significantly more nest zones than controls.

6.3 Results.

6.3:1 Part 1: Biological Edge Effects - An Analysis of the Plant and Tree Species and their Associations within the Four Study Aspects.

A total of 45 species were found within the four study aspects (Appendix 8.1). The total number of species found in each of the individual aspects showed variation; north-west 2 and the south supporting a more diverse mix of species than either the north-east or north-west 1 (Table 6.1). These relationships were found to be statistically significant (ANOVA F=

8.533; $p < 0.001$), *post hoc* analysis showing that the southern transects supported significantly more species than either the north-east ($p=0.002$) or north-west 1 ($p<0.001$).

Table 6.1: Total, mean and standard deviation of tree and plants species within the four sites.

Site	No. of Species	Mean	SD
South	32	25.67	1.53
North-East	14	11.33	2.31
North-West 1	21	15.33	3.10
North-West 2	37	25.66	4.04

The mean number of species found at each point along the edge to interior transects, in general, decreased with distance into the wood, although the trend was least noticeable in the east (Appendix 8.2). This relationship was statistically significant for all aspects (ANOVA $F= 7.106$; $p<0.001$), the sample points at 0m supporting a greater number of species overall than the sampling points at 80m or 160m ($p<0.001$).

The number of tree species found in the transect survey of the four aspects followed a similar pattern to the overall vegetation survey, with north-west 2 and the south having the greater number of species (Table 6.2).

Table 6.2: Total Number of Tree Species within the Four Sites.

Site	No. of Species
South	10
North-East	8
North-west 1	8
North-West 2	13

The number of tree species found at each sample point along the study site transects were significantly different from one another (ANOVA $F= 11.790$; $p<0.001$). *Post hoc* analysis showed that the southern transects supported significantly more tree species than those within the other study aspects ($p<0.001$). The overall trends between the sites differed. The mean number of tree species generally increased with distance along the southern transect. However, numbers in the north-east and north-west 1 remained fairly stable throughout. In north-west 2, diversity increased to 20m from which point numbers remained about the same (Appendix 8.3).

Regardless of trunk circumference the number of individual trees found along the transects within the four aspects were significantly different (ANOVA $F= 6.135$; $p= 0.001$). *Post hoc*

analysis showed that the south supported significantly more individuals than north-west 2 ($p=0.001$). The mean number of individual trees, although higher along the southern transects, did not follow the expected clearly defined trends, with the number of species decreasing with distance into the interior (Appendix 8.4).

Many of the individual trees within the study aspects were young, showing healthy regeneration around the wood. Therefore, to determine the number of mature trees, those with trunk circumferences of over 20cm were compared. These comparisons showed that there were significant differences between aspects (ANOVA $F= 11.525$; $p<0.001$). *Post hoc* analysis identified that the south had a greater number of individuals with trunk circumferences >20 cm than the other aspects ($p<0.001$). However, there were no significant differences in the number of individual trees with trunk circumferences >20 cm found within each 5m sampling point along the edge to interior transects (ANOVA $F= 0.626$; $p=0.680$) (Appendix 8.5).

The ground flora found along the edge to interior transects showed variation with aspect in the four sites (Appendix 8.6). There were also significant differences in the number of species found at each sample point along the edge to interior transects (ANOVA $F= 3.803$; d.f.3; $p=0.016$), *post hoc* analysis identifying that sample points at 0m supported more species than points at 80m ($p=0.019$) and 160m ($p=0.013$) (Table 6.3).

Table 6.3 : Number of species of plants in the ground flora found at each sample point of the edge to interior transects within the four study sites.

Site	Distance along transect						Total
	0m	10m	20m	40m	80m	160m	
South	15	8	8	8	9	3	22
North-East	8	2	2	2	2	3	8
North-West 1	14	5	3	2	1	1	13
North-West 2	21	14	11	12	1	4	23

Species Associations within the Study Aspects.

The different tree species found within the sample points of the edge to interior transects within the four aspects showed variation in both total number and the number of mature trees (trunk diameter >20 cm). Although north-west 2 had the most species, no species truly dominated (Figs. 6.1 and 6.2). *Rhamnus cartharticus* was the most numerous species, although most occurred as young individuals. The most common plantation species was *Pinus sylvestris*. In the south, *Ulmus* spp. were the most numerous, although occurring

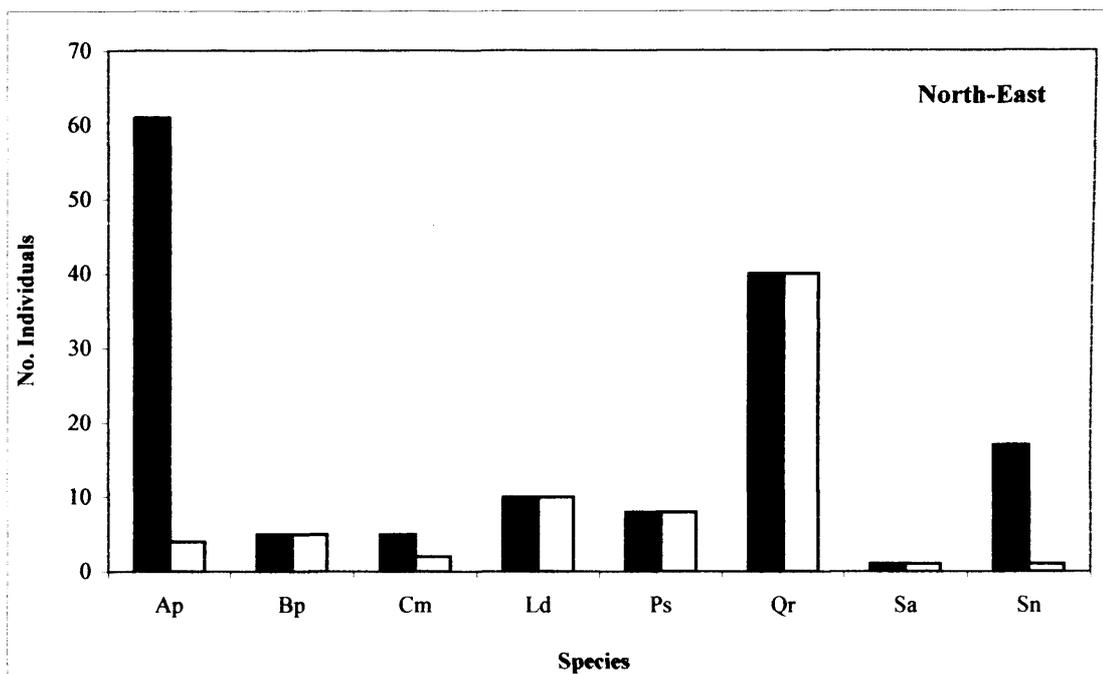
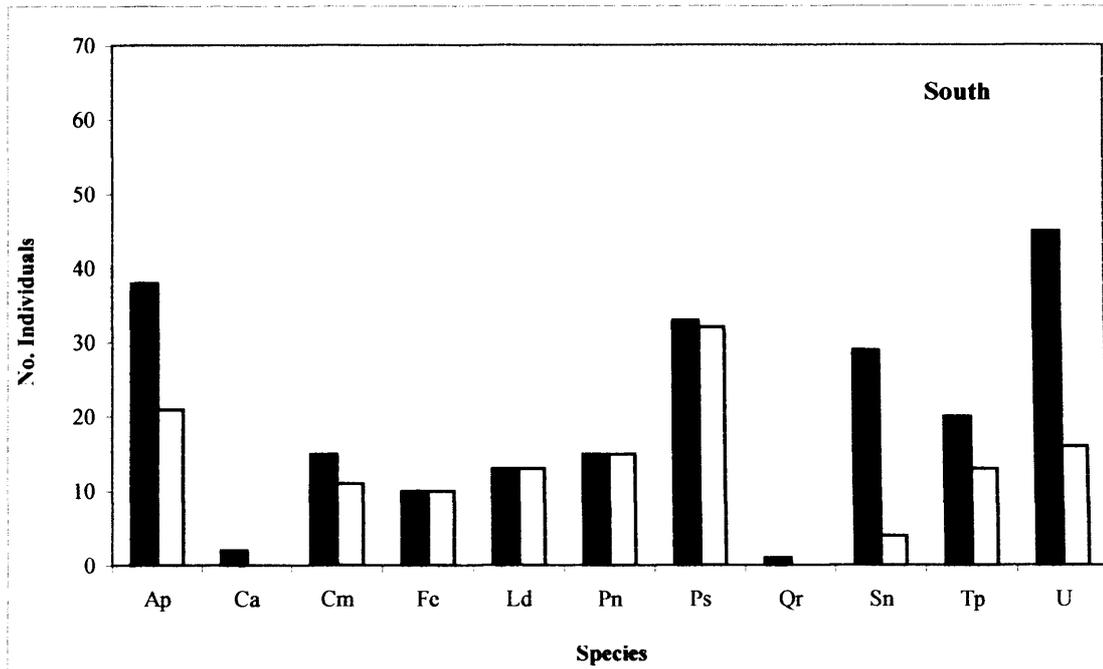


Figure 6.1 : Number of individual trees and trees with trunk circumferences >20cm from the transect sample points of the southern and north-eastern sites (Black bars denote total number of trees : white those with trunk circumferences of >20cm).

Key : AP- *Acer pseudoplatanus*; Bp – *Betula pendula*; Ca – *Corylus avellana*; Cm – *Crataegus monogyna*; Fe – *Fraxinus excelsior*; Ld – *Larix decidua*; Pn – *Pinus nigra*; Ps – *Pinus sylvestris*; Qr – *Quercus robur*; Sa – *Sorbus aucuparia*; Sn – *Sambucus nigra*; Tp – *Tilia platyphyllos*; U – *Ulmus* spp.

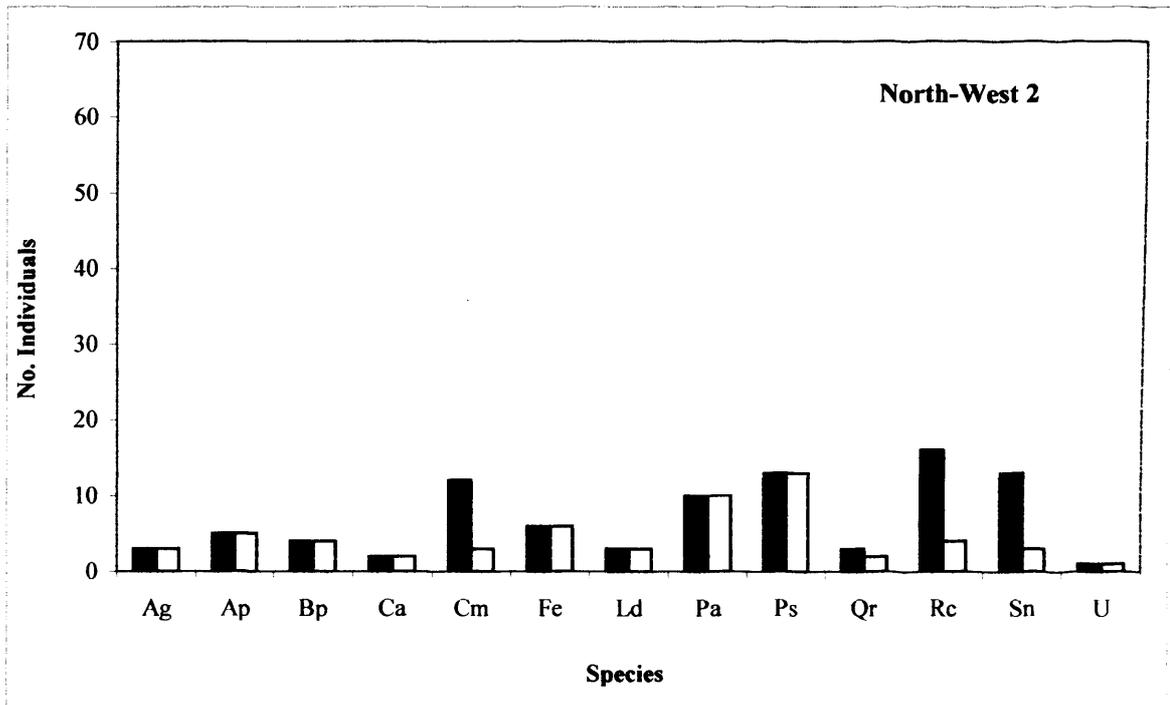
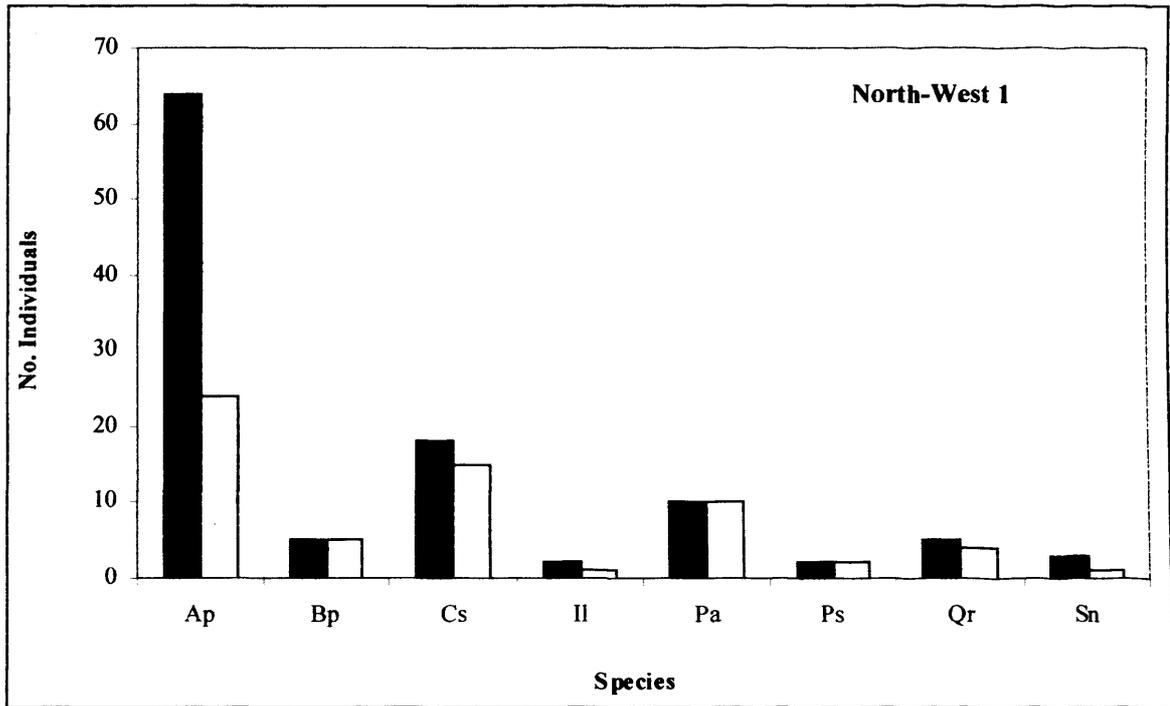


Figure 6.2 : Number of individual trees and trees with trunk circumferences >20cm from the transect sample points of the north-west 1 and 2 aspects (Black bars denote total number of trees : white those with trunk circumferences of >20cm).

Key : Ag – *Alnus glutinosa*; AP- *Acer pseudoplatanus*; Bp – *Betula pendula*; Ca – *Corylus avellana*; Cm – *Crataegus monogyna*; Cs – *Castanea sativa*; Fe – *Fraxinus excelsior*; Il – *Ilex aquifolium*; Ld – *Larix decidua*; Pa – *Picea abies*; Ps – *Pinus sylvestris*; Qr – *Quercus robur*; Rc – *Rhamnus cathartica*; Sa – *Sorbus aucuparia*; Sn – *Sambucus nigra*; Tp – *Tilia platyphyllos*; U - *Ulmus* spp.

between 0m and 10m from the edge. *A. pseudoplatanus* was the next most numerous deciduous species, with *P. sylvestris* the most abundant coniferous species. In the north-east, *A. pseudoplatanus* was the most numerous species, although *Q. robur* was the most dominant mature tree. *Larix decidua* was the most common plantation species. Once again, in north-west 1, *A. pseudoplatanus* was the most abundant species, but most occurred as young saplings. *Castanea sativa* was the dominant mature broad leaved tree, with *Picea abies* the most common plantation species (Figs 6.1 and 6.2).

Principal Component Analysis (PCA) of the original 45 species within the four aspects did not highlight any striking relationships, reducing the data to fifteen factors which accounted for 78.5% of the variation (Table 6.4 and Appendix 8.7). The failure to reduce the data set to a small number of factors indicates that the dataset is very complex. Nevertheless, the ordination diagram of the first two factor scores showed that vegetation on the southern and north-west 2 transects, for the most part, supported different species compositions than the north-east or north-west 1 (Fig 6.3). This was supported by statistical analysis of the individual species which were found to show significant variation around the four aspects within the PCA analysis (Table 6.5). This confirms that the distribution of some species is limited to certain aspects and that among them examples of ancient woodland indicators (AWI) exist (App 8.6). Analysis by distance along the transects when combining all sites tentatively showed that there were some differences in the species composition between 0m and 20m and the other distances. This would imply that no independent associations existed from at least 20m into the wood (Fig 6.4).

Summary of the Results - Part 1.

Overall, the southern and north-west 2 aspects supported more species than either the north-east or north-west 1. There were also significantly more species along the edge to interior transects in the south than in the north-east or north-west 1, but in all aspects, the reduction in the total number of species with distance along the transects was significant between 0m and 80 to 160m. The south supported significantly more tree species per sample point and along the transects than all other aspects. It also supported significantly more species of trees with trunk circumferences >20cm than the other aspects. The number of tree species decreased with distance into the wood, except in the south where a slight increase occurred. Species composition appeared to be different between the south and north-west 2, and between them and the north-east and north-west 1. The north-east and north-west 1 appeared to support

Table 6.4: Principal Component Analysis of transect vegetation data. Factors were extracted to a minimum eigenvalue of 1.0 to produce sixteen significant factors explaining 78.5% of the variation in the data.

Factor	Eigenvalue	% Variation	Cumulative % var.
1	7.6	16.6	16.6
2	5.1	11.1	27.7
3	3.4	7.4	35.1
4	2.4	5.4	40.6
5	2.2	4.8	45.3
6	2.1	4.6	49.9
7	2.0	4.3	54.3
8	1.9	4.1	58.5
9	1.6	3.6	62.0
10	1.6	3.4	65.4
11	1.4	3.0	68.5
12	1.3	2.9	71.3
13	1.2	2.6	73.9
14	1.1	2.4	76.3
15	1.0	2.2	78.5

Table 6.5: Significant results of Kruskal-Wallis tests to compare the vegetation along the transects with PCA scores of +/- 0.5 within the four study aspects (3 degrees of freedom).

Species	χ^2	p
<i>A. pseudoplatanus</i>	8.11	0.044
<i>A. maculatum</i>	22.93	<0.001
<i>C. sativa</i>	30.42	<0.001
<i>F. excelsior</i>	17.31	0.001
Filicospoda spp.	33.30	<0.001
<i>G. aparine</i>	16.93	0.001
<i>H. non-scripta</i>	38.41	<0.001
<i>L. decidua</i>	12.67	0.005
<i>P. abies</i>	17.13	0.001
<i>P. nigra</i>	42.60	<0.001
<i>P. sylvestris</i>	19.82	<0.001
<i>P. aquilinum</i>	20.18	<0.001
<i>Q. robur</i>	40.43	<0.001
<i>R. fruticosus</i>	18.33	<0.001
<i>R. ficaria</i>	26.62	<0.001
<i>R. obtusifolius</i>	9.80	0.020
<i>S. dioica</i>	9.26	0.026
<i>S. dulcamara</i>	22.93	<0.001
<i>S. media</i>	13.31	0.004
<i>S. nigra</i>	8.29	0.040
<i>S. vulgaris</i>	9.26	0.026
<i>T. platyphyllos</i>	19.36	<0.001
<i>U. dioica</i>	22.32	<0.001
<i>Ulmus</i> spp	12.19	0.007
<i>V. thapsus</i>	12.36	0.006

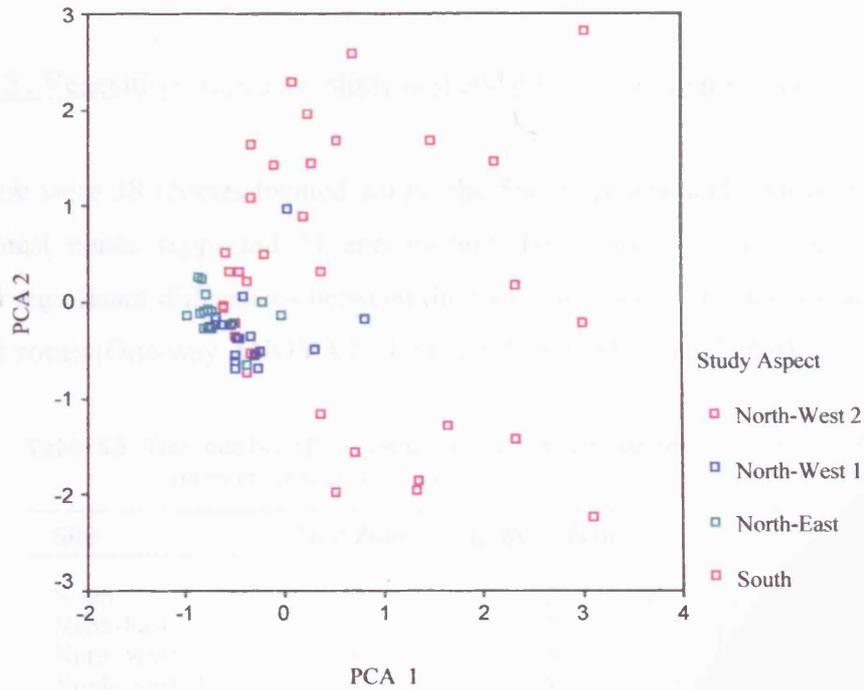


Figure 6.3: Relationships between the vegetation in the four study sites using Principal Component Analysis of the first two factor scores.

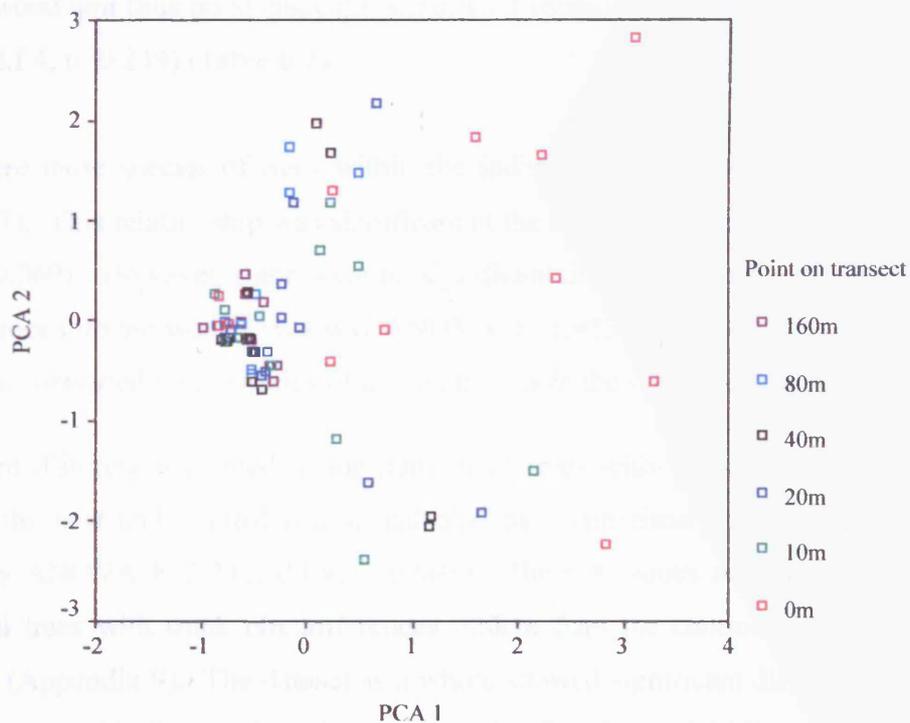


Figure 6.4: Relationships between the vegetation along the edge to interior transects of the four study sites using Principal Component Analysis of the first two factor scores.

similar species, although diversity was less in the north-east. There appeared to be slight differences in species composition between 0m to 20m and the interior of the wood.

6.3:2 Part 2 : Vegetation within the study nest and control point sample zones.

Overall there were 38 species located within the 5m study nest and control zones (Appendix 9.1). The nest zones supported 31 species and the controls 32 species. There were no statistically significant differences between the mean number of species found within the nest and control zones (One-way ANOVA $F=1.11$; d.f.3; $p=0.332$) (Table 6.6).

Table 6.6 Total number of species within the nest and control zones in the four study sites.

Site	Nest Zone	Control Zone
South	19	22
North-East	16	12
North-West 1	20	14
North-West 2	20	17

Individual nest zones supported significantly more species than the individual controls (One-way ANOVA $F=8.95$; d.f.19; $p=0.005$), but the total number remained similar with distance into the wood and thus no statistically significant relationship was found (One-way ANOVA $F=1.62$; d.f.4; $p=0.239$) (Table 6.7).

There were more species of trees within the individual nest zones than within the controls (Table 6.7). This relationship was significant at the 94% level (Two-way ANOVA $F= 3.713$; d.f.1; $p=0.060$). However, there were no significant differences in the number of trees found with distance into the wood (Two-way ANOVA $F=1.953$; d.f.4; $p=0.127$). The southern nest zones also supported more species of tree than nests in the other study aspects.

Significant differences existed in the number of trees with trunk circumferences of >20cm between the nest and control zones, and also by comparison with distance into the wood (Two-way ANOVA $F=3.741$; d.f.9; $p=0.003$). The nest zones supported significantly more individual trees with trunk circumferences >20cm than the control zones ($F=10.540$; d.f.1; $p=0.003$) (Appendix 9). The dataset as a whole showed significant differences in the number of tree species with distance into the wood ($F=4.849$; d.f.4; $p=0.004$), *post hoc* tests showing that the edge regions supported more species than sample points between 21 and 50m ($p=0.029$) and 91 and 160m ($p=0.011$) from the edge.

Table 6.7: Mean number of plants in the ground flora and tree species within the nest and control zones in the four study sites (St dev in italics).

	Site	Nest Zone	Control Zone
Ground Flora	South	3.6 <i>(1.5)</i>	3.4 <i>(3.4)</i>
	North-East	3.4 <i>(1.7)</i>	1.8 <i>(0.8)</i>
	North-West 1	4.4 <i>(2.3)</i>	2.4 <i>(1.5)</i>
	North-West 2	11 <i>(1.8)</i>	7 <i>(1.9)</i>
Tree Species	South	6.0 <i>(0.7)</i>	4.4 <i>(1.1)</i>
	North-East	4.4 <i>(0.5)</i>	4.0 <i>(0.7)</i>
	North-West 1	3.6 <i>(0.5)</i>	2.8 <i>(1.5)</i>
	North-West 2	3.8 <i>(1.6)</i>	3.4 <i>(1.5)</i>

There were no statistically significant differences in the mean number of species in the ground flora within the four aspects (One-way ANOVA $F= 0.818$; d.f.3; $p=0.548$) (Table 6.7). However, the ground flora within the nest and control zones showed variation around the four sites (Appendix 9.2). There were significant differences in the number of species of ground flora found within the nests and control zones (Two-way ANOVA $F= 3.471$; d.f.9; $p=0.005$); the nests supporting more species than the control zones ($F=8,828$; d.f.1; $p=0.006$). The number of species of ground flora tended to fall with distance into the wood, this relationship proving significant ($F=5.073$; d.f.4; $p=0.003$). *Post hoc* tests showed that the edge zones supported more species than sample points between 21 and 160m from the edge ($p=0.002$; $p=0.023$; $p=0.033$).

Species associations within the nests and control zones.

The only species of ground flora common to all nest zones were *Galium aparine*, *Rubus fruticosus* agg. and *Pteridium aquilinum* (Appendices 9.2). However, both *Galium aparine* and *Pteridium aquilinum* were also common to all control zones. No other species of ground flora showed any striking relationship with nest or control zones. *A. pseudoplatanus* was the most common tree found within the nest zones (Fig 6.5). *S. nigra* and *P. sylvestris* were the next most abundant, followed by *Q. robur*. *P. sylvestris* was the most abundant species within the control zones.

As differences between the sites with respect to ground flora were limited, Principal Component Analysis (PCA) was conducted using the tree species found within the nest and control zones only. PCA reduced the data to six factors accounting for 74.5% of the variation, ordination diagrams showing that no clearly discernable relationships existed between the first two factors representing species composition within the sample zones (Appendix 9.7 and Fig 6.6). However, comparing the number of individuals of each tree species within the nest and control zones was more meaningful and showed that only *A. pseudoplatanus* and *S. nigra* occurred in significantly greater numbers in the nest zones than in the controls (Table 6.8). *A. pseudoplatanus* was the most abundant occurring in the nest zones of all southern and north-west 1 nests, three north-eastern and two north-west 2 nests. PCA of the tree species found only within the nest zones at the four study aspects reduced the data to seven factors which accounted for 81.9% of the variation (Appendix 9.8). The ordination diagram of the first two factor scores showed that the southern cluster tended to separate from those of the other aspects, but otherwise no clear trends existed (Fig 6.7).

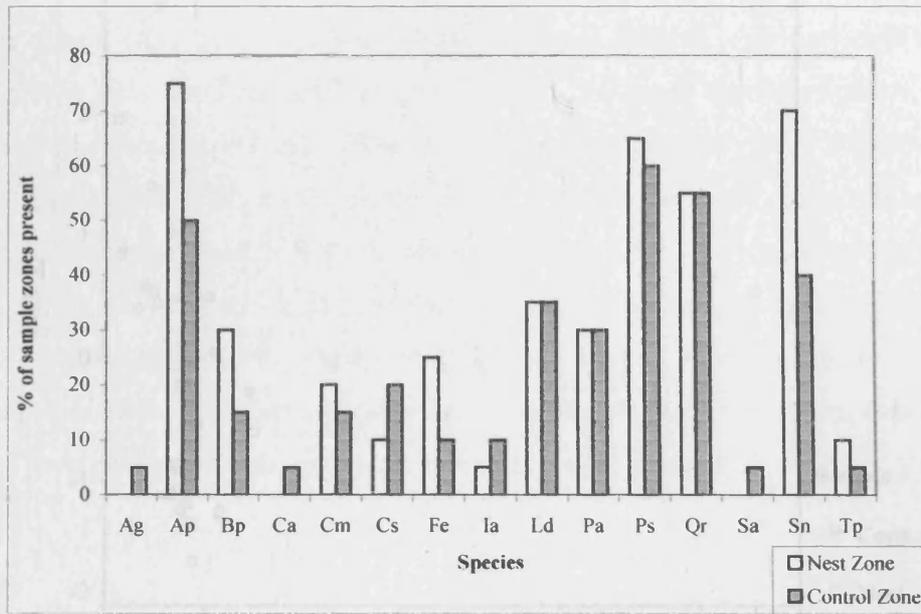


Fig 6.5: Number of individuals of each species of tree found within the sample zones.

Key: Ag- *Alnus glutinosa*; Ap- *Acer pseudoplatanus*; Bp - *Betula pendula*; Ca- *Corylus avellana*; Cm- *Crataegus monogyna*; Cs- *Castanea sativa*; Fe- *Fraxinus excelsior*; Ia- *Ilex aquifolium*; Ld- *Larix decidua*; Pa- *Picea abies*; Ps- *Pinus sylvestris*; Qr- *Quercus robur*; Sa- *Sorbus aucuparia*; Sn- *Sambucus nigra*; Tp- *Tilia platyphyllos*

Table 6.8: Results of the Kruskal Wallis tests to compare the abundance of tree species found in nest and control zones within the four study sites (all at 1 degree of freedom).

Species	χ^2	p
<i>Acer pseudoplatanus</i>	6.557	0.010
<i>Alnus glutinosa</i>	2.051	0.152
<i>Betula pendula</i>	2.289	0.130
<i>Crataegus monogyna</i>	0.151	0.698
<i>Fraxinus excelsior</i>	1.271	0.260
<i>Ilex aquifolium</i>	0.351	0.553
<i>Larix decidua</i>	0.031	0.861
<i>Picea abies</i>	0.001	0.973
<i>Pinus sylvestris</i>	1.136	0.286
<i>Quercus robur</i>	0.459	0.498
<i>Sambucus nigra</i>	4.920	0.027
<i>Sorbus aucuparia</i>	0.001	0.971
<i>Tilia platyphyllos</i>	0.425	0.515
<i>Ulmus spp.</i>	0.001	0.971

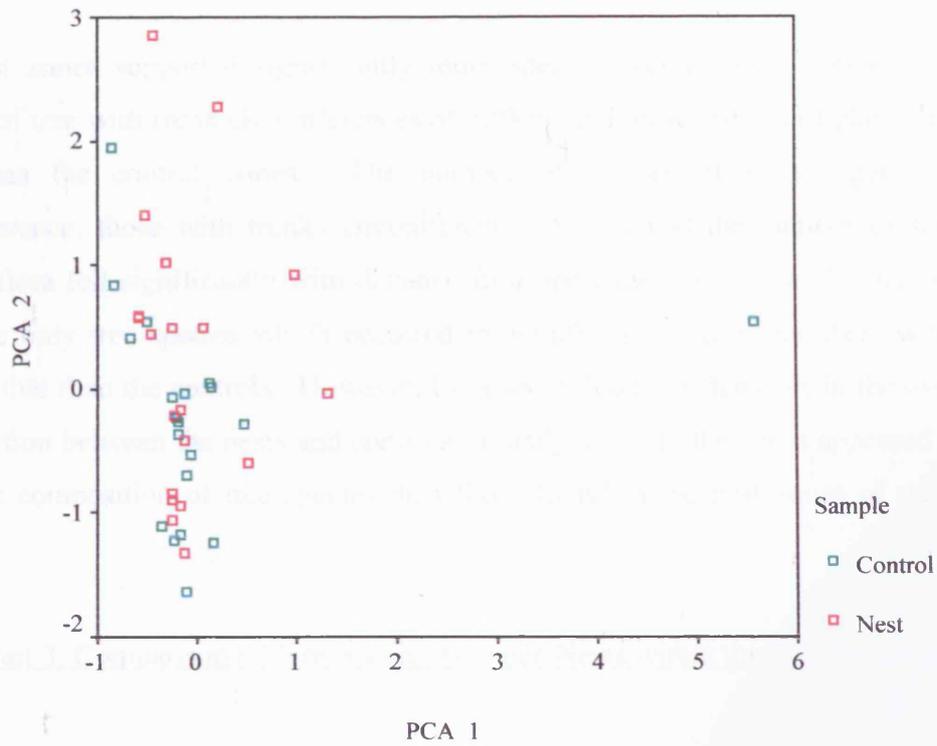


Figure 6.6 : Relationships between the tree species found in the nest and control zones using Principal Component Analysis of the first two factors.

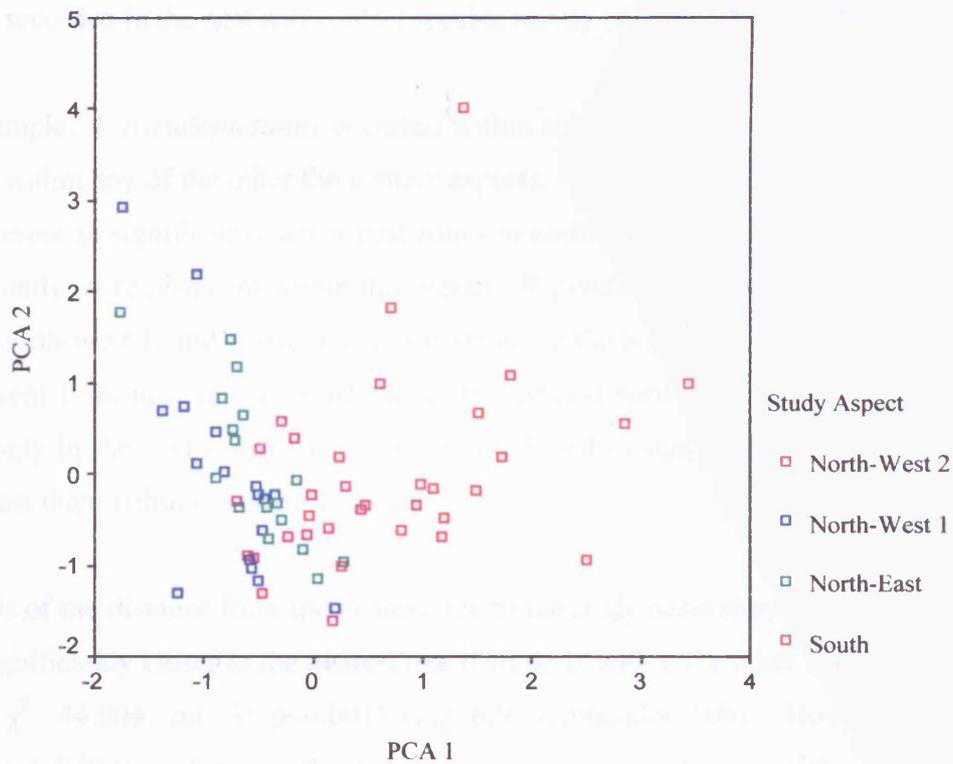


Figure 6.7 : Relationships between the tree species found in the nest zones using Principal Component Analysis of the first two factors.

Summary of the Results - Part 2.

The nest zones supported significantly more species overall, more species of tree, more species of tree with trunk circumferences of >20cm, and more species of plants in the ground flora than the control zones. The number of species of trees regardless of trunk circumference, those with trunks circumferences >20cm and the number of species in the ground flora fell significantly with distance from the edge. *A. pseudoplatanus* and *S. nigra* were the only tree species which occurred in significantly greater numbers within the nest zones rather than the controls. However, PCA identified no differences in the overall species composition between the nests and controls. Finally, nests in the south appeared to support a different composition of tree species than those found in the nest zones of the other study aspects.

6.3:3. Part 3. Comparison of Tree Species between Nests within the Four Study Aspects.

No new tree species were found within the 5m nest zones of the additional 62 nests (Appendices 10a). However, significant differences existed in the presence/absence of particular trees around the four study aspects, with variation occurring in 10 of the 15 tree species recorded in the nest and control species survey (Figure 6.8 and Table 6.9).

For example, *A. pseudoplatanus* occurred within significantly fewer nest zones in north-west 2, than within any of the other three study aspects. Two species (*L. decidua* and *P. sylvestris*) were present in significantly fewer nest zones in north-west 1, but *C. sativa* and *P. abies* were significantly more abundant within this aspect. *B. pendula* was less abundant in the south and within north-west 1, and *S. aucuparia* was absent in the South and the north-east. *F. excelsior* was absent from nest zones within the north-east and north-west 1, and *T. platyphyllos* was found only in the south. Finally, *Q. robur* was found in significantly more nest zones in the north-east than within the other three aspects.

Analysis of the distance from the nearest tree to the study nests showed that nests in the south were significantly closer to the nearest tree than nests within the other study aspects (Kruskal-Wallis χ^2 44.004; d.f. 3; $p < 0.001$) (Fig 6.9) (Appendix 10b). However, there was no significant difference between the distance from the nearest tree in relation to the distance of the study nests from the nearest edge (Kruskal-Wallis χ^2 1.919; d.f. 4; $p = 0.751$).

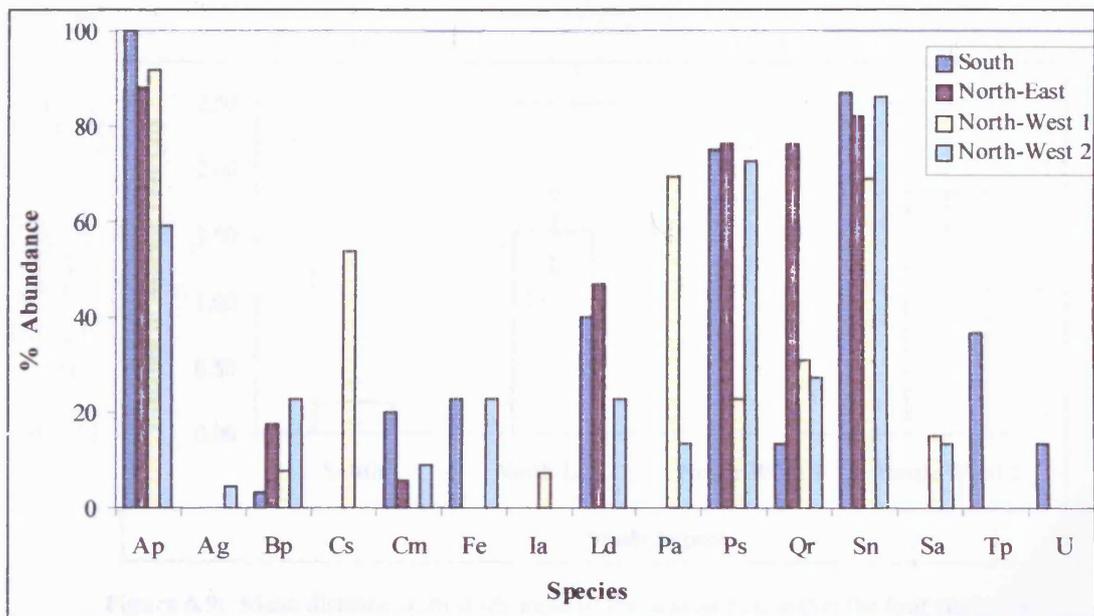


Figure 6.8: Percentage abundance of tree species within the 82 study nests within the four sample aspects.

Key: Ap- *Acer pseudoplatanus*; Ag- *Alnus glutinosa*; Bp - *Betula pendula*; Cm- *Crataegus monogyna*; Cs- *Castanea sativa*; Fe- *Fraxinus excelsior*; Ia- *Ilex aquifolium*; Ld- *Larix decidua*; Pa- *Picea abies*; Ps- *Pinus sylvestris*; Qr- *Quercus robur*; Sa- *Sorbus aucuparia*; Sn- *Sambucus nigra*; Tp- *Tilia platyphyllos*; U- *Ulmus* spp.

Table 6.9: Results of the Kruskal Wallis tests to compare the abundance of tree species found in nest zones within the four study sites (all at 1 degree of freedom).

Species	χ^2	p
<i>Acer pseudoplatanus</i>	19.816	<0.001
<i>Betula pendula</i>	9.059	0.029
<i>Castanea sativa</i>	40.059	<0.001
<i>Fraxinus excelsior</i>	7.989	0.046
<i>Larix decidua</i>	9.466	0.024
<i>Picea abies</i>	39.266	<0.001
<i>Pinus sylvestris</i>	8.769	0.033
<i>Quercus robur</i>	24.883	<0.001
<i>Sorbus aucuparia</i>	8.695	0.034
<i>Tilia platyphyllos</i>	21.685	<0.001

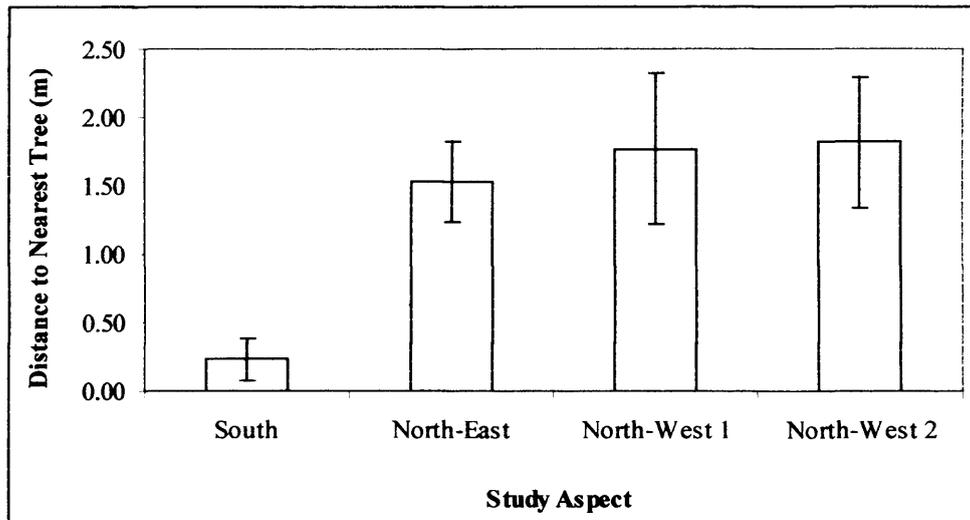


Figure 6.9: Mean distance from study nests to the nearest tree within the four study aspects.

The General Linear Model analysis of the differences in the tree species found within the study nest zones in relation to distance from internal and external edges showed that significant differences occurred (Table 6.10).

Table 6.10: Results of the General Linear Model analysis of the tree species found within the study nest zones in relation to distance from internal and external edges.

Factor	Species	F	p
Overall Model	<i>C. sativa</i>	3.802	<0.001
Distance from external edge	<i>C. monogyna</i>	3.242	0.018
Distance from internal edge	<i>C. sativa</i>	5.371	0.001
	<i>P. sylvestris</i>	4.104	0.005

Post hoc tests showed that *C. monogyna* was found only in external edge regions and that *C. sativa* was found in significantly greater number within 5m of an internal edge. In addition, *P. sylvestris* was more likely to occur between 21-50m from an internal edge, usually located in the centre of the sample study aspects.

6.3:4 Nest Persistence and Colony Structure.

Nest persistence over the two years showed stability, with nests present in 2000, for the most part, surviving to the beginning of 2002. However, forest management activities in spring 2001 severely damaged some nests, especially sample nests 3 and 7. After disturbance by damage to nests, the loss of forage trees or due to canopy opening, some colonies responded by producing numerous bud nests. Most of these were later abandoned, but some survived and were still in use at the beginning of 2002. After disturbance nest densities did

increase, with the exception of the north, which was largely excluded from management activities. Sample nest 7 was abandoned in favour of one of the buds during 2002, but otherwise, all study nests were still active at the beginning of 2004.

Colony structure showed great variation within the four study sites. The southern site contained a much higher percentage of polydomous colonies than the other sites. Colonies in the north and west especially favoured a monodomous strategy (Table 6.11 & Figures 6.10-6.13).

Table 6.11: Colony structure amongst colonies within the four study sites.

Site	Colonies	% Monodomous
South	37	39
North-East	16	69
North-West 1	14	79
North-West 2	22	82

6.3:5 Foraging Activity.

Foraging activity was first witnessed at nests in the south (Table 6.12). *A. pseudoplatanus* was the most common tree on which activity was first observed. Overall foraging activity appeared to be higher in the south, although these differences were not statistically significant (One-Way ANOVA $F= 1.673$; $d.f.3$; $p=0.205$) (Fig 6.14). The onset of first foraging activity around the four study aspects matched both the activity phase (see Chapter 5) and sycamore bud development data, although no relationship existed between first foraging and temperature measured at the UCN weather station and the individual nests (section 6.3:1) (Table 6.12).

At the beginning of the season, *A. pseudoplatanus* was the favoured broad-leaved species, but attention on this species diminished during the rest of the year (Figs 6.15 to 6.18). However, the most prolific foraging occurred on plantation species, most notably *P. sylvestris* and *L. decidua*, which appeared to be a very important food resource through until the late summer and autumn. Where *B. pendula* was present it was used extensively, and together with *Q. robur*, became more significant as the season progressed. Peak foraging activity in north-west 2 was one month behind those colonies within the other three study aspects.

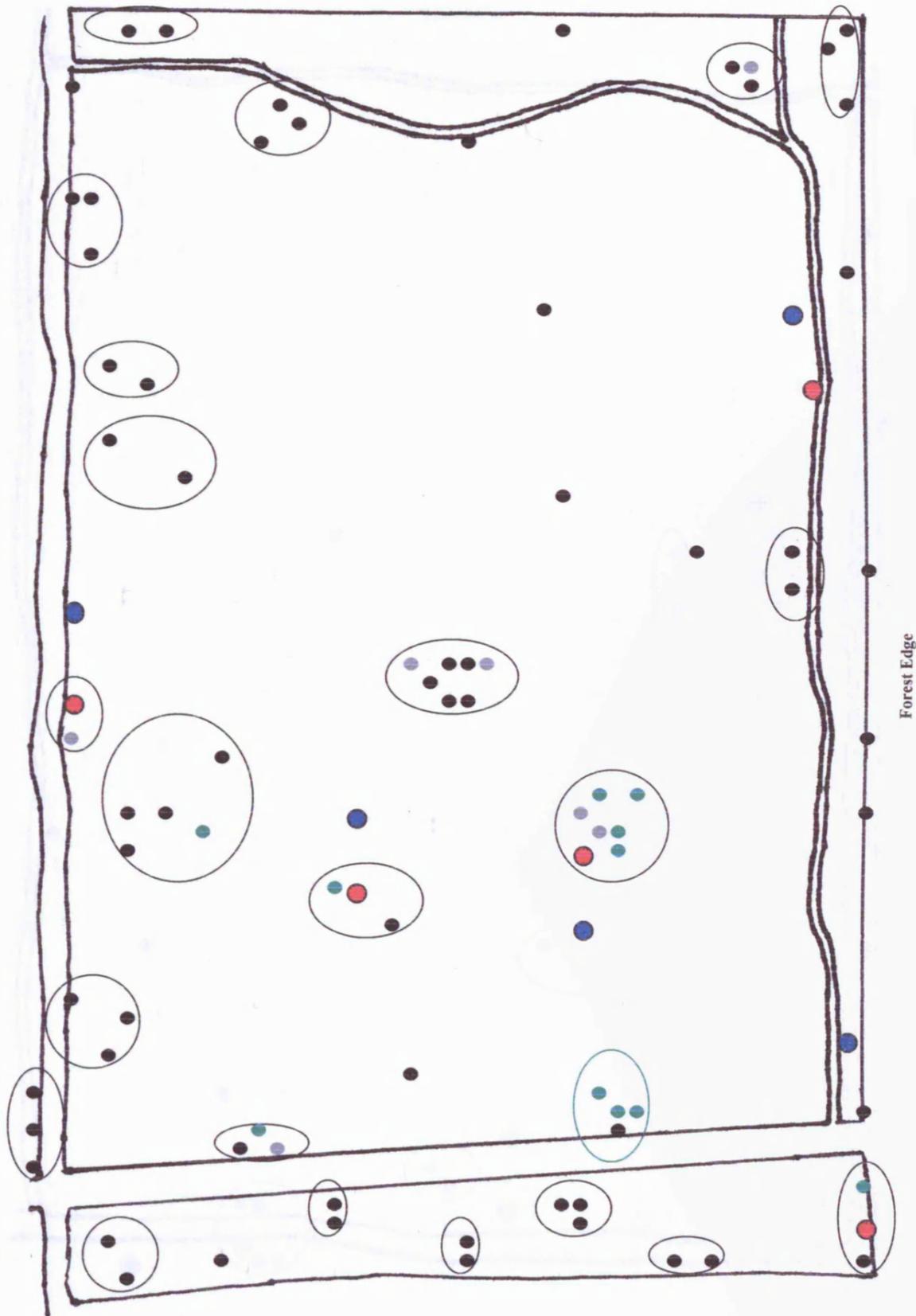


Figure 6.10: Approximate location of nests within the Southern site (Red - sample nests; Blue - controls; Green - permanent buds which developed in response to disturbance; Grey - nests from the original 2000 survey which were permanently abandoned; Rings indicate polydomous colonies). Measurements are accurate to ± 5 m

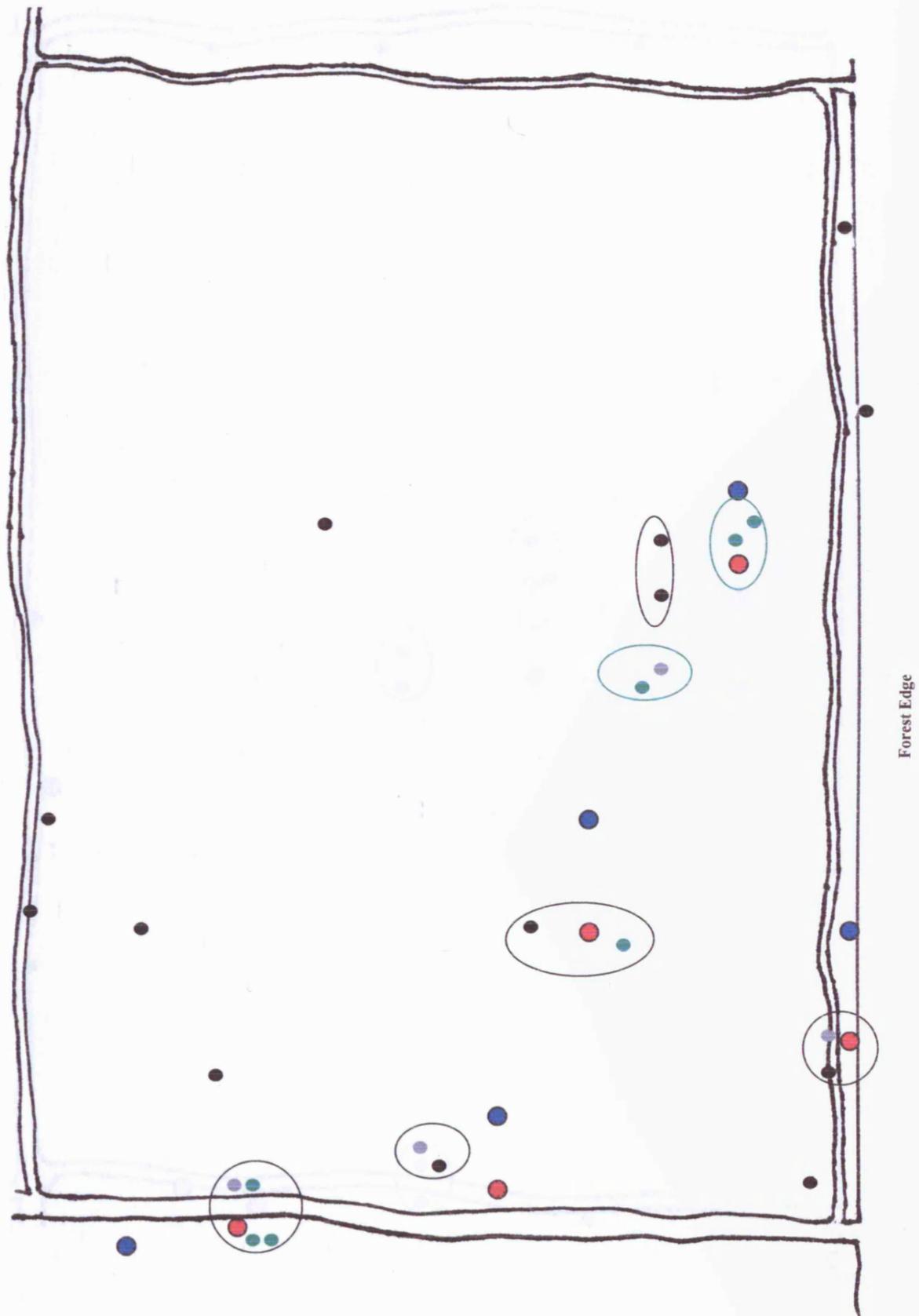


Figure 6.11: Approximate location of nests located within the North-Eastern site. (Red - sample nests; Blue – controls; Green – permanent buds which developed in response to disturbance; Grey – nests from the original 2000 survey which were permanently abandoned; Rings indicate polydomous colonies). Measurements accurate to ± 5 m

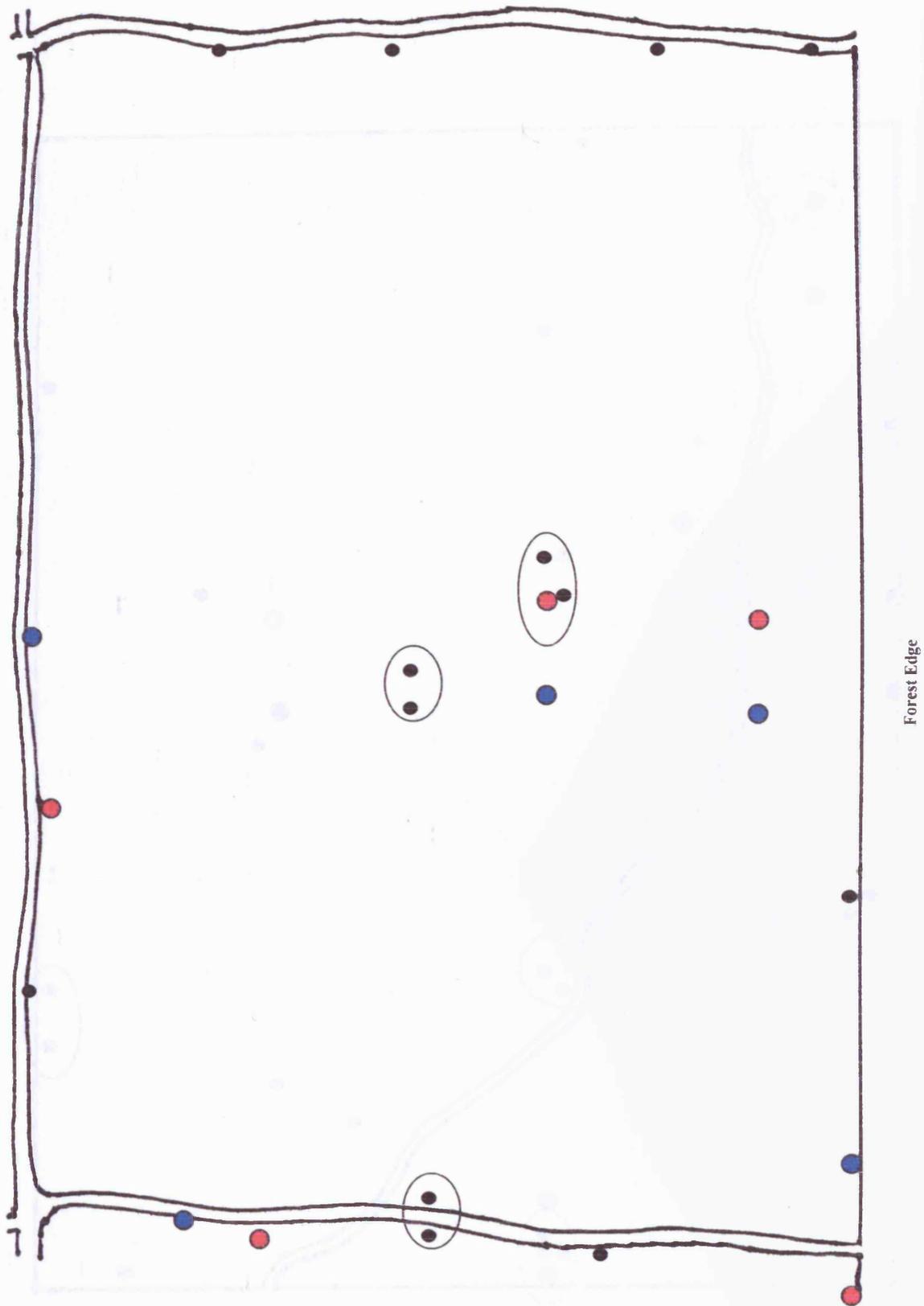


Figure 6.12: Approximate location of nests located within the North-West 1 site
 (Red – sample nests; Blue – controls; Rings indicate polydomous colonies)
 Measurements accurate to $\pm 5m$.

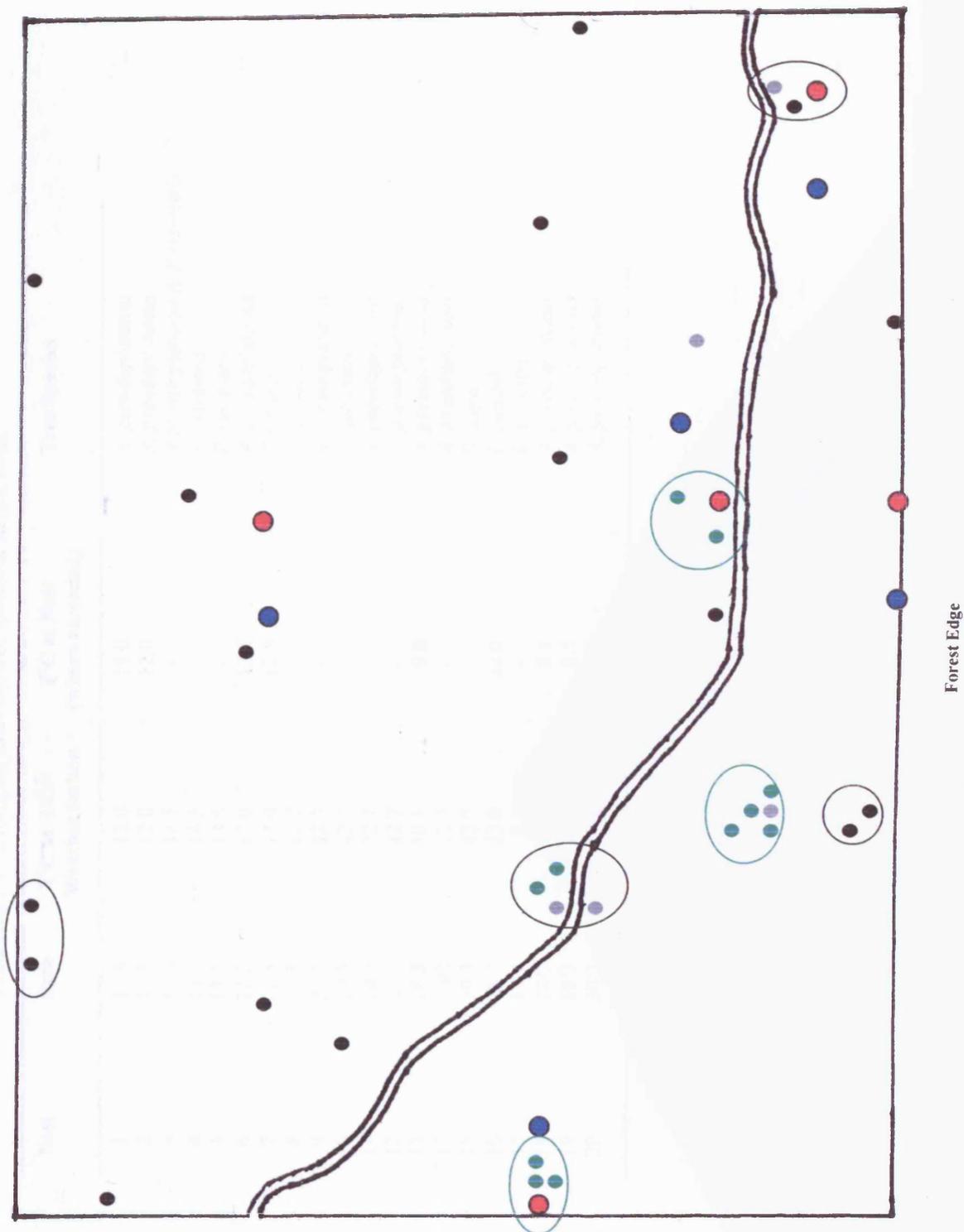


Figure 6.13: Approximate location of nests located within the North-West 2 site. (Red - sample nests; Blue - controls; Green - permanent buds which developed in response to disturbance; Grey - nests from the original 2000 survey which were permanently abandoned; Rings indicate polydomous colonies). Measurements accurate to $\pm 5m$.

Table 6.12 : First foraging dates and tree species at sample nests.

Nest	Date	T°C at UCN Weather station	T°C at Nest (where recorded)	Tree Species
1	11/3	12.0	14.0	<i>A. pseudoplatanus</i>
2	11/3	12.0	12.0	<i>A. pseudoplatanus</i>
3	13/3	14.5	-	<i>A. pseudoplatanus & P. sylvestris</i>
4	13/3	14.5	-	<i>P. sylvestris</i>
5	13/3	14.5	-	<i>P. sylvestris</i>
6	22/3	13.0	12.5	<i>A. pseudoplatanus</i>
7	22/3	13.0	12.5	<i>P. sylvestris</i>
8	20/3	12.7	-	<i>L. decidua</i>
9	20/3	12.7	-	<i>A. pseudoplatanus</i>
10	20/3	12.7	-	<i>P. sylvestris</i>
11	20/3	12.7	-	<i>A. pseudoplatanus</i>
12	20/3	12.7	-	<i>A. pseudoplatanus</i>
13	18/3	10.1	9.0	<i>A. pseudoplatanus</i>
14	20/3	12.7	-	<i>A. pseudoplatanus</i>
15	20/3	12.7	-	<i>S. nigra</i>
16	22/3	13.0	12.0	<i>B. pendula</i>
17	1/4	9.1	-	<i>P. sylvestris</i>
18	18/3	10.1	8.5	<i>A. pseudoplatanus</i>
19	18/3	10.1	8.5	<i>A. pseudoplatanus</i>
20	30/3	9.0	6.0	<i>A. pseudoplatanus</i>

Table 6.13 : Total number of foragers recorded on each tree.

Species	Total Foragers
<i>P. sylvestris</i>	9153
<i>B. pendula</i>	5082
<i>L. decidua</i>	4193
<i>Q. robur</i>	3112
<i>A. pseudoplatanus</i>	1734
<i>S. nigra</i>	1667
<i>P. abies</i>	1414

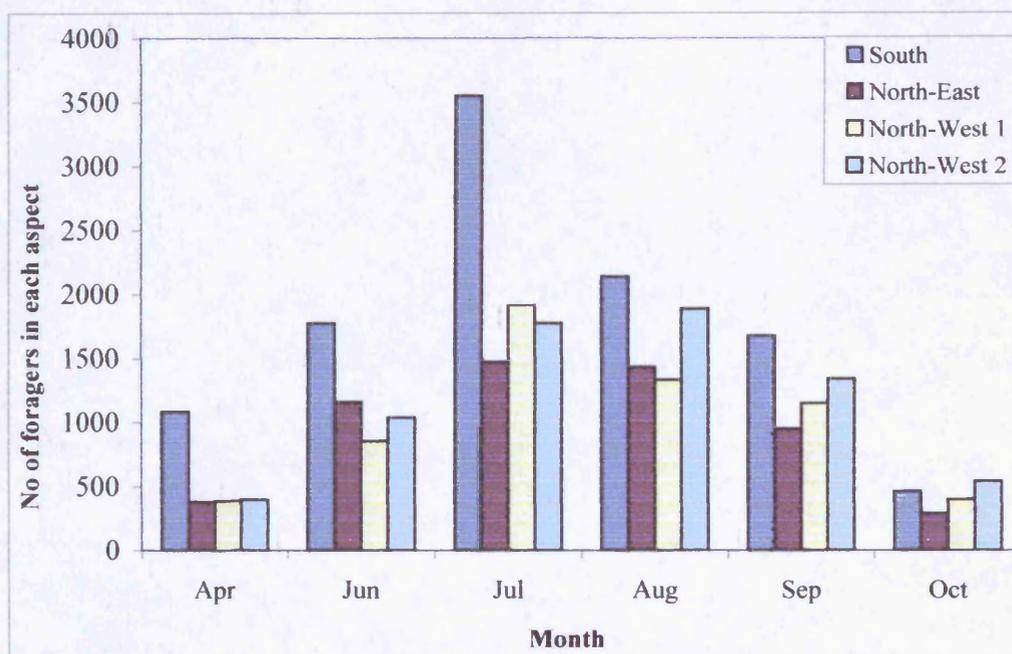


Figure 6.14: Total number foragers recorded on trees in each site through the year.

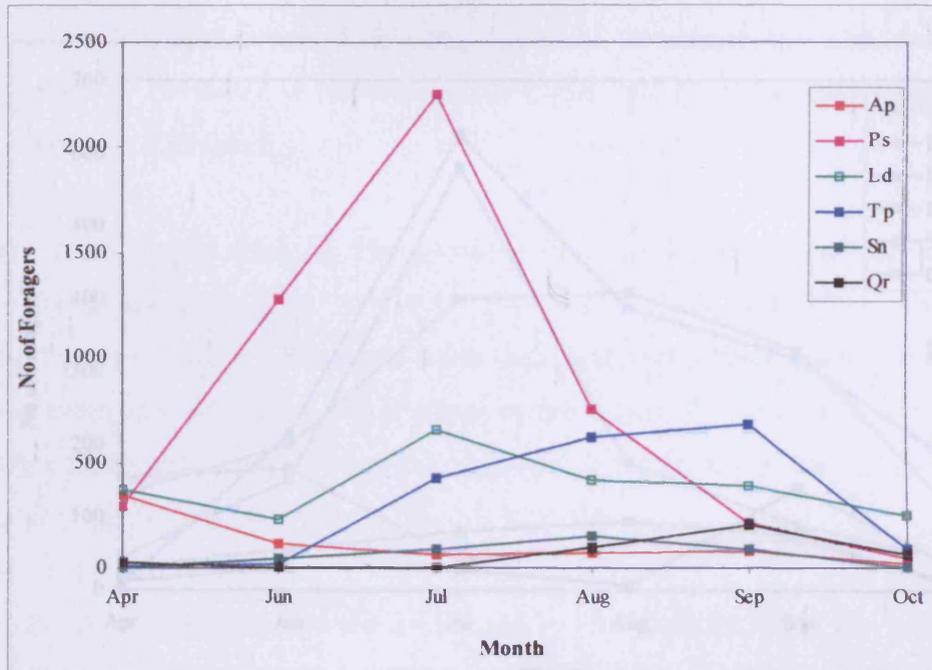


Figure 6.15: Mean number of foragers on each tree species through the year – South. *, **
 * Y-axis scale in the south do not correspond to the other sites to give better definition to the data.
 ** Error bars omitted for ease of visual presentation; see Appendix 5 for mean and 95% CI.

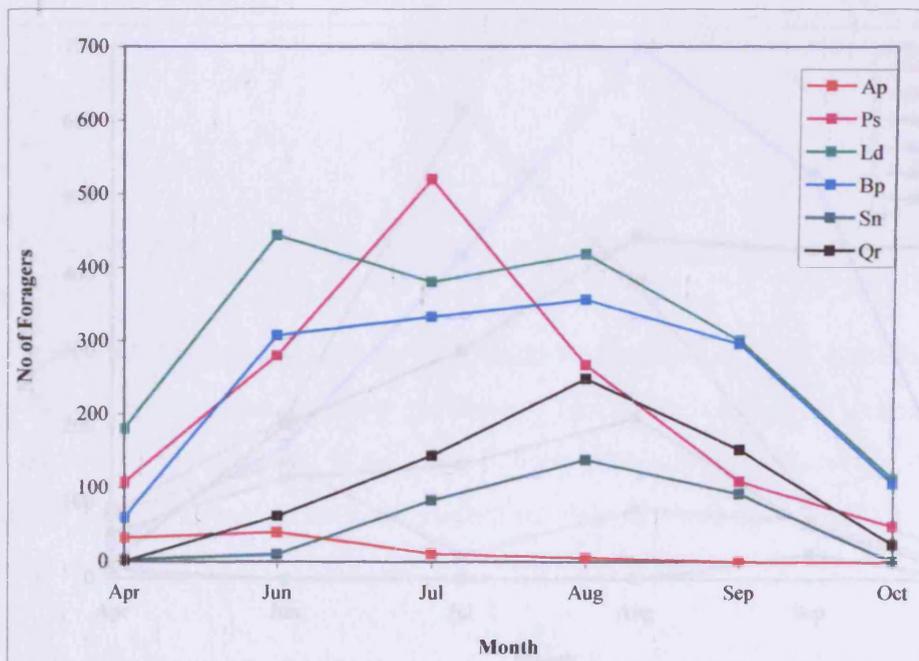


Figure 6.16: Mean number of foragers on each tree species through the year – North-East. *, **
 * Y-axis scale in the south do not correspond to the other sites to give better definition to the data.
 ** Error bars omitted for ease of visual presentation; see Appendix 5 for mean and 95% CI.

Key: Ap – *Acer pseudoplatanus*; Bp- *Betula pendula*; Ld - *Larix decidua* ; Ps – *Pinus sylvestris*; Qr – *Quercus robor*; Sn- *Sambucus nigra*; Tp – *Tilia platyphyllos*.

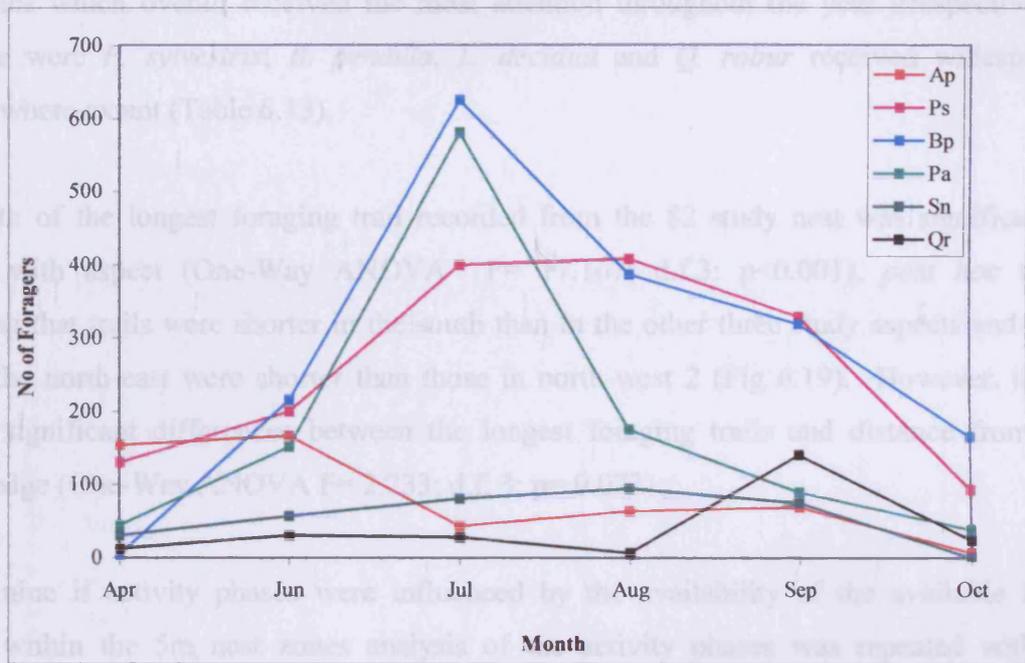


Figure 6.17: Mean number of foragers on each tree species through the year – North-West 1. *,**

* Y-axis scale in the south do not correspond to the other sites to give better definition to the data.

** Error bars omitted for ease of visual presentation; see Appendix 5 for mean and 95% CI.

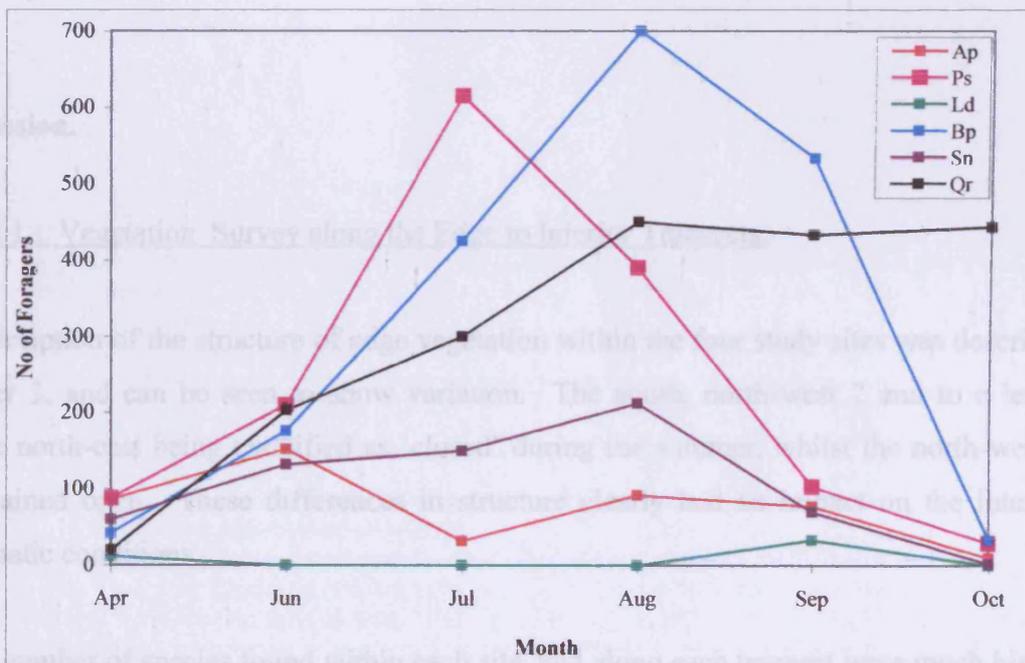


Figure 6.18: Mean number of foragers on each tree species through the year – North-West 2. *,**

* Y-axis scale in the south do not correspond to the other sites to give better definition to the data.

** Error bars omitted for ease of visual presentation; see Appendix 5 for mean and 95% CI.

Key: Ap – *Acer pseudoplatanus*; Bp- *Betula pendula*; Ld - *Larix decidua*; Ps – *Pinus sylvestris*; Qr – *Quercus robur*; Sn- *Sambucus nigra*.

The species which overall received the most attention throughout the year irrespective of study site were *P. sylvestris*; *B. pendula*, *L. decidua* and *Q. robur* received widespread attention where extant (Table 6.13).

The length of the longest foraging trail recorded from the 82 study nest was significantly different with aspect (One-Way ANOVA $F= 17.167$; d.f.3; $p<0.001$), *post hoc* tests confirming that trails were shorter in the south than in the other three study aspects and that trails in the north-east were shorter than those in north-west 2 (Fig 6.19). However, there were no significant differences between the longest foraging trails and distance from an external edge (One-Way ANOVA $F= 2.233$; d.f. 3; $p= 0.073$).

To determine if activity phases were influenced by the availability of the available food resource within the 5m nest zones analysis of the activity phases was repeated with *A. pseudoplatanus* and *S. nigra* acting as covariates. However, no significant relationships were identified and it is thus likely that activity patterns are directly influenced by aspect and distance related physical edge effects (Table 6.14).

6.4 Discussion.

6.4:1 Part 1 : Vegetation Survey along the Edge to Interior Transects.

A full description of the structure of edge vegetation within the four study sites was described in Chapter 3, and can be seen to show variation. The south, north-west 2 and to a lesser extent the north-east being classified as ‘closed’ during the summer, whilst the north-west 1 edge remained open. These differences in structure clearly had an impact on the internal microclimatic conditions.

The total number of species found within each site, and along each transect were much higher in the south and north-west 2. Significantly more species were found in the south than in the north-east and north-west 1, which given the southern microclimate, is no great surprise. The high number of species in north-west 2 is related to the age of the initial 30m of this part of the woodland. This initial zone is clearly much older than the remainder of the woodland, supporting many very old individual *Q. robur* and *F. excelsior* trees, and has therefore had more opportunity to accumulate species than the other aspects.

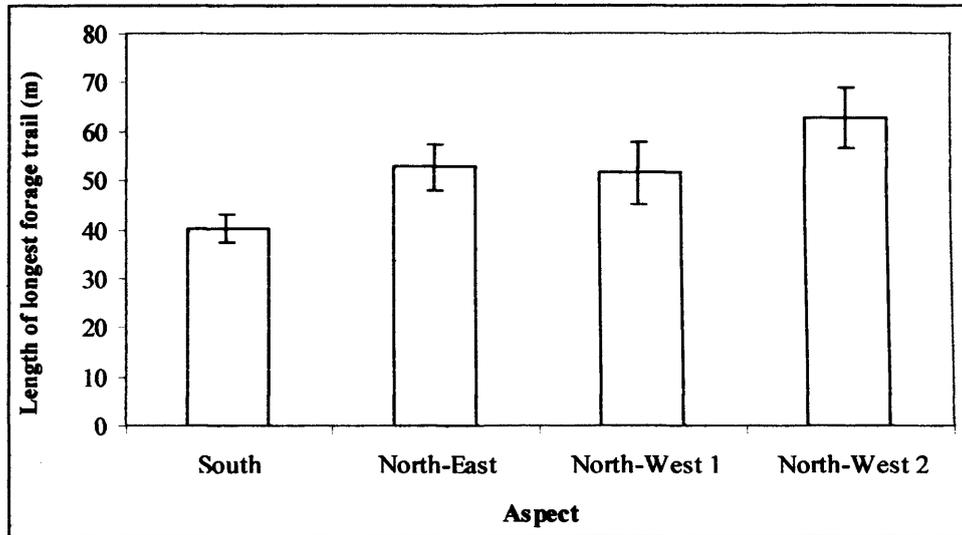


Figure 6.19: Mean distance of the longest foraging trails of study nests within the four sample aspects.

Table 6.14 : MANOVA Model results of *F. rufa* activity phases with *A. pseudoplatanus* and *S. nigra* as covariates.

	Activity Phase	F	p
Overall Model	First Activity 2000	4.706	0.114
	First Activity 2001	9.429	0.078
	First Mass 2000	1.669	0.375
	First Mass 2001	5.071	0.103
	First Alate Appearance 2000	2.251	0.275
	First Alate Appearance 2001	7.487	0.089
	Last Observed Activity 2000	1.078	0.550
	Last Observed Activity 2001	4.187	0.132

The mean number of species found along the individual transects generally fell with distance into the wood, the relationship being statistically significant (App 8.2). This is consistent with previous research, edges being found to support more species than the interior of a woodland and confirming yet again that both aspect and distance related edge effects are an active force within Harlestone Firs (Gysell 1951; Wales 1967; Matlack 1993, 1994; Fraver 1994; Camargo & Kapos 1995; Murcia 1995).

Analysis of the mean number of tree species within each site showed again that the south and north-west 2 supported the most species. However, significant differences did occur in the number of species found at each point along the transects, with the south supporting more species than the other sites (App 8.3). Again, these results are predictable given the character of the sites. In the south, it is evident that more successional development has taken place. Noticeably, where plantation trees have been removed they have not been replaced and the subsequent gaps have been colonised by deciduous tree species and shrubs. The greater light resource has apparently promoted this development, a factor also found by Matlack (1993). In contrast, the north-east is composed of established plantation, with limited deciduous development and in north-west 1, mature plantation dominates from about 60m into the site. In north-west 2, after the initial 30m characterised by a great diversity of species, mature extensive and uniform plantation, discourages the growth of deciduous species.

There were significantly more individual trees along the transects in the south than north-west 2 (App 8.4). The number of individuals remained fairly constant in the south, but fell with distance into the wood in the other aspects. Again, given the nature of the four aspects these results are quite predictable (see Chapter 4). The south again shows greater evidence of successional development in response to a more equitable microclimate. In north-west 2, although more species were found, the number of individuals were much lower, probably reflecting the greater age of the initial 30m. The lower numbers at 160m tend to support the general findings of Brothers & Spingarn (1992), Brothers (1993) and Fraver (1994), that fewer individuals are found within the woodland interior.

The results of analysis of the number of individuals with trunk circumferences >20m showed that the south had significantly more mature trees than the other aspects. However, there were no significant differences with distance along the transects. The results once more indicate that although more mature trees exist in the south, still greater successional development is occurring, and that this development is not limited to the edge (App 8.5). These results once more confirm the findings of previous research, confirming solar radiation

as the principle determinant of vegetational responses (Matlack 1993; Young & Mitchell 1994).

The number of species of ground flora found along the transects of the four sites followed a similar pattern to the tree species, the south and north-west 2 having the greater number. However, the number of species found within each sample point along the transects showed greater variation. The north-west 2 transects supported the greatest number of species over the first 40m, but numbers fell rapidly from this point until 160m. This is a direct result of the age of the initial part of the site. Beyond 40m the site was dominated by dense plantation and extensive stands of *Pteridium aquilinum*, reducing the available light dramatically, and therefore limiting the colonisation of species of ground flora.

In the south, although the number of species fell with distance along the transect, numbers remained very stable until 160m, where again, dense plantation became established. North-west 1 supported comparatively large numbers of species at the edge, but again, numbers fell sharply. This is probably due to the invasion of dense stands of *P. aquilinum* which dominate from 60m. From this point, quite dense plantation begins, effectively shading out the forest floor. In the north-east, numbers were the lowest, and ground flora was dominated by *P. aquilinum* and *Filicospoda* spp, which severely reduced the available light to the forest floor. The results are therefore entirely in keeping with the character of the sites, although in general, the number of species appears to be very low.

Species Associations

Comparing the species found along the transects of the four aspects confirms that the pattern of distribution and abundance varied around the wood (App 8.6). Species of ground flora common to all sites were either woodland specialist species, or in the case of *Rumex acetosella* and *R. obtusifolius*, species found on heaths or field edges (Rose 1981). Those species which were found only in the south were not normally associated with woodland habitats, and were most likely colonisers from the adjacent field which were able to survive at the very edge. The five species found only in the south, north-west 1 and north-west 2 were all associated with cultivation or disturbed ground. In all cases, these species were confined to the edge regions, confirming the ability of exotics to disperse into edge habitats reported by previous research (Brothers & Spingarn 1992; Brothers 1993; Matlack 1994; Murcia 1995).

In contrast, those species found only in north-west 2 were all associated with woodlands. In fact, three of the five (*Hyacinthoides non-scripta*, *Arum maculatum* and *Ranunculus ficaria*) were associated with well established woodland habitats. These results again, confirm that north-west 2 is the most established of the study aspects. The north-east had only a single unique species, *Mercurialis perennis*, which was found in limited areas along the boundary hedgerow. This boundary appears to date at least to the establishment of the woodland, the presence of several very old individual *Q. robur* suggesting that a boundary may have existed before that point. North-west 1 also had only a single unique species, *Rosa canina*, which again, occurred only in the boundary hedge.

Of the six species found only in the south and north-west 2, half were associated with woodland habitats (*Urtica dioica*, *Geum urbanum* and *Glechoma hederacea*), one with shady areas (*Geranium robertianum*), and two with bare and waste ground (*R. acetosella* and *Verbascum thapsus*). The results confirm the differences between the sites, for although these species were found only within the initial 40m in north-west 2, individuals were found at 160m in the south. As the south is free from dense plantation and receives much higher levels of solar radiation, a larger number of species can exist further inside this woodland compartment, once more confirming previous research (Murcia 1995).

The associations with tree species followed a noticeable pattern. In the south, with the exception of *Ulmus* spp., which were composed of young individuals found in two dense stands, deciduous species, such as *A. pseudoplatanus*, *Sambucus nigra* and *Tilia platyphyllus* were the most abundant. Three plantation species were found (*Pinus sylvestris*, *P. nigra* and *Larix decidua*). In the north-east, the deciduous species were dominated by *Q. robur* and *A. pseudoplatanus*. Two species were present in the north-east which were absent from the south, *Betula pendula* and *Sorbus aucuparia*. Conversely, several species found in the south were absent in the north-east (*Corylus avellana*, *Fraxinus excelsior*, *T. platyphyllus* and *Ulmus* spp).

In north-west 1, again *A. pseudoplatanus* dominated, but the majority were young saplings found close to the edge. Two species were found which did not occur elsewhere, *Castanea sativa* and *Ilex aquifolium*. The density of species, at least along the transects was low, and *Picea abies* dominated the plantation areas, casting a very heavy shade. In north-west 2, the pattern was very different. Here no species truly dominated, and the first 30m of the site had the greatest species richness. Species unique to north-west 2 were *Rhamnus cartharticus* and *Alnus glutinosa*, both of which were found in the damp edge region. It should be noted that

A. pseudoplatanus was least abundant in north-west 2. The plantation areas were dominated by *P. sylvestris* and *P. abies*, although *L. decidua* was found close to the edge.

Principal component analysis showed that the data points representing the southern and north-west 2 aspects were more similar to themselves than to the other study aspects. It would thus appear that these aspects have distinct species associations, confirming the earlier autecological descriptions. Analysis of the vegetation by distance along the transects did produce defined clusters and it is concluded that a relationship exists between species composition and distance. These differences in the plant communities between 0m and 20m and the woodland interior are simply linked to the presence of species such as, *Rhamnus cartharticus*, *Alnus glutinosa*, *Ulmus* spp, and the invasive plants which have colonised the edge zones. This is typical of the results of many previous edge effect studies around the world (Brothers & Spingarn 1992; Brothers 1993; Matlack 1994; Murcia 1995).

To summarise, whether the microclimates of the four aspects were influenced entirely by physical edge effects is unlikely, as clearly the mediating effects of the vegetation is playing an important role. It is thus concluded that differences between the aspects are related to species composition and to the physical characteristics of the sites, such as topography, but that edge aspect appears to be the most important factor contributing to the severity of edge effects within each aspect.

6.4:2 Part 2: The Relationship between the Vegetation at Nest and Control Points.

There were some differences in vegetation between the nest and control zones. Nests supported more species overall, more species of tree, and more individual trees with trunk circumferences >20cm. It is thus likely that colonies are selecting nest sites on the basis of foraging requirements, as well as on microclimate. However, although nests supported significantly more species of ground flora than control zones, no firm relationships appeared to exist. The greater number of ground flora species on and around nests is probably related to the wood ants' habit of carrying seeds back to the nests, and because the nutrient content of nests tends to be greater than the surrounding forest soils (Gorb & Gorb 1995, 1999, 2000; Gorb *et al.* 1997; Laakso & Setala 1998; Laakso 1999; Lenoir *et al.* 1999; Lenoir *et al.* 2001). Otherwise, species richness was found to decrease with distance into the wood, meaning that the potential food resources for colonies located further back from an edge were fewer (perhaps significant given the phenological data).

Only two species of tree had a statistically significant relationship with nests, *A. pseudoplatanus* and *S. nigra*. The relationship with *A. pseudoplatanus* was also confirmed in north-west England, where all study colonies were situated within 5m of this species (Skinner 1976, 1980a&b; Skinner & Whittaker 1981; Warrington & Whittaker 1985 a&b). *A. pseudoplatanus* is the first species each year to receive widespread foraging attention around Harlestone Firs, highlighting the importance of this species to the early season nutrient status of colonies.

That there were no distinct differences in the tree species composition between the nests and control zones is no great surprise and is probably a reflection of the small sample size. Clearly, some differences in species exist between the two but the abundance of certain species, such as *P. sylvestris*, *L. deciduas* and *P. abies* probably help to make the analysis less 'sensitive'. Analysis by nest zone only showed that the southern nest zones may possess a slightly different tree species composition. This is most certainly due to the greater abundance of *A. pseudoplatanus*, *S. nigra*, *T. platyphyllos* and *F. excelsior* and the absence or distinct reduction of species such as *P. abies*, *B. pendula* and *C. sativa* in the south.

It should also be noted that all southern and north-west 1 nests, but only three north-eastern and two north-west 2 nests were located within 5m of this species. However, whether this relationship is due to the greater abundance of *A. pseudoplatanus* within particular sites, or is a definite choice on the part of the *F. rufa* colonies is difficult to assess. However, certainly those colonies which are adjacent to this food resource appear to have some benefit. The relationship with *S. nigra* was also noted by Skinner (1976), but has received less attention elsewhere. Again, this species was present within in the 5m zone of 66% of nests and certainly appeared to be used extensively by the ants for foraging.

6.4:3 Part 3: Comparison of tree species between nests within the four study aspects.

The pattern of abundance and the number of trees found within the original 20 study nests was for the most part maintained in 62 additional nests within the four study aspects. For example, the distribution of species such as, *A. pseudoplatanus*, *T. platyphyllos*, *B. pendula*, *C. sativa*, *I. aquifolium*, and *P. abies* with the study aspects was the same. This confirms that the original sample nests are representative of nests within Harlestone Firs as a whole, lending credence to the conclusion that colonies are selecting nest sites initially on suitable microclimate and then by proximity to food resources. This is confirmed by the aspect driven data, where the southern nests in receipt of a more equitable microclimate are showing a

preference for nest sites situated close to *A. pseudoplatanus* and *P. sylvestris* which both provide valuable food reserves early in the year.

The distance from nests to the nearest tree (which in all cases was used for foraging) confirms the advantage that southern colonies possess over their more northerly counterparts. Nests in the south were significantly closer to trees than nests in the other three aspects. This trend once again confirms that with the benefit of a more suitable microclimate in relation to edge aspect, colonies are able to locate nests in positions which make foraging more efficient.

The apparent preference of certain trees for proximity to particular habitats in this study may be misleading. Certainly, the location of *C. monogyna* and *P. sylvestris* have an anthropogenic origin, the former planted as boundary hedges and the latter planted as a plantation species. However, the preference of *C. sativa* for internal edges may be of greater significance. The data here corresponds to this species' location within the north-west 1 aspect. Mature trees have shown evidence of having been planted, apparently to act as companion trees during the early plantation phase. Nevertheless, *C. sativa* has shown extensive regeneration in the regions close to a major forest ride which receives large amounts of sunshine from the south-west. In this warmer climate, *C. sativa* saplings are found in very high densities, showing evidence of extensive vegetative budding from the original colonisers. As *C. sativa* is an introduced species from more southerly areas of Europe this regeneration may well have occurred in this single area as a result of the more favourable microclimatic conditions and therefore can be linked to the influence of edge effects (Rackham 1986, 1990)

6.4.4 Nest Persistence and Colony Structure.

As the south is characterised by favourable ecological conditions and general stability, it would certainly appear to support the conclusions of previous research, that existing colonies have spread into available territories by budding (Fortelius *et al.* 1990). Here, nest buds have probably become functional nests, with colonies adopting queens and have therefore grown via secondary polygyny (Pamilo & Rosengren 1983, 1984). This strategy has been shown to develop in colonies of the *F. rufa* group living in favourable habitat patches across Europe, where single colonies can monopolise large areas of the local food resource (Puntilla 1996; Goropashnaya *et al.* 2001). For this reason, although the exact number of queens per colony could not be directly established, it is strongly suspected that each nest and 'bud' within the polydomous colonies have at least one functional queen.

Polydomous colonies in the other sites were far less common, but in every case, were located in warmer areas within each study site which were also close to several species of different tree which the workers used whilst foraging throughout the year. Again, it would appear that both microclimate and food resource are acting as a trigger for colonies to move towards polydomy. Although the number of queens within each of these colonies is not known, it is suspected that a move towards secondary polygyny began following the pattern described by Pamilo & Rosengren (1984) (See Chapter 6).

The persistence of nests during the study period showed great stability. Only twelve of the original survey nests were abandoned over the two year period, all but one from a polydomous colony. The monodomous nest in the north-west 2 which was lost represented a very small colony inhabiting an area of dense plantation. The loss of the colony may have been due to the unsuitable microclimate, or more likely, due to competition with the expanding polydomous colony of study Nest 18, which took over the former colony's forage trees (Elton 1932b; Skinner 1976).

In contrast, a total of twenty-nine 'buds' were produced during 2001 which were still active at the beginning of 2002. The proliferation of nests in 2001 was most certainly a response to forest management activities, and supports the findings of Czechowski (1975) and Vepsäläinen & Wuorenrinne (1978). Clearly, the colonies first response to severe disturbance was to 'throw out' numerous buds in an effort to ensure its long term survival. All but one study nest survived the duration of the study period, several showing signs of having occupied the same site for many years, which is consistent with the observations of many other researchers (Dreyer 1942; Haviland 1948; Imms 1947; King & Salee 1953; Klimetzek 1981). The sample nest which was abandoned, Nest 7, suffered severe damage when the tree around which it was built was removed. The colony attempted to rebuild the original nest, but as predicted, immediately produced numerous buds. In 2002, the colony eventually abandoned the original nest and moved to a new location 15m to the north, into a newly created gap with access to abundant sunlight.

6.4:5 Foraging Activity by Study Colonies within the Four Study Sites.

Foraging activity in the south was much more pronounced than in the other sites. This was probably a response of southern colonies to the more favourable ecological conditions,

colonies being able to grow much larger due to the abundant food resource and stable microclimate.

The first broad-leaved tree species to receive widespread foraging attention was *A. pseudoplatanus*. Unfortunately, foraging on this species was under recorded, as March and May were omitted from the survey. However, *A. pseudoplatanus* received the most attention of the broad leaved species in April in all but the north-eastern aspect. The fact that this species was one of only two which had a statistically significant relationship with proximity to nests, certainly reflects the importance placed upon *A. pseudoplatanus* by the colonies at the beginning of the season. The significance of this relationship was initially highlighted by Skinner (1976), working in north-west England, who identified that the mutualistic relationship between *F. rufa* and the aphid, *Periphyllus testudinaceus* was largely responsible for this pattern of foraging. It appears that in Harlestone Firs, close proximity to this tree at the beginning of the season provides access to a valuable high quality food resource, at a time when foragers are not able to travel great distances due to the lower early season air temperatures. The fact that such a high proportion of nests are located close to this species confirms this point.

Nevertheless, it is also clear that plantation species make an invaluable contribution to the wood ant colonies. *P. sylvestris* was by far the most foraged tree over the entire year, its peak utilisation being in July (July and August in north-west 1). This mid season relationship was identified by Skinner (1976, 1980b) and by Breen (1979a), the latter working on *F. lugubris* in Ireland. In addition to insect prey, the tended aphids of the genus *Cinera* provided massive amounts of honeydew to the local colonies.

B. pendula was the most extensively used broad-leaved species throughout the year, the ants using this species from June onwards. This relationship with *Betula* spp. was also identified by Sudd *et al.* (1977), Douglas & Sudd (1978), Fowler & McGarvin (1985) and Mahdi & Whittaker (1993). However, as the summer progressed, it became evident that the pattern of foraging preference had once again shifted, on this occasion to *Q. robur*. In all cases, in the latter stages of the season foragers travelled over large distances to this species, a habit especially noticeable in north-west 2. Many studies have identified a preference for *Quercus* spp. with their associated *Lachnus* sp. aphids, in addition to the normal abundance of insect prey which this tree supports (Skinner 1976; Welch 1978; Adams 1991; Cook 1998).

S. nigra, the other species with which nests had a statistically significant affinity, was also heavily used by *F. rufa* during the summer months, but unfortunately the method of recording activity did not show this relationship very well, due to the small size of the trunk. It should be noted that the leaves and branches of this species at times appeared to 'drip' with ants, as large numbers of workers clustered over the extensive groups of the aphid, *Aphis sambuci*. This attention, although reaching its height during the summer, was constant throughout the year.

A definite 'sequence of utilisation' of species through the year was found by Skinner (1976, 1980b), who showed that the ants focused first on *A. pseudoplatanus*, then *P. sylvestris* and finally *Q. robur*. In Ireland, Breen (1979a) did not report any particular sequence, and concluded that *P. sylvestris* was the most important species throughout the year. In this study, although Skinner's (1976) sequence appears to be in operation within Harlestone Firs also, the colonies were clearly taking advantage of insect prey and tended aphids as they became available, confirming their 'generalist' strategy (Brian 1977; Wells *et al.* 1983; Collins & Wells 1987; Fowles 1994; Skinner 1998). However, the greater density of *A. pseudoplatanus* in the south, clearly provides these colonies with an early season advantage over colonies in other sites, which they appear to maintain throughout the year.

The onset of foraging activity around the wood appears to be related to the response of the tree species in relation to the increasing light and temperatures of early spring. This is particularly true of *A. pseudoplatanus*, which along with *P. sylvestris* were the first trees on which foraging was observed. The aphid, *P. testudinaceous*, over-winters within the developing *A. pseudoplatanus* buds, and as soon as the tree begins to respond to the new season and mobilises rich phloem sap from its reserves, it leaves its shelter and begins to feed. It therefore appears that the aphid itself is not influenced directly by the climatic temperature, but rather by the response of the tree. Therefore, it is of no surprise that for the most part, first foraging dates correspond to the development of *A. pseudoplatanus* buds around the wood in response to both aspect and (to a lesser extent) distance. For those nests where the first foraging was observed on *P. sylvestris*, the situation is more complex, but is probably influenced by the same processes; higher spring temperatures and greater light increasing photosynthetic activity and the mobilisation of a more nutritional sap around the tree. In summary, first foraging dates are both directly and indirectly related to aspect and distance related edge effects.

The length of the longest foraging trails showed that the southern nests foraged over significantly shorter distances than colonies in the other three aspects. This is directly linked to the more favourable microclimatic conditions in the south, which allow colonies to select nest locations which are adjacent to the most valuable food resources. These length of forage trails are undoubtedly related to the density of nests, which would quite naturally result in smaller territories, but the differences in colony structure is playing an important role. As colonies have expanded and produced bud or satellite nests so as to monopolise large expanses of the available food reserves, the distance of the longest foraging trails has automatically decreased. From the view of the individual colonies, shorter foraging trails enables the overall territory to be defended more efficiently and thus reduces the direct competition and conflict with neighbouring conspecific colonies.

However, in the more northerly areas, where nest location is determined by the availability of a suitable microclimate, colonies must be prepared to forage over longer distances to obtain the food reserves that they require. Consequently, nest density will be lower and the number of colonies will in turn be reduced. Here, unless food reserves are concentrated, the development of large polydomous colonies is unlikely to occur, as satellites would be too far away to remain efficiently socially connected. Therefore, the overall length of foraging trails is likely to increase considerably.

This pattern appears to be occurring here and is confirmed by the fact that trails were significantly longer in north-west 2 than in the north-east. In the north-east, the microclimate is more favourable, nests are also closer to the nearest tree and there are a greater percentage of polydomous colonies. The higher incidence of *Q. robur* is also important. In the north-east, when foraging preference switches to *Q. robur*, colonies here have a distinct advantage as this species is more abundant than in north-west 2. In north-west 2, the distance to the nearest tree was the longest of the four aspects, the percentage of polydomous colonies was the lowest, the length of the longest foraging trail was the longest. In fact, in every case, the longest foraging trails in north-west 2 were all measured to *Q. robur*.

Finally, the retarded response to the least favourable microclimate in north-west 2 is further confirmed by the foraging activity throughout the year. In the south, north-east and north-west 1, peak foraging occurred in July. However, in accordance with the fact that colonies left hibernation, began foraging, began their reproductive cycle later and entered hibernation earlier, the peak foraging activity in north-west 2 was one month behind. This combined data confirms that although distance from external edges do have an important influence on *F. rufa*

colonies in Harlestone Firs, that it is edge aspect that is playing by far the most influential role.

6.5 Conclusion.

Overall, vegetation showed important differences around Harlestone Firs. The south and north-west 2 aspects supported more species than either the north-east or north-west 1. There were also significantly more species along the edge to interior transects in the south than in the north-east or north-west 1, but in all aspects, the reduction in the total number of species with distance along the transects was significant between 0m and 80 to 160m. The south supported significantly more tree species per sample point and along the transects than all other aspects. It also supported significantly more species of trees with trunk circumferences >20cm than the other aspects. The number of tree species decreased with distance into the wood, except in the south where a slight increase occurred. Species composition appeared to be different between the south and north-west 2, and between them and the north-east and north-west 1. The only specific associations between vegetation and nest sites is with the trees, *A. pseudoplatanus* and *S. nigra*, both more abundant in the south. It would thus appear that both edge aspect and distance related edge effects are in operation within the four study aspects.

The social structure of colonies showed variation around the wood, the favourable ecological conditions giving rise to a higher percentage of polydomous, and possibly polygynous colonies in the south. It is suggested that the earlier flight times and consequent 'temporal' isolation from colonies in areas to the north, may also have contributed to the development of polydomy.

Colonies tended to follow a predictable foraging sequence through the year, *A. pseudoplatanus* being utilised at the start of the season, *P. sylvestris* during the summer, and finally *Q. robur* from late summer until the end of the active season. However, the colonies also took advantage of insect prey and tended aphids on other species as they became available through the year. Although both *P. sylvestris* and *B. pendula* received the most foraging attention throughout the year, *A. pseudoplatanus* appeared to be very important for colonies, being the only tree which had a statistically significant relationship with nest mounds. The greater density of *A. pseudoplatanus* in the south, appeared to provide colonies with an early season advantage over colonies in other sites, which they appeared to maintain throughout the year.

Finally, the distance to the nearest tree and the length of the longest foraging trails from nests showed that the southern nests were significantly closer and that colonies foraged over shorter distances than those in the other aspects. Corresponding well with the microclimate data, north-west 2 nests were further from the nearest tree, had the longest foraging trails and had the lowest incidence of polydomous colonies. It is thus concluded that *F. rufa* appeared to be selecting nest sites firstly on the basis of a favourable microclimate and then with proximity to particular species of aphid supporting trees. These results again confirm that although distance and aspect related edge effects are in operation, aspect related edge effects have a profound impact on colonies living in Harlestone Firs.

Chapter 7:

General Discussion.

7.1 Introduction.

The impact of both aspect and distance related forest edge effects on ants in temperate regions has yet to receive any great attention. In the context of conservation efforts for species confined to isolated woodland fragments, this is a situation which requires greater research effort. Although *F. rufa* is not threatened nationally, it has been lost from many of its previous strongholds. Therefore efforts to conserve this species in its current habitats, and to attempt reintroductions to new sites, will require the development of coherent conservation strategies (Skinner & Allen 1996; Skinner 1998; Warwickshire County Council 2003). Thus the aim of this chapter is to revisit the initial research questions posed in the aims and objectives of this thesis, and to address some of the key conservation issues which impact upon the wood ant, *Formica rufa* L.

7.2 Outcomes of the Aims and Objectives of the Thesis.

7.2:1 The Extent of Physical Edge Effects within the Four Study Aspects.

The initial thrust of the study was to determine the extent of any physical edge effects within the four chosen study aspects around Harlestone Firs. Analysis over two years highlighted that physical edge effects played a significant role in moderating microclimate around the woodland (Figure 7.1). Firstly, wind speed was significantly higher in north-west 1, where the open structure of the edge itself allowed higher wind velocities to penetrate deep into the sampling area. In contrast, winds were lightest in the south, where due to the more sheltered nature of the immediate landscape and the closed edge structure, winds could not easily penetrate into the wood following canopy closure. Light intensity was also significantly different, with the southern site recording the highest values at the beginning and end of the sampling period. It is concluded that edge aspect is the most important physical factor determining the severity of edge effects in a particular sampling location. These results are entirely consistent with the findings of previous studies (Matlack 1993, 1994; Young & Mitchell 1994; Murcia 1995; Chen *et al.* 1995).

North-West 2 Aspect

Closed edge.
Least internal edges.
Lowest edge light values at start and end of year.
Initial 20m highest soil moisture.
Edge region older containing ancient woodland indicators, higher species diversity and most mature trees (*Quercus*).
Alnus found only close to the edge in this aspect.
Acer pseudoplatanus occur in lowest numbers.
Rhamnus carharticus most numerous broadleaf.
Pinus sylvestris dominant plantation sp.
Nests furthest away from internal edges.
Highest percentage of monodomous colonies
Longest foraging trails.
Height of foraging activity retarded by one month.

North-West 1 Aspect

Open Edge – wind penetration 40m
Highest wind speeds – lowest humidity values
Lowest number of nests and colonies.
Mostly monodomous colonies.
Lowest average nest heights.
Castanea sativa dominant broadleaf.
Picea abies dominant plantation sp.



South-East Aspect

Closed edge.
Highest average light intensity, temperature and humidity values.
Lowest wind speed.
Statistically the highest diversity of plant species.
Highest diversity of trees with trunk circumference >20cm in transect sample points.
Ulmus spp and *Acer pseudoplatanus* most numerous broadleaf spp.
Pinus sylvestris most common plantation sp.
Acer pseudoplatanus bud development advanced earlier.
Nests on average higher temperatures, light intensity & humidity values.
Nest received lowest wind speeds.
Highest number of nest, colonies and nest densities.
Characterised by higher percentage of polydomous colonies.
Nests face closer to south than NW1 and NW2 nests
Nests closest to trees – shortest foraging trails.
Nest statistically taller.
Ants leave hibernation earliest – active season longest.
Begin 'spring mass' earliest.
Alates appeared first on southern nests.
Nuptial flights occur earlier and colonies are reproductively isolated from those in the other aspects.
First foraging activity occurs earlier.

North-East Aspect

Partly closed edge.
Ancient boundary hedgerow with *Mecurialis. perennis*.
Quercus robur dominant broadleaf.
Larix decidua dominant plantation sp.
Nests face closer to south than NW nests.
Mostly monodomous colonies.



Figure 7.1: Summary of the characteristics of the four aspects from the results of the thesis.

The results of the soil analysis around the four study aspects showed that soil moisture was significantly higher in north-west 2 than in the south or north-west 1 in 2000 and significantly higher than all other aspects in March. This is simply linked to the topography of the site which lies at the bottom of a small but steep valley, and to the presence of a small stream which flows along the edge. Moisture moving down-slope from either side of the edge is thus responsible for elevating soil moisture in the initial 30m of this study aspect, which is especially noticeable during the early sampling period after the damp winter months. As soon as warmer, drier conditions arrive and the moisture drains away, the significant differences between aspects are reduced.

No significant differences were found in soil pH in the four aspects, but values were higher in the edge regions of north-west 2. This is probably due to the presence of greater amounts of organic matter/debris from the broadleaf species which proliferate in this region which rapidly decomposes due to the more moist conditions. Otherwise the chemical composition of soils around the four study aspects remained very similar.

Edge Width along the Transects around the Four Study Aspects.

Light intensity and wind speed showed significant differences between edge and interior in all Periods of both years. In addition, temperature was also significantly different in Period 4 of 2001. The light intensity and wind speed data follow the expected trend which had been identified in many previous temperate region edge effect studies (Matlack 1993; Murcia 1995).

The actual area influenced by these distance related edge effects did show variation depending upon the time of year and the impact of minor forest management activities in April 2001. In the south, north-east and north-west 1 in both years light intensity, for the most part, remained stable from 10-20m inside the edge. The exception was the notable 'peaks' in the south in 2001, between 40-80m were due to the thinning of the crown canopy during management operations. North-west 2 showed the greatest variation, with edge width moving between 10 and 80m in both years. Although some variation in 2001 was due to forest management, it is likely that topography and crown and side canopy development were responsible for the fluctuations in north-west 2.

Edge width in relation to wind speed showed reasonably stable patterns in the south, north-east and north-west 2, with any fluctuations related to the prevalent weather systems, the

development of the side canopy or minor forest management. The greatest wind penetration occurred in north-west 1 where the edge effect extended consistently to at least 40m inside the edge.

The significant distance relationship in the temperature profiles in Period 4 of 2001 was probably related to the particularly warm spell of weather, allowing warm exterior air to penetrate inside the edge to produce an enhanced temperature gradient across the forest edges. Clearly, distance related edge effects were in operation during both years in Harlestone Firs.

7.2:2 Differences in Vegetation in Response to Edge Effects.

Vegetation within the four study aspects was influenced by both aspect and distance related edge effects. Edge structure varied around the four aspects, the southern and north-west 2 edges being classified as 'closed', the north-eastern edge as 'partly closed' whilst the north-west 1 edge remained 'open'. The southern edge, in receipt of the highest solar input, supported a dense growth of understorey, mid-canopy and canopy trees, the adventitious limbs of which sealed the edge by way of a side canopy. The north-west 2 edge was characterised by mature trees whose adventitious limbs reached far out into the adjacent field. A remnant boundary hedge and invasive shrubs sealed the edge down to the ground. The north-eastern boundary again supported numerous mature trees whose limbs sealed the upper part of the side canopy. The mature boundary hedge sealed the mid-canopy but offered little protection at ground level, hence the classification of 'partly closed'. The north-west 1 edge remained open, with the limited edge trees producing fewer adventitious limbs and limited shrub development. Trees were much more likely to produce limbs reaching back into the wood than out towards the edge. Whether this was a response to lower available light or due to effects of high winds striking an abrupt edge is difficult to determine, but does confirm that edge aspect was the principal factor driving edge effects (Sigmon *et al.* 1984; Matlack 1993).

The total number of plant species found within the southern and north-west 2 sample aspects were higher than within the north-east or north-west 1. The southern diversity is in response to higher temperatures and light availability. The north-west 2 diversity is likely to have been a response to the age of the edge, evidence suggesting that woodland boundary, the edge of which follows the line of the small stream, existed in the initial 30m of the site many years before large scale afforestation in the rest of Harlestone Firs in around 1850AD (Laundon 1964; Hillsden 1975). This area supports a ground flora more indicative of mature woodland, but has gained arable and early successional species over the years. The north-east

and north-west 1 supported the fewest species, with a much greater density of *Pteridium aquilinum* shading the ground. Similar to many previous studies, edge regions of all aspects contained more species than the interior, supporting the view that both aspect and distance related edge effects influenced the vegetation structure within Harlestone Firs (Gysell 1951; Wales 1967; Matlack 1993, 1994; Fraver 1994; Camargo & Kapos 1995; Murcia 1995).

The southern and north-west 2 sample aspects again supported more tree species than the north-east and north-west 1. However, the south supported significantly more species at each individual distance along the transects than the corresponding distances within the other aspects. The south also supported significantly more individual trees than the other aspects, probably confirming that the more favourable microclimate in the south has led to greater successional development. North-west 2 again, supported a diverse mix of trees within the initial 30m of the edge probably due to its age, but diversity fell rapidly after 40m, where mature plantation and dense *P. aquilinum* were dominant. In the north-east and north-west 1, mature plantation and dense stands of *P. aquilinum* again limited the light resource reaching the ground and appear to have hindered widespread successional development. The results are consistent with previous studies, confirming the role of both aspect and distance related edge effects in influencing edge vegetation (Matlack 1993; Fraver 1994; Young & Mitchell 1994).

7.2:3 The Influence of Edge Effects on *F. rufa* Nest Location.

Nest Location and Microclimate.

The results confirmed that microclimate dictated nest location in *F. rufa* colonies within the four study aspects. Nest locations were selected so as to ensure that direct sunlight could penetrate to the nest surface and in areas which appeared to offer shelter from high winds. These results are not unexpected and reflect the findings of a large body of research spanning the last 150 years (Forel 1874, 1920; McCook 1877; Andrews 1926, 1927; Elton 1932b; Dreyer 1932; Weber 1935; Scherba 1958, 1959, 1962; Kneitz 1964; Adlung 1966; Finnegan 1975; Skinner 1976, 1987, 1998; Douglass & Sudd 1977; Breen 1979b; Brandt 1980; Coenen-Stass *et al.* 1980; Rosengren *et al.* 1987; Adams 1991; Fowles 1994; North 1996; Pontin 1996; Cook 1998; Robinson 2001).

However, the results of this study show that higher light levels are particularly important during the initial period of colony activity. This situation is consistent with the ecological

strategy of *F. rufa* group species, which are dependent upon elevating internal nest temperatures well above ambient early in the season to facilitate the development of the season's brood, and to ensure that the reproductive period can begin as early as possible (Hölldobler & Wilson 1990; Heinze & Hölldobler 1996). From the point when brood development is well underway and large scale foraging activity has begun (normally well before canopy closure or the development of dense *P. aquilinum* stands which shade nests), the light resource has already become less important, as ambient air temperature is sufficient from this point to maintain colony activity. This explains why during the summer, colonies continue foraging throughout the night and many nests are covered entirely with vegetation, commonly *U. dioica* (Rosengren 1970; Skinner 1976). Therefore, it is concluded that forest edge effects related to edge aspect influence *F. rufa* behaviour, and colonies inhabiting the southern regions of woodlands can be expected to have an advantage over those in the more northerly regions.

Nest Characteristics.

Nests in north-west 1 tended to be significantly lower in height than those in the other study aspects. This is due to a number of factors. Firstly, nests were located in more open areas, in many cases close to internal or external edges which consistent with other studies, led to them failing to attain the characteristic dome (Brian 1977; Skinner & Allen 1996). It is likely that the higher average wind speeds within this aspect would also have contributed to these lower nest forms. However, the positive relationship between light intensity and nest height seems to be a compelling one, as in the south, nests further back from edges or those which received lower light intensity values were the tallest. This confirms the influence of both aspect and distance related edge effects.

There was no evidence that nest dimensions or the angle of the shallowest slope were influenced by aspect. Nest dimensions are probably more related to the age and size of a particular colony, social structure and the amount of available light which the nest receives and thus all study nests, regardless of aspect, would have responded in a similar manner. Again, as the angle of the shallowest slope is associated with the amount of available sunshine it is not surprising that no significant relationships were identified within the study aspects.

Nest orientation nevertheless did vary significantly with aspect, the southern and north-eastern nests facing significantly closer to the south than either of the north-western aspect nests. The southern colonies orientated nests closer to the south than those of their more

northerly counterparts, highlighting the optimal conditions available to southern colonies which was manifested in the higher nest densities and differences in colony social structure. Nests in the other aspects needed to locate nests wherever access to direct sunlight for at least some part of the day allowed, as overall surface and air temperatures were lower. This had the 'knock on' effect of retarding areas of foraging behaviour and the phenology of activity phases (discussed in later sections).

The distance of nests to the nearest external edge did not prove statistically significant with aspect. The relationship with internal edges was not particularly useful, as the significant differences between the north-east and north-west 2 nests were more to do with the characteristics of the two sites, north-west 2 having one less internal edge. The large number of nests which were situated within the centre of sample aspects, in areas where light intensity values were high during the early part of the year, indicate that although Adlung (1966) and Robinson (2001) suggest that *F. rufa* is a shade tolerant species, this tolerance only applies to the summer months once ambient temperatures are high enough to support activity without the need of direct sunshine. Therefore, nests in deep shade during the summer are not a good indication of shade tolerance through the year.

Species Associations at Nest Sites.

Nest zones supported significantly more species of plants and trees than their corresponding controls but overall, no different species associations were evident between nests and control zones. Statistically, only *A. pseudoplatanus* and *S. nigra* were found in higher abundance in nest zones than controls, suggesting that colonies were selecting nest locations on the basis of microclimate and favoured foraging resources. These relationships were also found by Skinner (1976) in North West England, but were not evident from studies on *F. rufa* in Essex or Kent where *Quercus robur* was favoured (Welch 1978; Adams 1991; Cook 1998), or *F. lugubris* in Yorkshire (Sudd *et al.* 1977) and Ireland (Breen 1979b), where *Betula* spp. or *P. sylvestris* were favoured, respectively. This would suggest that the actual species of forage tree favoured is site or region-specific, in keeping with the known generalist strategy of members of the *F. rufa* group (Brian 1977; Skinner & Allen 1996; Skinner 1998).

The pattern of species abundance was retained across the 62 additional nests, with *A. pseudoplatanus* remaining the most common tree within the 5m nest zone around the four aspects. The analysis of the distance from nests to the nearest tree showed that southern nests were significantly closer to trees than nests in the other three aspects. This confirms that the

more equitable southern microclimate allows colonies to locate nests closer to foraging resources rather than being solely dependent upon nest locations which offer suitable microclimatic conditions. This consequently had important implications for nest density and colony social structure (discussed in a later section). As no related distance relationships were found it is concluded that aspect driven microclimatic edge effects alone are most important in influencing nest location in *F. rufa*.

The apparent preference of certain trees to internal or external edges was not of great significance. Only three species were statistically linked to edges, the location of two of these (*C. monogyna* and *P. sylvestris*) being of anthropogenic origin and the third (*C. sativa*) most significantly related to it being a naturally more southern species that was more at home along a sunny internal edge. Therefore, it is concluded that nest location and the proximity to notable trees is not coincidental, but rather a definite selection by *F. rufa* colonies.

The Pattern of Foraging within the Four Study Aspects.

It was shown that foraging activity in the south was much more pronounced than in any of the other study aspects in response to the more favourable microclimate and abundant food resources. There was a well defined 'sequence of utilisation' of tree species throughout the year. Ant attention focused first on *A. pseudoplatanus*, before turning to *P. sylvestris* during the late spring and summer, and finally to *Q. robur* during the summer and autumn. This foraging preference appears to follow that described by Skinner (1976), and is probably linked to the aphid habit of host alternation (Thacker & Hopkins 1998).

The significant relationship between nest sites and *A. pseudoplatanus* (a pattern also shown across the additional 62 nests), and the preference shown for this species early on in the year suggests that the close proximity of nests to this tree confers an advantage to colonies. High *A. pseudoplatanus* densities in the south certainly favoured earlier foraging activity in this region. It thus appears that there is a reliance on the aphid *P. testudinaceous* on this species, which provides access to a high quality food resource when foragers are unable to move large distances away from the nest due to low ambient temperatures. In the absence of *A. pseudoplatanus*, colonies were forced to wait until the plantation species *Cinera* spp. aphids begin activity, or until aphids on other species of broad-leaved tree become available. Although this will not deter *F. rufa* from particular woodlands, it may well act to lower the maximum nest densities which are found, which appears to be the case at Bedford Purlieus.

However, in Harlestone Firs, plantation species contribute vastly to the nutrient status of *F. rufa* colonies with *P. sylvestris* being the most utilised tree through the year across the woodland. This has important implications for *F. rufa* conservation across the UK (dealt with in a later section). *B. pendula*, where it was present, was also used preferentially, in agreement with the findings of Sudd *et al.* (1977), Douglas & Sudd (1978), Fowler & McGarvin (1985) and Mahdi & Whittaker (1993). *S. nigra* was found in significantly more nests sites than control points and was used widely for foraging throughout the year, again making a massive contribution to the colony's food resources.

The length of the longest foraging trails around the four study aspects showed that southern colonies foraged over significantly shorter distances than colonies elsewhere. The longest foraging trails were in fact found in north-west 2, which again confirms the role of aspect related edge effects. Colonies to the north, in the absence of optimal microclimatic conditions are forced to locate nests where a suitable microclimate exists and to travel to the food resources. This has important implications again for nest density and the manifestation of colony social structure (dealt with in a later section).

7.2:4 Nest Density, Persistence and Edge Effects.

Nest densities in the south were very high, comparable with the highest values found in the UK and Europe (Welch 1991; Cook 1998). In contrast, nest density in the other three aspects were around average for the UK (Elton 1932a; Peterken & Welch 1975; Welch 1978). This observation appears to be a direct consequence of the more favourable ecological conditions within the south, where colonies need to travel shorter distances to locate abundant food resources thus providing space for a greater number of nests to exist. This once again confirms the conclusion that aspect driven edge effects are most important in determining *F. rufa* behaviour within Harlestone Firs.

Nest location showed great persistence during the study, with only twelve nests being abandoned over the two year study period, only one of which represented a monodomous colony. This is consistent with observations of many other studies (Dreyer 1942; Imms 1947; Haviland 1948; King & Salee 1953; Skinner 1976). Nevertheless, it is unlikely that edge effects are directly responsible for nest persistence in the short term.

7.2:5 Colony Structure in Relation to Edge Effects.

The study has highlighted that forest edge effects related to microclimate and vegetation dynamics have influenced the mode of social structure utilised by colonies within the four sample aspects. The south, characterised by favourable ecological conditions, has given rise to the development of polydomy within colonies, probably as a result of polygyny via the adoption of queens, as described by Pamilo & Rosengren (1984). This has allowed colonies to monopolise large areas of the abundant food resources by forming bud nests to which functional queens have probably been moved. This strategy has been shown to develop across Europe in this and other species, which occupy stable but patchily distributed habitats (Hölldobler & Wilson 1977; Pamilo & Rosengren 1984; Elmes 1987; Chapisat *et al.* 1997).

In contrast, colonies within the other three aspects were mainly monodomous, except in limited areas where microclimate and concentrated food resources again promoted a move towards polydomy. However, because in general, microclimatic conditions in these study aspects are less favourable than in the south, nest density and thus the number of polydomous colonies has remained low, suggesting the influence of aspect related edge effects as a major trigger in colony social structure within Harlestone Firs.

7.2:6 The Impact of Edge Effects on Activity Phases around the Wood.

A. pseudoplatanus Bud Development.

Bud development showed a relationship with both aspect and distance related edge effects. In both years leaves on sample trees were fully open within the edge region in all four aspects on the same day. However, although leaf development was completed basically on the same day in the south and north-east, interior regions in both north-west aspects were retarded by 11 and 12 days during both years. The southern, north-eastern and north-western edge region results are probably explained by the higher temperatures and potentially more important, higher light intensities which these areas received. However, although the results are consistent with previous research they do show that the factors which trigger bud burst are complex.

F. rufa Activity.

There were profound differences between the onset of particular activity phases in *F. rufa* colonies inhabiting the four study aspects. Southern colonies left hibernation significantly earlier than colonies in all other aspects. The spring massing occurred earlier in the south, significantly so compared to colonies in north-west 2. Alates appeared significantly earlier in the south than colonies occupying the other aspects. Colonies in the south also entered hibernation later than colonies in the north-east and north-west 2 in 2000 and those within all aspects in 2001, giving southern colonies the longest active season. These differences are a direct consequence of the more favourable microclimatic conditions which occurred in the south and thus initially confirms aspect as the key determinant of *F. rufa* behaviour. It should also be noted that although differences in light intensity were highly statistically significant, that the differences in temperature were clearly biologically significant, the arbitrary selection of 95% confidence limits being insensitive to the scale of differences which influence the ants.

This is perhaps confirmed by the distance relationships which existed in activity patterns of the southern nests. Here, a positive relationship was found between the first observed worker activity and light intensity and temperature profiles. Workers from nest 1, located at the forest edge (which was consequently warmer and received significantly more light than nests 3 (30m), 4 (81m) and 5 (160m)), left hibernation earlier. Although differences in first worker activity between nests 1 and 2 (8m from the edge) could not be attributed to significant differences in light or temperature, internal nest temperatures would have been depressed in nest 2 due to the much higher moisture levels which were found there. This slight drop in both air temperature and light intensity values, together with lower internal temperatures within nest 2, was sufficient to retard activity slightly in this nest and confirmed that distance relationships may also be important in determining the phenology of activity phases in *F. rufa*.

Breeding times also showed variation around the wood, flights occurring earlier in the south in both years, with little or no apparent overlap with reproducing colonies within the other study aspects. This again appears to be a direct response to the higher temperatures, itself a product of higher light intensity values, in the south.

Peak foraging activity was retarded by one month in north-west 2. This is certainly in response to the later first worker activity, first worker foraging dates and retarded breeding

phase, again confirming aspect as the major determinant. It should also be noted that initial early season activity in north-west 2 may be related to the very boggy conditions in the initial 30m, where foraging would certainly have been limited and less efficient over the wet soils.

7.3 Key Aspects of the Thesis.

7.3: 1 Physical and Biological Edge Effects from the Perspective of Landscape Ecology.

This study is one of only a few in the UK which has provided data on the impact of edge effects on a fragmented woodland. In so doing it provides a very useful comparison with equivalent North American studies, showing evidence that physical edge effects, especially those related to light intensity and wind speed, do indeed influence edge regions, but that their impact is less severe in Central England (Gysell 1951; Matlack 1993; Murcia 1995; McCollin 1998). Whether this is due to the design of the analysis or the difference between continental interior and oceanic climates is difficult to determine (although both factors clearly play a part), but it does show that woodland management techniques should take into account both aspect and distance related edge effects, especially in remnant ancient woodlands embedded with modern fragmented landscapes.

The study also provides a useful comparison with studies which have focused on the responses of vegetation (Wales 1967, 1972; Brothers & Spingarn 1992; Brothers 1993; Fraver 1994; Matlack 1994). The results showed that the invasion of exotics was most likely in edge regions, with the exception of the south, where the warmer and brighter environmental conditions allowed field species to invade deep inside the wood. The study showed that the number of tree species increased in edge regions, the numbers decreasing with distance into the wood and that regeneration was more likely to occur in edge regions. This confirmed overall that both aspect and distance related edge effects were influencing species diversity and abundance.

In addition, the results showed that historical factors were also very important. The south which was scrubby heathland until the 1850s, when it was planted as a conifer plantation has accumulated invading species relatively quickly. It was actively managed for many decades before being largely left to successional development over the last 20 or so years. Here species associations are largely confined to invasions from the exterior of the wood. In contrast, the initial 30m of north-west 2, which along with the south had the greatest number of species, is a remnant boundary area which was wooded well before the rest of the site was

planted. Here, the very edge (perhaps 10m or so) has escaped any planting by conifers and has simply accumulated species overtime, many of which are agricultural ‘weeds’ from the surrounding fields. However, in this aspect species associations just inside the edge confirm the more ancient origin of this region, it being home to many woodland specialists not found elsewhere in the wood. The combination of historical factors and the influence of both aspect and distance related edge effects have provided an interesting comparison with the north-eastern and north-west 1 study aspects where diversity is low, mostly confined to the older boundary hedges. Again, these results provide a valuable insight into the responses of vegetation to the differences in microenvironmental conditions in southerly and more northerly study sites which will be valuable when designing management plans to both remnant and plantation woodland sites.

Finally, the data regarding the bud development on *A. pseudoplatanus* is novel and provides further insight into the factors that trigger bud burst and how this is influenced by both aspect and distance related edge effects. In so doing, it provides valuable baseline data which can be easily extended to cover other species in other parts of the UK.

7.3:2 The Influence of Aspect and Distance Related Edge Effects on the Ecology of *F. rufa*.

This is first study to try to determine the influence of forest edge effects on the ecology of the wood ant, *Formica rufa*. For this reason many of the results can be considered novel, although some data confirm the findings of previous research,.

Previous studies have highlighted that wood ants do tend to select nest locations which are warmer and receive direct solar input (Breen 1979a; North 1996; Pontin 1996; Skinner & Allen 1996). This study has found largely similar results, but by approaching this area from the view of edge effects, it has also provided greater definition to current knowledge. Colonies are tending to select nest sites on the basis of light availability, and therefore temperature, but also locations which offer shelter from the wind. However, there certainly appears to be a threshold beyond which selection on the basis of microclimate becomes secondary to proximity to food reserves (confirmed by the data on foraging preference, distance to the nearest tree and length of longest foraging trail). This threshold was found to be aspect driven, which has important implications for conservation and management strategies for *F. rufa* populations, especially at the northern end of this species’ range in the UK.

In addition, the literature concerning the impact of shading on *F. rufa* colonies suggests that direct sunlight is a requirement throughout the year, but the results of this thesis do not support this suggestion. With the possible exception of colonies living at the northern edge of the species' range, it appears that shading is only a factor during the early part of the season, and certainly by the time that *P. aquilinum* (often claimed to deter colonies) is fully established, colonies appear to be little affected by its close proximity to nests.

This study has identified that only two species of tree, *A. pseudoplatanus* and *S. nigra* were found in significantly more nests than control zones. *A. pseudoplatanus* was also the most common and abundant tree within the nest zones of the additional 62 nests. In addition, *A. pseudoplatanus* was also the most common tree to receive the first foraging attention in the year, and was preferentially selected for foraging by colonies in the first two months of activity. These results confirm Skinner's (1976) observation, but provide greater definition as his study was based on fewer than 10 nests. Clearly, *F. rufa* colonies, especially in the northern area of their range, gain an advantage by utilising *A. pseudoplatanus*, which due to its early leaf development and the presence of the abundant and prolific honeydew producing aphid, *P. testudinaecous*, provides a valuable food reserve from very early on in the new active season (Skinner 1980 a&b; Skinner & Whittaker 1981). Colonies that are able to locate nests close to this species therefore are able to obtain high energy food reserves early, which in turn helps to elevate internal nest temperatures (Skinner 1998). The current drive to remove invasive tree species (of which *A. pseudoplatanus* is considered to be one), from northern woodlands in an effort to reduce shading to *F. rufa* nests may therefore be misguided and could be contributing to the loss or reduction in existing populations (UKBAP 2004).

The great differences in the phenology of *F. rufa* activity phases across Harlestone Firs are of great significance. This is the first study which has shown that aspect, and to a lesser extent distance from the edge, can have such a profound impact on the behaviour of *F. rufa* populations. Although previous studies have commented that wood ant colonies are most common on southern facing edges or slopes (Elton 1932b; Scherba 1958; Adlung 1966; Finnegan 1975; Sudd 1977; Douglas & Sudd 1978; Breen 1979a; Cook 1998), no direct comparisons have been made with the responses of colonies occupying more northerly facing orientations and thus this study provides valuable insight into the factors which trigger changes in behavioural patterns. It also provides actual data to support the isolated observation of Scherba (1958) that colonies with only a northern exposure tended to lag behind those facing south in activity. It is interesting to note that peak foraging activity in north-west 2, which was the most retarded activity, was one month behind that in the other

three aspects. This largely confirms the accuracy of the microclimate and activity phase data and means that this study will have great application to future conservation efforts.

The differences in breeding times across a single isolated woodland fragment is of great significance and again has not been reported before. One of the major problems of isolated populations is the likelihood of inbreeding depression and so evidence of the further isolation of breeding populations within an already fragmented woodland has very serious implications. This has even greater significance at Harlestone Firs, where the loss of habitat due to planning applications for the southern portion of the wood, could result in the loss of a discrete breeding unit, leading to a further reduction in genetic variation within the remaining population (Chapuisat 1996; Gyllenstrand *et al.* 2002, 2004; Goropashnaya *et al.* 2001, 2003). These results should therefore prompt greater research effort in the area of *F. rufa* population genetics.

In addition, the great variation in the timing of breeding activity in this study may well explain the findings of Woyciechowski (1990) in the Polish Carpathians. He found through trapping reproductives during their nuptial flights, that *F. rufa* breeding times varied from year to year and that the reproductive phase lasted for up to 2.5 months in some years. He could provide little explanation for these observations. The results of this present study may well lend an explanation, that simply colonies whose nests tended to have a more southerly aspect were further advanced and therefore were breeding early. Those colonies utilising more northerly slopes lagged behind in their activity phases and therefore the later reproductives represented individuals from these populations. The onset of the reproductive phase would initially be determined by the climatic conditions, and thus in good years, reproduction would commence earlier.

The factors which trigger a switch in colony social structure in *F. rufa* are not particularly clear. *F. rufa* colonies in mainland Europe tend to be monodomous or very weakly polydomous (Adlung 1966; Welch 1978; Rosengren & Pamilo 1983). This is most likely due to competition with other highly polygynous and polydomous species, such as *F. aquilonia*, *F. lugubris* and *F. polycтена*, which according to Adlung (1966), confine *F. rufa* populations to the woodland interior. Applying these observations to the results of this present study may therefore provide an insight into what triggers a colony to switch to a polydomous (and polygynous) social structure allowing the following hypothesis to be proposed.

Colonies in the south, with the advantage of a suitable microclimate, can select nest locations on the basis of food resource, rather than exclusively on solar input. Therefore, foraging trails do not have to be so long and consequently territories are smaller. In this optimum habitat the best option for newly inseminated queens is to return to their own nest, or to join the nest of a nearby conspecific, as resources in the immediate area are abundant. For the workers of existing colonies then the best option is to recruit sister reproductives, enabling more of their genes to be passed to future generations. The greater number of reproductives are provided for by raising a larger worker brood, which is also supported by the abundant resources. Therefore, satellite nests closer to favoured forage trees are formed, which reduce the distance of forage trails, increasing foraging efficiency and making territory defence more effective. Over time, colonies shift from the monodomous-monogynous models to polydomous-polygynous model, increasing nest densities and allowing individual colonies to monopolise large areas of the local food resource. This scenario shows a similar response to optimal local conditions which is found in other highly polygynous wood ant species. However, the difference is that some species, such as *F. aquilonia* form strikingly polygynous colonies even in Fennoscandia. Therefore, in *F. rufa* there is clearly a microclimatic threshold below which polydomy does not develop.

This is confirmed by the north-eastern, north-west 1 and north-west 2 populations, where the incidence of polydomy is much lower. In these areas, colonies are forced to select nest locations which provide access to solar input, and therefore higher surface temperatures, rather than food resources. As in more northern areas of Britain, the number of available nest sites is lower so colonies must therefore travel much greater distances to obtain the resources that they require, making colony territories much larger. In the absence of abundant resources, (in the case of Harlestone Firs due to the reduction in key broadleaved species) colonies are much less likely to adopt new queens, as there is a limit to the number of brood that can be successfully raised from the available resources. Therefore, for newly inseminated queens the likelihood of finding a welcome conspecific nest is lower and the strategy of long distance dispersal is more profitable. Thus nest densities are lower, because as nest sites are limited, forming satellites is not viable, except in those areas where the food resource is concentrated and the microclimate favourable. Therefore, the development of polydomy and polygyny is reduced.

This scenario certainly explains the difference in observed polydomy between populations in Southern England, which form strikingly dense aggregations in many woods, and those in the Midlands and especially Northern England, where colonies tend to be obligately

monodomous (Elton 1932a; Collingwood 1955, 1964; Satchell & Collingwood 1955; Peterken & Welch 1975; Skinner 1976; Welch 1978; North 1993b; Fowles 1994; Edwards 1997; Cook 1998; Robinson 2001; UKBAP 2004). It is therefore notable that the colonies at the southern edge in Harlestone Firs are behaving in a similar fashion to populations in Southern England, and those colonies in the more northerly areas of the wood are more representative of populations in Wales and the Lake District.

It is clear from this study that aspect is the most important factor in providing the favourable conditions for the development of polydomy. That microclimate may influence social structure has been proposed previously in other species (Elmes & Petal 1990), but that it may make such a large difference to *F. rufa* colonies has not been previously demonstrated.

7.4 Critical Evaluation of the Study.

The use of four study sites was a controversial one, but stemmed from a desire to provide comparable data to previous studies on the impact of edge effects from around the world, listed by Murcia (1995) as a key recommendation for future studies. In addition, this study did try to overcome the problems of previous research, related to what Murcia (1995) described as 'pseudo-replication'. Thus the study aspects were selected to ensure that, where possible, the forest edges maintained consistent characteristics, that from the outset the actual location of the forest edge was defined and described, and that common sampling points were used throughout the study. Therefore, by selecting a four aspect approach, this study did overcome many of the criticisms levelled at previous research.

With the benefit of hindsight this approach may have hindered the study of the impact of edge effects on the wood ant population. The suggestion that the use of transects which ran from north to south and east to west through Harlestone Firs would have made the comparison of the impact of microclimate with distance from the edge easier and the differences in nest characteristics more simple, but perhaps would not have made the differences in colony structure, nest density and the wood ant activity phases as clear. In addition, the use of more random points located throughout the woodland was also not possible due to the necessity of using instantaneous measurements. The selection of a further ten points, for example, would have added approximately 1.5 hours to the necessary sampling times, which would have introduced unacceptable degrees of error into an already tight sampling schedule. Any differences between sample points would then have been equally due to the time of day, rather than actually microclimatic differences around the woodland. Therefore, as with any

study, although improvements could have been made, it is considered that the approach used here was appropriate and beneficial, providing an insight into *F. rufa* ecology which has not been previously shown.

However, the selection of the study aspects was not without difficulty and was hindered by the shape of the woodland boundaries and the problem of access to the adjacent land. This meant that none of the sites faced a cardinal compass point. The similarity in the aspect of north-west 1 and 2 especially, could have influenced the accuracy of the results, but it should be noted that the microclimatic conditions were very different between the two aspects and still provided a valuable contrast consistent with many other studies (e.g. Barry & Chorley 1992). The southern site, facing more towards the south-east retained a representative southern microclimate consistent with previous research (Matlack 1993; Murcia 1995). It is thus considered that the results provided an accurate assessment of the general woodland conditions around the edges of Harlestone Firs and that the differences between the northern and southern woodland microclimate and vegetation structure were accurately represented.

A consistent observation throughout the study was that although apparently playing a key role in *F. rufa* activity and behaviour, differences in temperature between study sites, and nests compared to control points, were not often statistically significant. Given that significant differences in light intensity did exist this is rather surprising. However, it is likely that this situation has arisen due to the sampling protocol adopted during the study. The measurement of the air column temperature (0.6m) is likely to give much lower values throughout the year than would be obtained from measurements of soil surface temperatures (Barry & Chorley 1992; Ahrens 1994). This compromise between a sampling height which provided data for both forest edge effects studies and which accurately reflected conditions directly affecting the ants was difficult to obtain, given the limitations imposed at Harlestone Firs (Bernstein 1979; Murcia 1995). Future studies would benefit from the use of data logging equipment and the measurement of the four microclimatic variables at several different heights at regular intervals over longer periods of time. A useful future analysis would be to devise an 'index of exposure' which took into account the combined effects of temperature and wind speed. This would provide a useful comparison with the pure 'aspect' generated data. However, it is concluded that overall, the results obtained during this study provided an accurate, but conservative, assessment of the woodland microclimate due to both sampling height and the timing of microclimate measurements. Thus more detailed studies may find greater variation in the four variables throughout the year.

The analysis of foraging preference in general provided an accurate reflection of observed behaviour throughout the year. However, the omission of March and May meant that foraging on *A. pseudoplatanus* was under-recorded, which was unfortunate in the context of comparisons of the overall utilisation of tree species. Foraging on *S. nigra* was also under-recorded due to the difficulty in counting worker trails on very small stems or trunks. As *S. nigra* is generally quite a low growing species perhaps counting the number of foragers actually tending aphids would have been a more useful approach. The use of 'intervention' type studies, which remove foragers descending the trunks over a given time period to enable the chemical analysis of the carbohydrate content of the crop, has the potential to provide more accurate results. However, there are several drawbacks to this approach. Firstly, the losses to colonies through the year should be considered unacceptable, especially in high summer where several hundred to a thousand workers per colony would be taken every week. Secondly, it would be impossible to ensure that all descending foragers could be collected from very busy trees as the numbers would be too great, and therefore in practice, results would probably not be much more accurate than have already been achieved here.

Analysis of the activity phases in general provided an accurate assessment of colony responses to differences in microclimate across the woodland. Although it is conceded that perhaps activity was missed in the more northerly areas due to the timing of the measurements (perhaps an observation was missed due to worker responses to early morning or late afternoon direct sunlight), it is believed that the standardisation and rotation of the measurement period was the best approach in this study. In defence of missed activity in the north it is argued that in the early and late periods of the year, southern activity had an equal or even greater chance of being missed, because in many cases, direct sunlight would have been received at the nests up to 3 hours before activity was classified. This would mean that again, these results are potentially quite conservative, and perhaps the differences in the timing of activity are more pronounced.

Reproductive behaviour was perhaps the most difficult parameter to measure accurately. Again, although every effort was made to ensure that the recording effort was directed to the actual timing of flights across the wood, it is inevitable that flights were missed. However, it is highly probable that the vast majority of notable flights were recorded, meaning that for the most part, only individual alate take offs were omitted. This study was ambitious in trying to classify flight times across so many sample nests as both Breen (1979a) and Talbot (1959, 1971, 1972) focused only on single or limited numbers of nests, and thus increased their chances of accuracy. Nevertheless, it is considered that this study has provided a good

indication of the reproductive behaviour in *F. rufa* in Harlestone Firs and that the potential for isolation of colonies in the south is genuine.

7.5 Thesis in Context of Conservation Issues.

Formica rufa L. is a priority species in the UK Biodiversity Action Plan (BAP) (UKBAP 2004). Although not threatened within its strongholds in the south of England, colonies have been lost from Wales, the Midlands and North West England, prompting widespread attention from conservation bodies in these areas (Fowles 1994; Robinson 2001; Warwickshire County Council 2003). The findings of this thesis will provide many insights into future conservation strategies.

Insensitive woodland management measures have had a negative impact on many vulnerable colonies, and the current drive to replace large areas of coniferous plantation with broad-leaved species in older sites, has been highlighted as a possible cause of the species' decline (Edwards 1997; UKBAP 2004). This poses the question, can *F. rufa* colonies survive in the absence of plantation species? Initial observations suggest that the presence of plantation is vital. For example, in Bedford Purlieus and Maulden Wood, colonies are found only in compartments which have plantation species. Certainly in the post-glacial forests of the mid-Holocene, *Pinus* species would have been more common and could have facilitated the expansion of *F. rufa* group species through Britain during those times (Rackham 1986, 1990). However, there are many sites in the south of England which do not support abundant plantation but which possess healthy *F. rufa* colonies, and thus this initial observation does not reflect the entire situation (Welch 1978; North 1996; Cook 1998; Skinner 1998).

The current 'purge' of *A. pseudoplatanus* throughout British woodlands by conservationists may also be relevant in this context. Listed as an invasive species, *A. pseudoplatanus* casts a deep shade, usually earlier in the year than many other broad-leaved deciduous species, making it unpopular with many (Rackham 1990). However, as it is one of the first broad-leaved species to support valuable ant-tended aphid colonies each year, it has become an important species for *F. rufa*, and thus its removal from wood ant inhabited woodland is significant (Skinner 1976, Warrington & Whittaker 1985a&b). Colonies in both this and Skinner's (1976) study utilised *A. pseudoplatanus* preferentially in the early part of the year and an advantage was gained from doing so. It is thus proposed that although not vital for the development of the new season's reproductives (fed by the storage or replete workers), the

sooner food reserves are returned to the nest, thus initiating widespread activity, the earlier the consequent increase in the colony's metabolic activity occurs. This helps to elevate nest temperatures at this vital stage of the year. Colonies failing to increase internal nest temperatures early are vulnerable to extremes of weather, listed as a potential reason for losses in some woodlands in Fennoscandia and North West England (Vepsäläinen & Wuorenrinne 1978; Robinson 2001).

In Europe, where conifers are natural components of the forest ecosystem, the loss of key broad-leaved species may not be so important (although research is lacking in this area). However, in Britain, where *A. pseudoplatanus* is not present, *S. nigra* and *Betula* spp. become important early in the season, provided that they exist in sufficient numbers to support population requirements (Skinner 1976; Sudd *et al.* 1977; Fowler & McGarvin 1985). *Quercus* spp. support important aphid species, but the main utilisation period on this species, especially in the Midlands and Northern England, commences from May or June; before this point interest appears to be less widespread. Otherwise, plantation species provide a season long valuable supply of honeydew from aphids of the genus *Cinera* (Breen 1979b). It is thus proposed that at the northern end of the range, the loss of key tree species which limits the overall food resource, will reduce potential nest densities. Lower temperatures and less available forage trees will promote monogynous colonies which have a finite life span, and thus nests will be inevitably lost over time (Skinner 1998). If numbers fall below a critical threshold, the impact of poor weather during the early season would be sufficient to promote losses, especially if this occurred in consecutive years (as proposed by Robinson 2001). Low internal nest temperatures due to limited early season foraging opportunities and lower light intensities would most certainly make a colony vulnerable under these circumstances (Vepsäläinen & Wuorenrinne 1978). It is thus important that the removal of key tree species in wood ant inhabited woodland in the North is limited until further research is carried out.

The fact that aspect related forest edge effects greatly influence the ecology of *F. rufa* is an important issue for conservation, as it is likely that populations inhabiting different parts of a woodland require different conservation strategies. For example, colonies in the more northerly sites of Harlestone Firs are more vulnerable to insensitive management and severe disturbance than colonies inhabiting the south. The response of southern colonies to a more favourable microclimate in the timing of events also confirms this point. Woodland management activities scheduled to minimise disturbance to colonies living on one side of the wood, may well have a severe impact on colonies in other areas. This is especially true of the reproductive phase of *F. rufa* colonies, where there is a clear distinction in the breeding

seasons between north and south. Conservation strategies should therefore seek to determine the extent of any phenological differences within populations and ensure that mitigating measures are taken to protect individual sub-populations within woodland fragments.

This is particularly important in the context of climate change. According to the Intergovernmental Panel on Climate Change (IPCC) (2001), many species are already responding to climate change at the local scale showing a shift in phenology, such as earlier breeding and first flowering dates. Their data showed that 46 species of invertebrate in Europe were already showing changes in their ecology that could be linked to climate change. Evidence from this study suggests that the wood ant group can act as a very useful indicator species, especially as their conspicuous colonies make observation relatively easy.

7.6 Recommendations for Future Research.

This study has shown that aspect related forest edge effects greatly influence the ecology of the wood ant, *Formica rufa* L. It has also highlighted some areas which would benefit from further research to strengthen the present understanding of the ecology of this species.

Although proving significant in many areas, the distance relationship did not influence *F. rufa* behaviour as much as aspect. However, there was sufficient evidence that distance from the edge is an important factor for wood ants and therefore further research is required. It is proposed that the use of transects which bisect the wood from north to south and east to west may give better definition to the impacts of distance related forest edge effects. Another useful comparison would be to investigate colonies which survive outside of normal woodland environments, such as those which inhabit the remaining pockets of heath in the south of England. In these locations an investigation of the role of nest aspect would highlight further key trends, especially those related to the wood ant phenology.

The role and importance of different trees and shrubs in *F. rufa* colonies requires more investigation throughout its range. This study has highlighted trends which support that the relationship with different forage trees is linked to microclimatic conditions. It would therefore be of great use to determine *F. rufa* utilisation of a variety of broad-leaved and coniferous tree species throughout the UK to confirm if inappropriate management is the cause of the current northern losses. Within locally inhabited woodlands around Harlestone Firs it would be of great use to repeat this study with data from a complete year which

incorporated more nests throughout the woods. An extension to include the *F. rufa* utilisation of aphids on various woodland herbs and woody plants through the year, to clarify the impact of aphid host alternation on seasonal foraging preference, would also be of great use to future conservation strategies.

The influence of aspect related edge effects in triggering differences in colony social structure is also an area which would benefit from further investigation. Although this observation is supported by this and preliminary investigations at Bedford Purlieus, this relationship ideally needs to be tested across a larger sample of woodlands in the UK, as it has great relevance for the persistence of colonies in isolated and fragmented woodlands. It would be especially useful to determine on how many occasions colonies living in warmer southern facing areas do display a different social structure to the more northerly facing colonies. The re-investigation of a number of aspects of wood ant ecology from the stand point of both aspect and distance related edge effects may highlight important additions to the current understanding of this group.

At present, no meaningful data exists on the genetic status of fragmented populations of *F. rufa* across the entire UK. It is therefore very important to carry out genetic analysis on colonies from isolated woodlands from southern England, the Midlands, Wales and north-west England, to determine the extent of 'inbreeding' and/or gene flow within these populations. The use of microsatellites and Inter Sample Sequence Repeats (ISSRs) are both valuable tools in this type of analysis and in the case of the latter, could provide meaningful genetic data rapidly and relatively cheaply. These data will enable more effective future conservation strategies to be developed.

This study is the first to have generated data which confirms the link between microclimate and activity (first mentioned by Scherba in 1958) over small spatial scales, and it is clear that much more data are needed from *F. rufa* colonies across the UK to enable a greater understanding of this phenomenon. It is recommended that detailed studies of wood ant phenology be carried out in many more populations, especially those in vulnerable areas. This is especially important as it would appear that wood ants are reacting to local climatic change. As wood ant colonies are on the whole quite conspicuous, making observation easy, and their entire ecology is based on the rapid development of the reproductive brood early in the year, these species may have an important role as indicator species in future climate change studies.

8.0 References

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