Analysis of the ecological principles underpinning forest landscape restoration:
A case study of Wood cricket (*Nemobius sylvestris*) on the Isle of Wight (UK)

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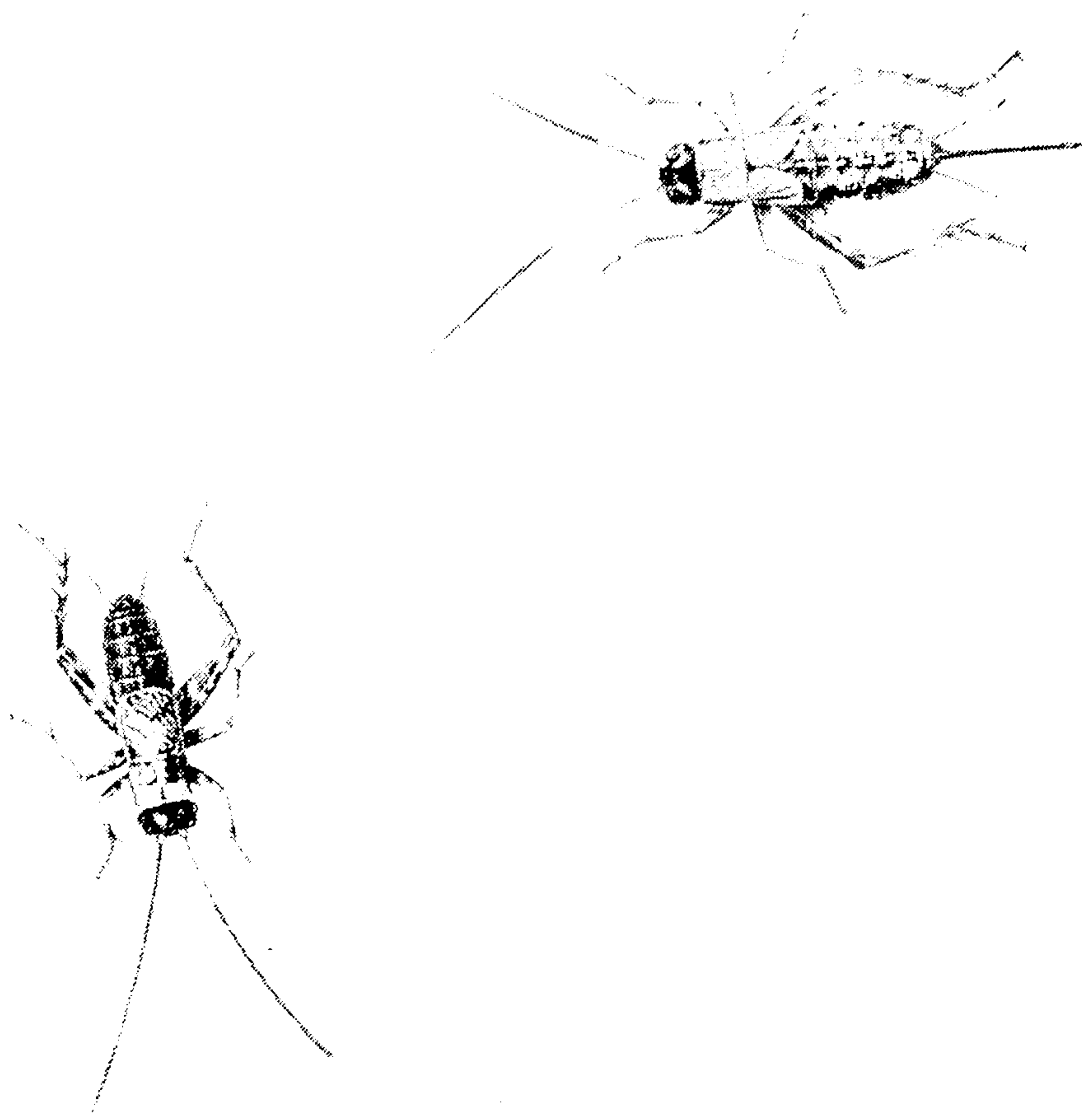

Wood cricket female (top) & male. Scale: 2 : 1

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Abstract

Current woodland restoration programs are increasingly focussing on the creation of habitat networks in order to increase woodland cover and connectivity. However, the basic assumptions underpinning such strategies are largely untested for species associated with woodland habitat. For many woodland invertebrate species, local scale processes are potentially more important than processes operating at the landscape scale in terms of species persistence, especially for those species that show high dependence on woodland habitat conditions and have limited dispersal ability. The applicability of landscape-scale approaches to woodland restoration therefore needed to be evaluated in relation to the ecological characteristics of invertebrates. This thesis examines these issues and provides a quantitative analysis of the factors influencing presence of wood cricket (*Nemobius sylvestris*) at multiple scales within the landscape.

The investigation was conducted in woodland habitats on the Isle of Wight in the south of the United Kingdom. A landscape-scale survey indicated that wood cricket was found predominantly in large woodland fragments situated in close proximity to each other, with ancient woodland characteristics and with a high amount of edge habitat. The current pattern of distribution of wood cricket suggested that most woodland fragments in the agricultural matrix are effectively isolated from each other, indicating the importance of maintaining a high level of connectivity between habitats for this invertebrate species.

An investigation within woodlands indicated that locations with permanent low cover of ground vegetation, low canopy closure and high availability of leaf litter were the preferred habitat conditions for wood cricket. Ride and track edges, woodland peripheries and open areas created and maintained by management activities were found to be the main habitat locations for wood cricket. It was further found that wood cricket was mainly present at permanent edges or in close proximity to these locations, indicating the importance of maintaining these habitat features for this species.

The mean dispersal rate for dispersing wood cricket obtained from a series of field experiments was found to be similar to that of other ground-dwelling invertebrate species that were strongly associated with woodland. This level of habitat specialism was consistent with the habitat preferences found for wood cricket, and therefore wood cricket can be seen as representative of this particular group of woodland-associated invertebrates. Comparable to wood cricket, the dispersal ability for species of this group was found to be limited. Few individuals of nymph (i.e. juvenile) and adult wood cricket populations were found to disperse. Wood cricket was found able to disperse up to 55 m into non-woodland habitat and mature habitat corridors were found to be used by wood cricket, but not new immature woodland plantings.

The results of this investigation indicate that the overall success of woodland conservation for woodland invertebrates lies in adopting a multi-scale and multi-management strategic approach. The current initiatives focussing on restoration and re-instatement of traditional management activities within existing woodlands were found to be highly beneficial for wood cricket. Corridors were found to facilitate movement if suitable woodland habitat conditions were provided. Creation of woodland habitat networks might therefore be beneficial for wood cricket if given enough time to develop.

Keywords: woodland, forest, fragmentation, landscape, habitat network, connectivity, corridor, scale, dispersal, movement, invertebrates, wood cricket, *Nemobius sylvestris*, Isle of Wight

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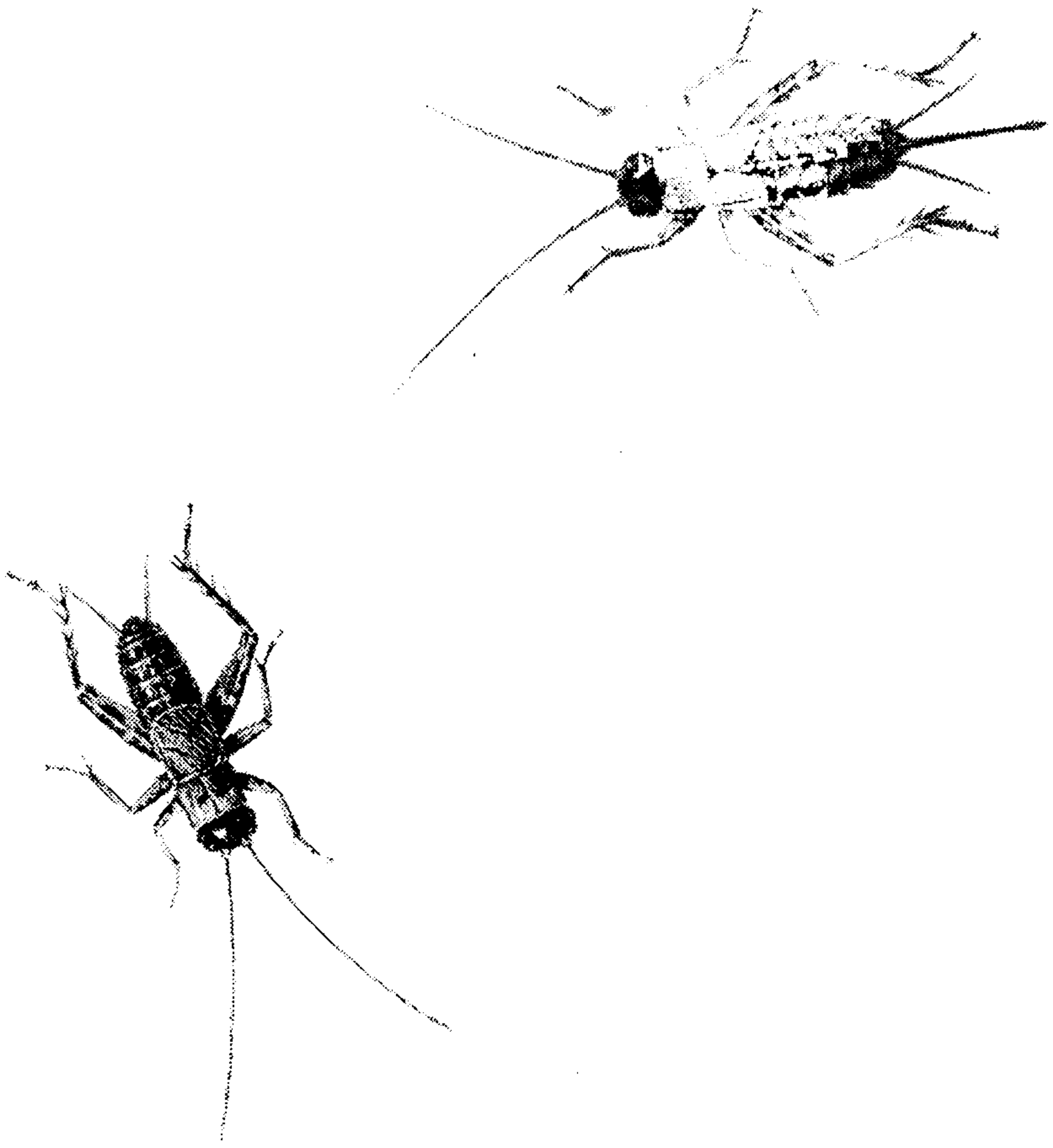


1 Thesis introduction

1.1 Background

1.1.1 Scale

The importance of scale in natural sciences is a recurring point of interest especially in ecology (Levin, 1992; Scott et al., 2002). Working across scales is one of the most challenging subjects in ecology, such that scale issues could become a primary field of research in itself (Wiens, 1989). Choosing the right scale is a key issue in every ecological study (Wiens, 1989; Levin, 1992). The scale of a study is primarily determined by its research aims (Turner et al., 2001; Morrison, 2002). However, if a specific species is the point of interest, then choosing the right scale should primarily be informed by understanding the habitat requirement of the study species used. Species interactions with and perception of the environment (Levin, 1992; Hanski & Gilpin, 1997) as well as relationships between species and environmental factors often change across scales (e.g. Wiens, 1989; Morrison, 2002; Bossenbroek et al., 2005). However, most studies are conducted at only one often-small spatial scale. Translating results obtained at one scale across a range of scales in most cases has proven to be unrealistic (Wiens, 1989; Levin, 1992). Addressing this problem should be a focus in empirical and modelling studies (Wiens, 2002b), especially in the context of generating appropriate tools for conservation management. Ultimately, every study needs to carefully define the appropriate scale that will fit the issues or problems the study is meaning to address.

1.1.2 Theory

In natural sciences, theories are considered the cornerstones for research. Influential theories specifically incorporating or based on scale are increasingly the focus of attention in ecological applications (Turner et al., 2001). For instance, fractal dimension theory (Mandelbrot, 1977) and hierarchy theory (Urban et al., 1987) are being used to analyse patterns in landscapes across scales. Another theory increasingly applied in ecology is percolation theory (With et al., 1997; McIntyre & Wiens, 1999). Percolation theory focuses on how spatial structure of, for example, habitat patches influences the level of connectivity within a heterogeneous landscape. This theory can be used to extract parameter estimates such as thresholds (With, 2002), for process-specific connectivity over a range of spatial scales (Gardner et al., 1989). Furthermore, in conservation management specific key species are often used to inform decisions. Two important theories explicitly incorporating a spatial element in relation to species are the island biogeography theory (MacArthur & Wilson, 1963; 1967) and metapopulation theory (Hanski & Gilpin, 1997; Hanski, 1998). Key features of both theories are based on the spatial arrangement of habitat patches related to species diversity, presence/absence and persistence.

1.1.2.1 Island biogeography theory

Island biogeography theory was developed by MacArthur and Wilson (1963; 1967), and is based on the study of species assemblages on islands. The key principles are based on the influence of island size and distance from the mainland on species diversity. Generally, this theory assumes that large islands sustain more species than smaller ones and islands far away from the mainland have fewer species than islands that are near. A positive linear relationship exists between species richness and area and a negative exponential relationship with distance in this respect. These factors act on the rate of immigration and extinction and ultimately determine how many species are present in time and space for every individual location (MacArthur & Wilson, 1963; 1967). These basic principles of the theory were applied and tailored to terrestrial environments and have been widely used to inform and direct conservation efforts (e.g. Diamond et al., 1976; Bennett, 1999, 2003; Freemark et al., 2002).

1.1.2.2 Metapopulation theory

Metapopulation theory has increasingly replaced the position of classic island biogeography theory in informing conservation efforts (Hanski & Simberloff, 1997; Turner et al., 2001; Breininger et al., 2002). However, the basic principles of island biogeography form the basis of metapopulation theory (Hanski & Gilpin, 1997; Turner et al., 2001). The principal idea of a metapopulation is that landscapes can be considered as a matrix of unfavourable habitat surrounding distinct habitat patches that sustain local species populations. However, a 'classic' metapopulation structure only exists when species dynamics between the habitat patches is such that frequent extinction and recolonisation events occur at the level of individual patches (Hanski & Gilpin, 1997; Hanski, 1998). The main differences with island biogeography are that within a terrestrial landscape metapopulation theory specifically addresses (1) interactions between multiple patches instead of one island relative to a primary mainland source, and (2) focuses on the dynamics/persistence of individual species rather than overall species diversity (Hanski & Simberloff, 1997).

1.1.3 Landscape ecology

Principles derived from a variety of research fields have informed the developing field of landscape ecology. Landscape ecology differentiated itself as a distinct sub-discipline of ecology when the importance of adopting a cross-scale landscape approach in addressing environmental management issues became apparent. Landscape ecology specifically addresses the interactions between spatial patterns and ecological processes within heterogeneous landscapes, across a range of often large spatial scales (Urban et al., 1987; Turner et al., 2001). Although widely applied and accepted, landscape ecology still lacks a strong theoretical basis (Wiens, 1992; Hanski, 1998; Turner, 2005). Theory development aims at simplifying processes in order to identify generalisations relevant to many different situations. When considering a landscape, increasing spatial and temporal scales largely increases the number and complexity of the processes and patterns involved. This might indicate why the field of landscape ecology struggles to produce its own body of theory (Wiens, 2002a). To date landscape ecology is restricted to using relevant theory drawn from other intellectual fields (Turner, 2005) and this can be considered as one of its main weaknesses, potentially undermining its general acceptance in conservation management (Gutzwiller, 2002b). Therefore, many authors repeatedly stress the importance of producing relevant theory within the field of landscape ecology (e.g. Gutzwiller, 2002a; Turner, 2005) to strengthen its position as a subdiscipline of ecological science.

1.1.3.1 Theory integration

Landscape ecologists deal with realistic complex landscapes, and focus on understanding/analysing landscape structure and the interactions between individual landscape features, whereas metapopulation theory focuses on the dynamics of individual populations (Hanski, 1998). It is increasingly recognised that considerable overlap exists in the basic principles used within the fields of landscape ecology and metapopulation biology (Pickett & Cadenasso, 1995; Hanski & Gilpin, 1997; Turner, 2005). However, landscape ecology and metapopulation biology largely evolved independently from each other (Hanski & Simberloff, 1997). Whereas some point out the reluctance of landscape ecologists to incorporate basic metapopulation principles in their research (Hanski & Simberloff, 1997), others point out the fundamental difference between the two fields in regarding the landscape (Forman, 1995; Wiens, 1997), as the main reason for this. Metapopulation ecology essentially views the landscape as holding distinct habitat patches embedded within a homogeneous 'hostile' landscape matrix, where landscape ecologists try to value all landscape features individually. Metapopulation biology clearly is stronger in terms of underpinning theory (Hanski, 1998). However, landscape ecology seems to have established itself firmly within the field of ecology, increasingly by integrating relevant principles and theory from other fields (Pickett & Cadenasso, 1995; Turner, 2005). Combining principles developed in both metapopulation biology and landscape ecology as well as with theories from other scientific fields, shows potential (e.g. in modelling; see With et al., 1997) and should become more accepted (Wiens, 1997), especially in terms of better informing conservation management strategies (Breininger et al., 2002).

1.1.3.2 Landscape simplification

Realistically simplifying the structure of a real landscape is one of the major challenges in landscape ecology. The pattern in the landscape is primarily driven by geological processes, natural disturbances and most of all, anthropogenic influences (Forman & Godron, 1986; Forman, 1995; Pickett & Cadenasso, 1995). Human impacts have, in many areas around the world, resulted in increasingly fragmented landscapes (Forman, 1995). Technological advances in geographic information systems (GIS) and readily available satellite imagery have made it possible to easily quantify this landscape pattern (Turner et al., 2001). The simplest way to quantify landscape pattern is to divide landscapes into distinct patches (e.g. woodland stands) lying within a dominant contrasting matrix (e.g. agricultural land). This oversimplification of landscape pattern is directly rooted in the island biogeography approach and is the basis of metapopulation theory (Hanski & Gilpin, 1997). Another approach often used is to identify additional corridor features in the landscape and is referred to as the patch – corridor – matrix model (Forman, 1995). In this model, patches are regarded as distinct non-linear areas differing from their surroundings (e.g. small woodland patches in an agricultural matrix), corridors are linear features in the landscape distinctly differing from their surroundings (e.g. hedges or roads), and the matrix is the dominating landscape feature in which the patches and corridors are embedded (e.g. agricultural land). This basic simplification of the landscape is often used in modelling efforts and as a basis for analysing how underlying ecological processes relate to landscape pattern (e.g. Hanski & Gilpin, 1997; Scott et al., 2002). However, from a species perspective, differences between matrix, patches and corridors as separate landscape features are often not as distinct.

Landscapes are more likely to act as a mosaic of different habitats interacting with each other (Dale et al., 2000), where each feature has a certain level of suitability for each species to exploit and/or move through (Hobbs, 2002).

1.1.4 Connectivity

Connectivity can be considered in two different ways. It can be looked at from a purely structural/physical or from a functional point of view (Crooks & Sanjayan, 2006). Structural connectivity only considers the pattern and the amount of particular landscape elements, and therefore focuses on the physical level of connectivity. Functional connectivity indicates the level of connectivity based on processes and movement of organisms, influenced by the structural configuration of the landscape elements. In a fragmented landscape, the amount and the spatial configuration of habitat patches determines how they will interact with each other and their surroundings. The key element in this respect is the degree of connectivity between habitat patches (Forman & Godron, 1981; Bennett, 1999, 2003; Crooks & Sanjayan, 2006). This degree of connectivity determines how well nutrients, materials or energy can flow through a system (Forman & Godron, 1986). For functional connectivity, as a rule of thumb, if a particular habitat patch is situated close to another similar patch, it is likely to be more connected in terms of ecological interactions than if it is situated further away. However, the spatial arrangement of habitat patches can be such that distances between patches might be large, but small similar habitat fragments situated in between act as 'stepping stones' facilitating flows and subsequently increasing the degree of connectivity (Forman, 1995). Furthermore, linear features connecting patches might also increase connectivity by acting as a conduit/corridor between them (Bennett, 1999, 2003; Crooks & Sanjayan, 2006). Finally, every landscape feature lying between habitat patches will influence the level of connectivity, based on the resistance it poses to the process under study (i.e. its permeability) (Hobbs, 2002). This level of permeability determines to what extent the feature functions as a conduit or poses a barrier to the flows in the system. Altogether, this means that hypothetically a habitat patch can functionally be more connected to a distant neighbour than to one situated closer by.

1.1.4.1 Species perspective

In conservation, from a species point of view, one aspect determining the level of functional connectivity between habitat patches is how these patches are structurally or spatially arranged within the landscape (Bennett, 1999, 2003; Crooks & Sanjayan, 2006). The main goal of conservation is essentially to provide enough habitat for species to sustain viable and temporal stable populations. So in a fragmented landscape the key questions to be answered are: (i) is there enough habitat available, (ii) at what spatial scale can it be exploited, and (iii) can it be accessed by the species in such a way that it can sustain a viable population? How species experience different landscape features is another issue that has to be determined (Freemark et al., 2002). Every feature between habitat patches will influence the level of functional connectivity in this respect. A key question in this context is whether the species is willing and/or able to exploit and/or move through a particular feature (i.e. how permeable the feature is for the species). A component to be incorporated in determining this level of permeability of landscape features is the movement strategy of individual species. Issues such as how a species moves and how fast it can move through landscape components are critical to determine how permeable a habitat feature is for the species and if it can be used for dispersal (Turchin, 1998). Incorporating the level of permeability in spatially realistic models might highlight the features that need to be targeted and improved in this respect. Overall, increasing the level of functional connectivity by making the intersecting habitat features more accessible or permeable for a species is one aspect that might prove to be an essential focus point for conservation efforts (Bennett, 1999, 2003; Dale et al., 2000).

1.1.5 Habitat networks

Internationally the recent trend in conservation science and practice highlights the importance of reversing habitat loss by preserving, expanding and re-connecting habitat fragments at a landscape scale in order to halt the continuous decline in species diversity. Traditionally, individual habitat patches and/or reserves have been managed regardless of the surrounding landscape. However, research has highlighted the importance of surrounding landscape features acting upon the processes within and between individual reserves (Turner et al., 2001), and the extent of different features functioning as conduits or barriers (Hobbs, 2002). Furthermore, insights developed in the field of landscape ecology have indicated the potential benefits of the development of links or corridors to increase connectivity, reducing the effects of fragmentation (Bennett, 1999, 2003; Crooks & Sanjayan, 2006). Therefore, a trend in conservation policy and practice has developed focusing on the creation of habitat networks (Bennett, 1999, 2003; Hobbs, 2002; Bennett, 2004a; Crooks & Sanjayan, 2006). The principles behind this concept are rooted in the model of distinct habitat patches lying within a more-or-less hostile matrix within the landscape. The primary aim of this concept is to connect individual patches to such an extent that they can interact with each other and form a functional 'network' for species and processes. The concept of developing habitat networks is further supported by insights in ecology that emphasise the positive role of size and negative role of isolation of habitat patches in the wider landscape in terms of species diversity, persistence and occurrence (MacArthur & Wilson, 1967; Forman & Godron, 1986; Hanski & Gilpin, 1997; Turner et al., 2001). Furthermore, connectivity of habitat patches and the permeability of the landscape matrix are considered to be key factors influencing the population dynamics of species within fragmented landscapes (Forman & Godron, 1986; Hanski & Gilpin, 1997; Turner et al., 2001). These insights have resulted in conservation management plans increasingly incorporating the 'network' concept across a range of spatial scales.

Projects following the habitat network approach have been initiated worldwide. Local, regional, nation and continent wide plans have been designed and launched (Bennett, 1999, 2003; Vos et al., 2002; Jongman et al., 2004; Crooks & Sanjayan, 2006). An excellent review on the background of these initiatives is given by Bennett (1999, 2003), including a set of current examples (Vos et al., 2002; also see Hobbs, 2002; Bennett, 2004a; Bennett, 2004b) such as the development of a National Ecological Network in the Netherlands (Jongman, 1995). Designing and implementing network projects often becomes more difficult with an increasing scale (Hobbs, 2002), mainly because of the increasing number of stakeholders involved. Nonetheless, in Europe, a growing number of countries including the United Kingdom, have committed themselves to a landscape-scale approach to conservation of natural resources under the European Landscape Convention (Council of Europe, 2007). Similar commitments have been made focusing on sustainable management of forests (MCPFE, 2003). To date, several continent-wide habitat network schemes have been initiated under the Convention, including the Pan-European Ecological Network and the Emerald Network (Council of Europe, 2007; Jones-Walters, 2007) and forests are incorporated as an integral part of these networks.

1.2 Woodland conservation in the United Kingdom

In the United Kingdom, woodland conservation is currently focusing on efforts to reduce and reverse current fragmentation and habitat loss (Peterken, 2002). This has resulted in the development of several policy initiatives focusing on the concept of creating Forest Habitat Networks (FHN) (Humphrey et al., 2005). These initiatives support the development of new woodland designed to link existing woodland patches or fragments together (Peterken, 2002; Humphrey et al., 2005). This is based on the belief that creating new native woodland on strategic locations reduces the negative effects of habitat fragmentation on woodland biodiversity by providing links and 'stepping stones' between isolated populations of woodland species (Spellerberg & Gaywood, 1993; Kirby & Rush, 1994; Peterken, 1995; Kirby, 1995).

One of the main conservation initiatives in the UK is the Biodiversity Action Plan (UK BAP) (Bendall et al., 1994; UK BAP, 2008). This initiative identifies several ancient woodland types as priority habitat for conservation. Over 30% of all individual species mentioned in the UK BAP are related to woodlands and are indicated as target species for conservation (Forestry Commission, 2005). The England Forestry Strategy (EFS) (Forestry Commission, 1998) and the revised UK Forestry Standard (Forestry Commission, 2004) point out that many of the UK's native ancient and semi-natural woodlands are fragments of historically more extensive woods. Restoring and increasing the total amount of woodland area is therefore one of the main conservation targets in the UK (Forestry Commission, 2004). As a result, one of the objectives identified in these policy initiatives is to target grants through the England Woodland Grant Scheme (EWGS) (Forestry Commission, 2006a) and the Environmental Stewardship (Rural Development Service, 2005) to reverse the negative effects of habitat loss and fragmentation by promoting the creation of new woodland, expanding existing ancient and native woodlands (Defra, 2005). Careful planning and targeting suitable areas for restoration is a key element of achieving these policy goals (Petit et al., 2004; Lee & Thompson, 2005).

The targeted approach in the development of habitat networks was adopted by the Forestry Commission and resulted in the 'JIGSAW' Challenge (Joining and Increasing Grand Scheme for Ancient Woodlands) (Forestry Commission, 2005), which was an initiative developed under the Woodland Grand Scheme (WGS) (Forestry Commission, 2003). To contribute to sustainable forest management, this initiative implemented landscape ecological principles by funding the expansion and linkage of semi-natural woodland in key areas of special conservation concern (Forestry Commission, 2005). This initiative together with the WGS is now included in the EWGS. A further aim is to restore planted ancient woodland sites (PAWS) by removing non native tree species in order to preserve their remaining ancient characteristics and biodiversity (Defra, 2005). The Forestry Commission has included similar targets in their long-term Forest Design Plans (Forestry Commission, 2007), aiming at restoring Forestry Commission woodlands on historical ancient woodland sites. The Woodland Trust has adopted similar approaches in their strategic conservation policy, which refers to increasingly incorporating a landscape-scale approach in their conservation efforts (Woodland Trust, 2003). To support this initiative, in 2004 the Woodland Trust organised an international conference in collaboration with the International Association for Landscape Ecology (IALE (UK)), which focused on the landscape ecology of woodlands (Smithers, 2004). Throughout the UK, landscape-scale strategies are being adopted in numerous local initiatives (Humphrey et al., 2003) and are presently the main mechanism for reversing the negative impacts of woodland habitat fragmentation.

Although the value of restoring, expanding and linking woodland fragments has a strong theoretical basis, little empirical evidence is available to support the application of these principles in practice (Bennett, 1999, 2003; Dolman & Fuller, 2003; Bailey, 2007). This raises the question whether current policy and related strategic plans and initiatives are going to deliver their intended results, and highlights the need for more empirical studies on species and communities particularly across a range of spatio-temporal scales (Wiens, 2002b). Furthermore, research is lacking on the factors influencing movement of woodland species at the landscape scale (Dolman & Fuller, 2003). The basic aim behind reversing the effects of fragmentation and creating habitat networks is to increase connectivity, which is assumed to be beneficial for species persistence by enhancing migration between populations (Bailey, 2007). However, Bailey (2007) also stresses the need to further strengthen the empirical evidence base for the development of habitat networks in order to decide what management strategy is likely to provide the highest conservation return. How woodland species move through the landscape is a key question that needs to be addressed in this respect. However, the understanding of and factors acting on the dispersal ability of many woodland taxa are still poorly understood (Dolman & Fuller, 2003). This lack of knowledge stresses the need to test the assumptions on which current conservation management and policy is based.

1.3 Project outline

1.3.1 Project objectives

1. To review the empirical evidence regarding the dispersal ability of different species and functional groups of organisms, in relation to their ecological traits and the characteristics of wooded landscapes.
2. To analyse the key factors influencing species colonisation of woodlands, with particular reference to processes operating at the landscape scale, through a programme of field-based research.
3. To examine the potential impacts of current approaches to development and management of wooded landscapes on species composition.

1.3.2 Context

Species greatly differ in their habitat needs. Relatively small animal species often use habitats at small spatial scales, only needing a few different resources during their, often short, life-cycle. Large animals generally live longer and operate at large spatial scales, utilising a wider array of resources compared to smaller species. Conservation efforts therefore require information on the amount and distribution of habitat that is necessary for a particular species at a variety of different spatio-temporal scales. Furthermore, our understanding of the dispersal abilities of many taxa is severely limited (e.g. Bowne & Bowers, 2004) and the mechanisms that contribute to low dispersal are often poorly understood (Turchin, 1998; Dolman & Fuller, 2003). Studies on large mammals and birds account for the majority of previous investigations (Scott et al., 2002; Bowne & Bowers, 2004); however these species are relatively mobile and are therefore capable of readily crossing unsuitable areas (matrix) to reach their preferred habitat patches. To address these issues for woodland species, Dolman and Fuller (2003) suggest that more studies are necessary on a variety of woodland taxa to provide a firmer basis for current management strategies. Specifically studies on woodland invertebrate species are underrepresented in the scientific literature (Mazerolle & Villard, 1999; Bowne & Bowers, 2004).

Previous research has indicated that woodland invertebrate specialist species show a decline in species diversity with an increase in habitat loss and subsequent fragmentation (Niemelä et al., 1988; Lövei & Cartellieri, 2000; Magura et al., 2001; Barbaro et al., 2005). Whereas generalist species generally use both habitat inside and outside woodlands (Magura et al., 2001), woodland specialist species often demonstrate very specific habitat requirements and therefore occupy only very specific habitat niches within the interior of woodlands (Ranius, 2002). This makes them vulnerable to changes in their environment specifically because of their often low dispersal ability (Magura et al., 2001; Ranius & Kindvall, 2006). Species intermediate in their degree of habitat specialism but limited in their dispersal ability have largely been ignored as study species in previous research, but might benefit most from current conservation efforts (Bailey, 2007). Developing habitat networks by linking woodland fragments with corridors is unlikely to facilitate dispersal of species that are dependent on woodland interiors, at least in the short term (Dolman & Fuller, 2003). However, it might potentially benefit species that are not able to cross a hostile matrix (e.g. arable land) but can traverse through relatively new woodland and/or semi-natural habitat (Bailey, 2007). How the intermediate group of relatively immobile woodland species utilise the landscape remains a gap in knowledge that needs to be addressed.

1.3.3 Choice of experimental species

To address this gap in knowledge, a suitable study candidate needed to be identified. An initial meeting with local stakeholders and specialists held on the Isle of Wight on the 4th of April 2005 resulted in a shortlist of candidate species. In this meeting, it was recognised that woodland invertebrates were a good candidate group for study. These species are a dominant and important group within woodland ecosystems, for example by serving as a food source for many other woodland organisms (Warren & Key, 1991). A further meeting with a local entomologist (Adam Wright; Ventnor, Isle of Wight) resulted in a shortlist of candidates extracted from the BAP species list for the Isle of Wight (Isle of Wight Biodiversity Action Plan Steering Group, 2000). The candidate invertebrates were selected following a set of criteria based on the species characteristics and known distribution on the island. The following selection criteria were used in order of decreasing importance: the species had to (1) be affiliated with deciduous woodland for most of their life-cycle, (2) have restricted dispersal ability, (3) be of national and/or local conservation concern, and (4) be present in sufficient numbers in order to permit experimental analyses. Additionally, to increase the time for conducting experiments, species with a relatively long lifespan were preferred over species with a short activity window. The final selection of the candidate species was based on a literature review to verify if all criteria would be met.

The species that was selected meeting all these criteria was the woodland invertebrate species, the wood cricket (*Nemobius sylvestris*). Wood cricket are bound by their life-cycle requirements to woodland habitat, because it needs a well-developed leaf litter layer to reproduce (Brown, 1978). Wood cricket have restricted dispersal ability, being small and flightless (Richards, 1952). These characteristics suggest that it is a species that might be expected to benefit from the existence of a wooded habitat corridor in order to move between habitat patches. In the UK the species is classified as nationally scarce and is both nationally and locally designated as a Species of Conservation Concern (Isle of Wight Biodiversity Action Plan Steering Group, 2000; NBN Gateway, 2007). Furthermore, when present at an area where habitat conditions are suitable, population densities are often high (Gabbutt, 1959). This is especially beneficial in terms of being able to locate, catch and use individual specimens for more detailed study without having a significant impact on their overall population persistence. In addition, the constant stridulation of the males in the summer makes it easy to quickly establish their presence at a woodland site (Proess & Baden, 2000).

1.3.4 Wood cricket (*Nemobius sylvestris*) biology

Wood cricket can be considered as intermediate between woodland generalist and specialist species. It is not a woodland specialist *per se*, in that it is not restricted to a small habitat niche in the interior of woodlands but is predominantly found on wooded edges (Richards, 1952). During their entire life-cycle, wood cricket can be found in wooded areas within a matrix of open and closed canopy habitat. Wood cricket lives on the ground and is strongly linked with, but not restricted to, deciduous and often oak- (*Quercus spp.*) dominated woodland. Wood cricket prefers a well-developed leaf litter layer that is used for shelter and serves as food source, although the species is omnivorous (Richards, 1952; Gabbutt, 1959; Proess & Baden, 2000; Koehler & Samietz, 2006). Viable wood cricket populations are restricted to locations with a well-developed leaf litter layer, which is used as a breeding ground and as a nursery (Brown, 1978) (see Appendix III).

Both Gabbutt (1959) and Brown (1978) studied the life-cycle of wood cricket in the UK. In Britain, wood cricket has a two-year (semi-voltine) life-cycle involving two overwintering stages. The life-cycle includes eight nymphal (i.e. instar) stages. In the first year from August to November, adult wood cricket lay their eggs in the soil beneath the litter layer after which the eggs go into diapause and overwinter. The next year in late June, the eggs hatch and the juveniles (i.e. nymphs) develop throughout the summer and autumn by means of moulting up to the 5/6th instar stage. Moulting ceases completely in September where the nymphs will overwinter finding shelter in the litter layer. The second year of its development starts in spring, where the nymphs continue to develop from April onwards. After the last instar stage (8th), the first adults appear in July/August and are reproductively active through to September/October. Occasionally adults overwinter, however are unable to reproduce and soon die-off in the following spring. This semi-voltine life-cycle results in the coexistence of nymphs of the 1st – 5/6th instar and adult wood cricket during the second half of each summer. The adult wood cricket grows up to approximately 0.9 – 1.1 cm in body size, males being always slightly smaller than females (Richards, 1952) (see Appendix III). They are unable to fly and move by way of walking or hopping (Richards, 1952). The male adult wood crickets produce a soft chirping sound (stridulation) by rubbing their wing remains together. This stridulation is associated with territorial and competitive behaviour amongst the males and is also thought to have an attracting effect on female wood crickets (Richards, 1952). The produced sound is very characteristic and is easily distinguishable from grasshoppers and other crickets (Proess & Baden, 2000). Furthermore, this stridulation is readily audible from 15 °C and above and is produced both during the day and during the night (Richards, 1952).

1.3.4.1 European distribution

Wood cricket is found both on mainland Europe and Britain (including the Isle of Wight) indicating that it was probably already present on the UK mainland before separation of the landmasses, which took place more than 7000 years ago (Scaife, 2003). In Europe the species is widespread from the Mediterranean to northern Europe, reaching its Northern limit in the United Kingdom, Holland, Germany and Poland (Chinery, 1977; Brown, 1978; Marshall & Haes, 1988; Wallaschek, 1997). In the UK wood cricket was first recorded in the New Forest (Richards, 1952; Marshall & Haes, 1988). The species is found in three main areas in the South of Britain (Marshall & Haes, 1988). The largest continuous area where wood cricket is found is in the New Forest (Hampshire), the other locations being South Devon and the Isle of Wight (Marshall & Haes, 1988; NBN Gateway, 2007).

1.3.5 Study area

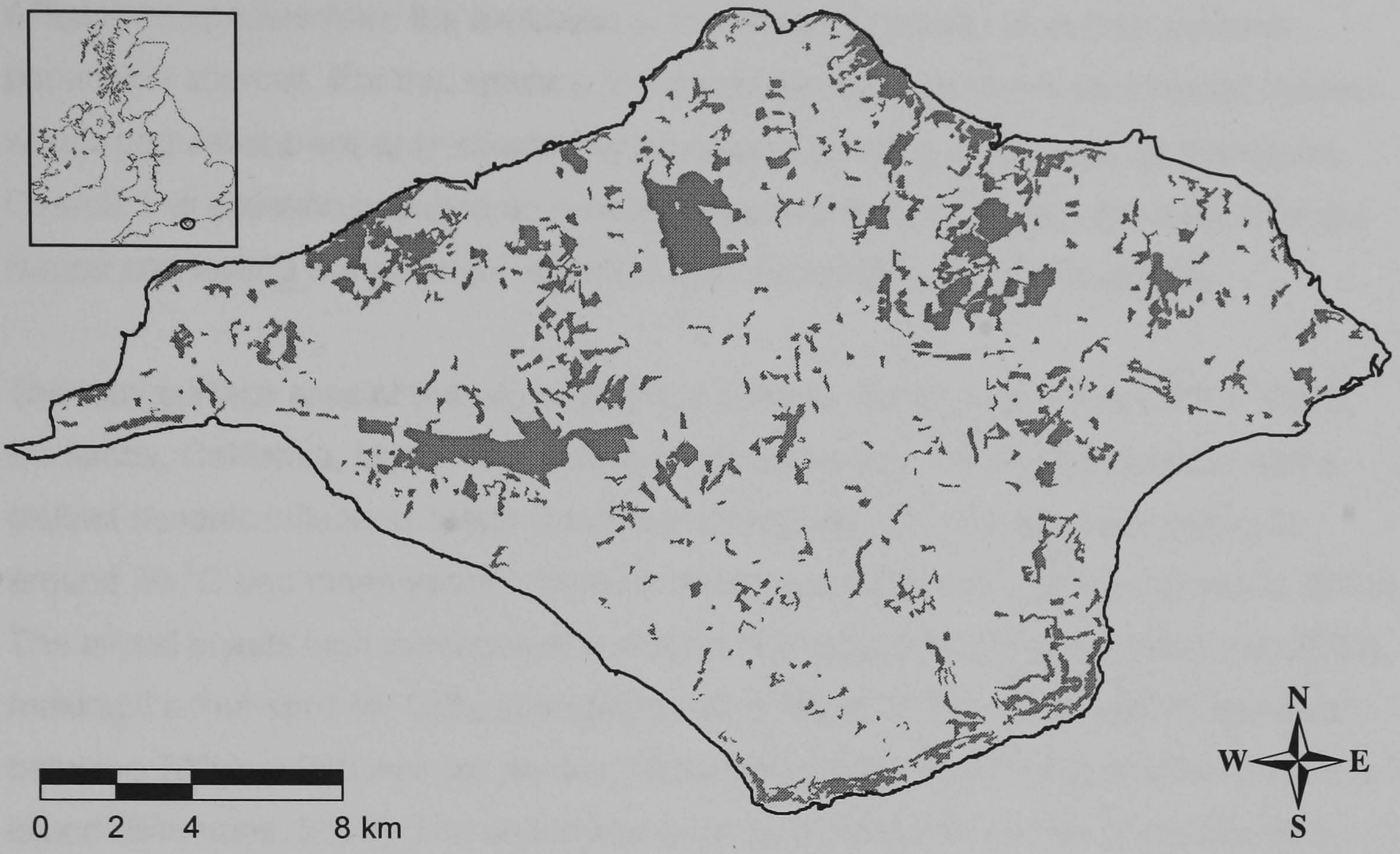


Figure 1: The woodland fragments on the Isle of Wight. Derived from digital maps based on the National Inventory of Woodland and Trees (NIWT) (Smith & Gilbert, 2003).

The research was undertaken on the Isle of Wight situated between 50° 39' N, 1° 35' W and 50° 40' N, 1° 04' W in the South of the United Kingdom (Figure 1). Selection of this study area was based on the following criteria. The study area needed to provide a landscape characterised by the impacts of fragmentation, with a range of different native woodland fragments varying in size and degree of isolation (Figure 1). Furthermore, the area needed to be a targeted site of active woodland restoration and reforestation. For wood cricket, only three candidate areas were available, and of these, only the Isle of Wight met all of the criteria. The fragmented structure of the landscape on Isle of Wight made it ideal for a landscape-scale research approach (Figure 1). It was further selected because the area was one out of eight key areas receiving special conservation efforts regarding woodland creation targeted under the 'JIGSAW' scheme (Forestry Commission, 2005) and has since been the focus of ongoing conservation management involving woodland habitat restoration and expansion (Forestry Commission, 2006a). A number of woodland areas scattered over the island were specifically targeted in order to increase connectivity between woodland fragments (Quine & Watts, 2007), making these sites ideal for more detailed study on the dispersal abilities of wood cricket. Additionally, the majority of woodland sites on the

Isle of Wight supporting wood cricket populations have some form of national protection status (NBN Gateway, 2007). Further benefits of working on an island using a flightless species were the exclusion of the effects of immigration from external population sources. For this species, the island can be considered as a closed system where populations are only affected by processes working at the scale of this island. Overall, this situation provided an excellent opportunity for research focusing on scale issues and testing the potential effectiveness of current conservation efforts.

The total surface area of the Isle of Wight is 388 km² (estimated in ArcGIS 9.1; ESRI, Redlands, California, USA). The area is characterised by a temperate climate with a distinct oceanic influence. Mean maximum temperatures in the warmest month lie around 20 °C and mean yearly minimum temperatures around 7.5 °C (Simmons, 2003). The Island boasts high averages of sunshine of around 5 hours daily (Simmons, 2003), making it a 'hot-spot' for Orthoptera (Marshall & Haes, 1988). Mean rainfall levels lie between 700 and 900 mm per annum, dependant on the topographical location on the island (Simmons, 2003). The underlying geology of the northern half of the island is dominated by Tertiary clays and the southern part by Lower Greensands (Insole, 2003). A central Chalk ridge divides the northern and southern part of the island. The soils in the southern half are light sandy and well-drained, whereas the northern soils are mainly poor draining heavy clays and silts (Insole, 2003). These characteristics make cultivation difficult, hence most native woodlands are situated/survived on the northern half of the island (Insole, 2003).

The landscape matrix is dominated by urban and agricultural land with a scatter of woodland patchily distributed across the island (Figure 1). The total woodland area including recent new planted sites currently covers 51.2 km² (5120 ha) or 13% of the island surface. Following the classification of the 'Ancient Woodland Inventory' (English Nature, 1998 - 2006; Smith & Gilbert, 2003), based on continuous woodland cover since 1600 AD, of the total woodland area, 68% of the woodlands on the island are of secondary origin. The remaining 32% still retain ancient woodland characteristics, of which 17% is classified as ancient semi-natural woodland (ASNW) and 15% as planted ancient woodland sites (PAWS) (i.e. planted with non-native, mainly coniferous, tree species) (all percentages estimated in ArcGIS 9.1, ESRI, Redlands, California, USA). Historically, the vegetation on the northern half of the island was dominated by deciduous woodland and flower-rich meadows, and the southern half by extensive heathland and acidic wetland vegetation (Pope, 2003). At present only small fragments of semi-natural habitat remain in the predominant agricultural matrix. The presence of open woodland species such as Narrow-leaved Lungwort (*Pulmonaria longifolia*) and Wood Anemone (*Anemone nemorosa*) indicate that the majority of woodlands on the island historically were coppiced, however this practice has been mostly abandoned (Pope, 2003). The current deciduous woodlands in the northern half are dominated by Pedunculate oak (*Quercus robur*) and Ash (*Fraxinus excelsior*), with frequent occurrence of Field maple (*Acer campestre*). In the southern half Pedunculate oak (*Quercus robur*) with Birch (*Betula* spp.) and bracken undergrowth are dominant, and Willow (*Salix* spp.) and Alder (*Alnus glutinosa*) are frequent in the woodlands situated on the more humid soils around the river valleys (Pope, 2003).

1.3.6 Single species approach

The decision to investigate a single species rather than multiple species was based on a number of factors. This choice was informed by following a reverse planning strategy, which is a useful approach for planning ecological field studies (Sutherland, 2006). This strategy involves a process of systematically assessing what is necessary to reach the objectives of the study and most importantly, what is possible in terms of the time that is available (Sutherland, 2006). The key topics that had to be addressed in this project were landscape-scale processes acting on species colonisation and related ecological traits, such as dispersal, that influence colonisation in wooded landscapes (see 1.3.1 Project objectives). First and foremost, landscape-scale surveys and dispersal studies are known to be highly time consuming (Turchin, 1998). Therefore, these time restrictions had to be considered in order to design appropriate and realistic census strategies to address the key topics of this project. Many species particularly restricted to woodland habitat are often so specialised that they only inhabit a small niche and occur in small numbers, making individuals difficult to locate and posing particular challenges for detailed study (Ranius, 2006). When assessing multiple woodland species, rapid surveys are therefore impossible and this poses restrictions on the scale of the study, in terms of the area that can be included. The possibility of including more species simultaneously within a study could potentially be achieved when examining highly specialised species inhabiting one specific habitat substrate (e.g. Rukke, 2000; Ranius, 2002). However, because dispersal traits are generally highly species-specific, detailed studies on dispersal still need to be carried out on individual species (Turchin, 1998; Ranius, 2002). Assessment of the dispersal ability of a species needs in depth knowledge of their biology (Turchin, 1998). Therefore, dispersal studies are recognised to be very time consuming and often difficult to perform (Turchin, 1998).

Furthermore, using a single species has the great benefit of being able to examine both patterns and processes in greater depth (e.g. Ranius, 2000b; Berggren, 2001). Single species can be used to investigate species traits and factors affecting species dispersal ability and colonisation across a range of scales (Ranius, 2000b; Berggren, 2001). Multi-species studies lack this possibility of in-depth exploration of movement traits, especially across different scales. Performing research across a range of scales makes it possible to identify at what scale a particular process operates and permits an evaluation of its importance in terms of conservation efforts. However, it is recognised that a single species study should not be the sole basis of informing management actions (James & McCulloch, 2002). The particular limitation of single-species studies is that the results obtained may have limited wider applicability. However, by comparing findings of similar studies, generalisations can be made by identifying groups of species with matching habitat preferences that operate at similar scales and in similar ways. In the current investigation, this was achieved by undertaking a systematic review, focussing on identifying groups of woodland invertebrates living in temperate forest ecosystems that were similar to wood cricket in terms of habitat preferences and dispersal ability.

1.4 Thesis structure

1.4.1 Work sequence

Studies on wood cricket examining the factors influencing its distribution across a range of scales and its dispersal ability through different habitats outside and within woodlands have never been conducted previously. In fact, such an integrated assessment of factors affecting movement has rarely been undertaken with any woodland invertebrate species.

At the outset of the investigation, the available information of wood cricket presence on the Isle of Wight was scattered and largely outdated (NBN Gateway, 2007). Therefore, a survey was carried out in the summer of 2005 to determine the landscape-scale distribution of wood cricket focusing on the woodland fragments present on the Isle of Wight. After establishing their presence and absence at the landscape scale, a study was conducted in 2006 focusing on three separate woodland fragments aimed at analysing the factors influencing their distribution at fine scales within woodlands. To provide a wider context for this study, in 2006/2007, a systematic review of the literature was conducted with the aim to identify similarities between wood cricket and other woodland-associated species focussing on their habitat specialism and related dispersal ability. Finally, informed by the findings of the systematic review, in 2007, a series of experiments were undertaken to examine the dispersal ability and role of specific factors influencing movement and dispersal of wood cricket within features represented by a wooded 'network' landscape. The overall rationale behind the research strategy/sequence described here was to examine processes and factors influencing dispersal ability of wood cricket across a range of different spatial and temporal scales, informed by observations made in the field. The ultimate aim of this strategy was to understand the processes influencing wood cricket distribution and to inform conservation efforts, specifically the design of woodland habitat networks.

1.4.2 Chapter outline and aims

Chapters 2 – 6 are structured as individual papers that will be submitted for publication in scientific journals (see Appendix I). The original project objectives of this study (1.3.1 Project objectives) are addressed as follows. Each chapter presented in this thesis addresses one or a specific part of the original project objectives. For each chapter, these objectives were translated into specific aims matching the context of the individual investigations and species used. Objective 1 is addressed in Chapter 4; Objective 2 is addressed in Chapters 2, 3, 5 & 6; and Objective 3 is addressed in Chapter 7. The individual aims addressed in Chapters 2 – 7 are listed below.

Chapter 2 focuses on the landscape scale distribution of wood cricket addressing the following aims:

1. To determine the landscape scale distribution of wood cricket on the Isle of Wight.
2. To test the relationships between wood cricket presence/absence and (*a*) patch area, (*b*) isolation (i.e. Euclidean distance) (*c*) measures of habitat availability, and (*d*) patch age.
3. To develop a deterministic model for wood cricket presence.

Chapter 3 focuses on habitat requirements and the distribution of wood cricket within woodlands addressing the following aims:

1. To test the relationships between wood cricket presence/absence and (*a*) ground habitat (i.e. leaf litter depth and volume), (*b*) vegetation structure (i.e. ground vegetation cover, vegetation height, canopy closure), and (*c*) isolation measures (i.e. Euclidean distance).
2. To develop a deterministic habitat suitability model.

Chapter 4 presents a systematic literature review of empirical evidence on movement rates of woodland invertebrates addressing the following aims:

1. To systematically identify studies within the published scientific literature providing direct measures of movement for woodland invertebrate species.
2. To examine whether ground-dwelling woodland invertebrates can be grouped based on movement rate (m day^{-1}) (i.e. dispersal ability) and habitat specialism.
3. To examine the relationships between movement rate, body size and habitat specialism.

Chapter 5 focuses on the movement strategy of wood cricket nymphs and adults through different ground surface habitats addressing the following aims:

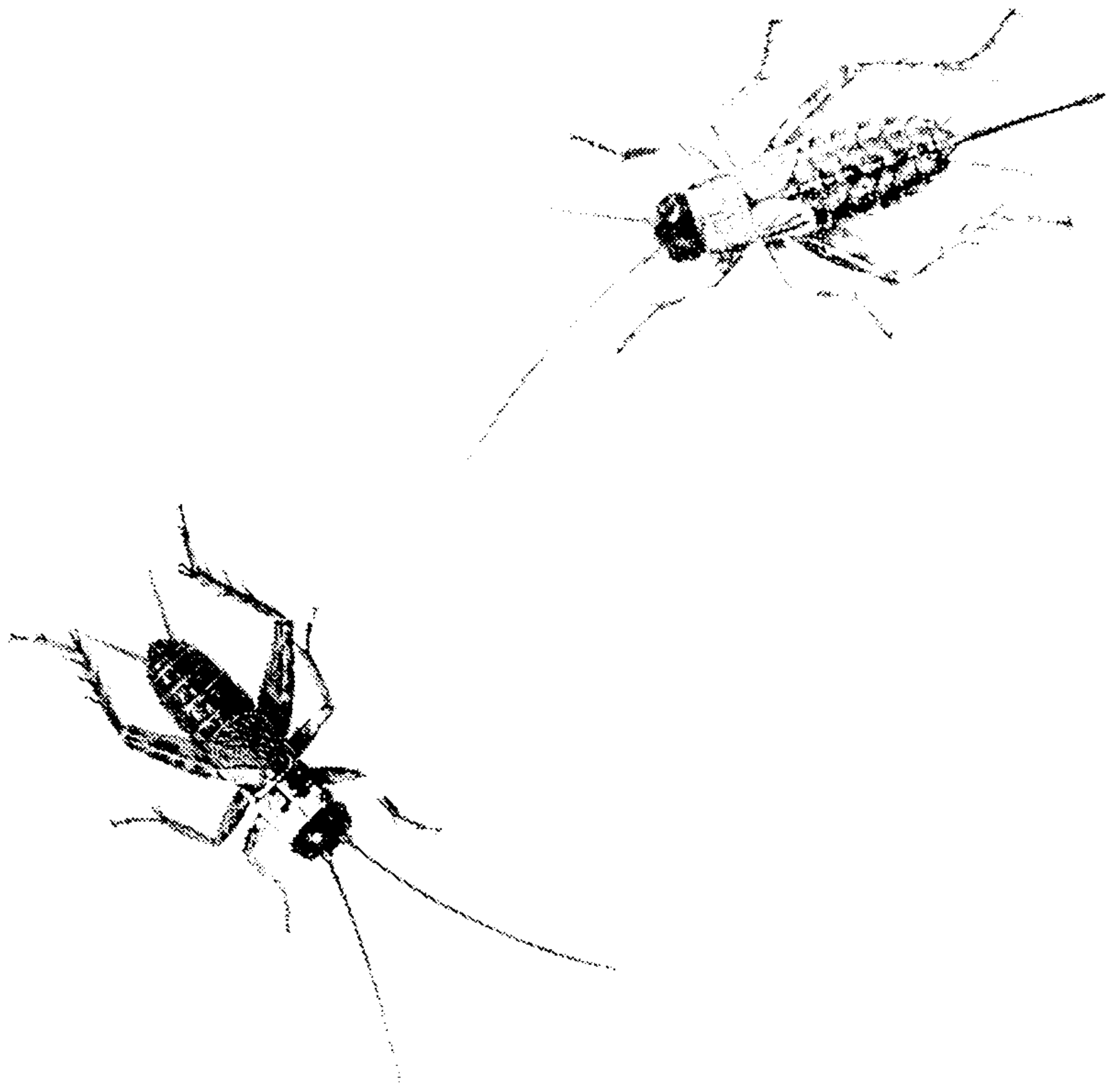
1. To explore the movement strategy of wood cricket nymphs and adults under different ground cover conditions.
2. To determine the rate of movement for both nymphs and adults under different ground cover conditions.
3. To determine the preferred ground cover/habitat of both adults and nymphs when presented with a choice.

Chapter 6 focuses on factors influencing dispersal of wood cricket addressing the following aims:

1. To model empirically the dispersal of wood cricket nymphs and adults (males and females).
2. To determine to what extent wood cricket nymphs and adults (males and females) move along corridors and through sub-optimal habitat.
3. To determine what factors influence their choice of habitat.
4. To determine whether wood cricket nymphs and adults (males and females) can cross a water barrier.
5. To what extent adult wood cricket are able to orientate themselves in the landscape.

Chapter 7 integrates and discusses the results of chapters 2 – 6 and focuses on assessing whether current woodland management initiatives and policy are appropriate for the conservation of wood cricket and similar woodland invertebrate species. The aims addressed here are:

1. To determine the appropriate scale for conservation directed at wood cricket and associated invertebrate species.
2. To evaluate the potential gain of creating forest habitat networks for wood cricket and associated species.



2 The influence of habitat and landscape structure on the distribution of wood cricket (*Nemobius sylvestris*) on the Isle of Wight, UK

2.1 Introduction

In recent years, many habitats and species have been subjected to increasing anthropogenic pressure. Activities such as agricultural intensification and exploitation of natural resources have resulted in substantial habitat loss and fragmentation of natural habitats (Forman & Godron, 1986; Andrén, 1994; Forman, 1995; Pickett & Cadenasso, 1995), which are both increasingly being recognised as principal drivers of worldwide biodiversity loss (Hanski, 1998; Fahrig, 2003). These effects are typically evident at the landscape scale, with many landscapes now being characterised by a mosaic of different agricultural land use types, often with fragments of native habitat embedded within them. Examples of historic and ongoing fragmentation acting on natural habitats include the tropical rainforest landscapes in Amazonian Brazil (Michalski & Peres, 2005), south temperate and tropical montane forests (Newton, 2007), the Rocky Mountains (Reed et al., 1996) and the fragmented woodlands in the British countryside (Peterken, 2000; Smith & Gilbert, 2003).

In a fragmented landscape, the biodiversity supported in remnants of natural habitat is commonly influenced by the quality and amount of habitat available within individual habitat fragments, and the spatial configuration of the fragments within the landscape (Andrén, 1994; Fahrig, 2003). In terrestrial environments the most common relationships explored for predicting species diversity at the landscape scale are based on fragment or patch area and measures of connectivity, and a substantial body of literature is now available highlighting such relationships (Andrén, 1994; Mazerolle & Villard, 1999; Bennett, 1999, 2003; Ewers & Didham, 2006; Bailey, 2007). Many studies have recorded a positive relationship between species diversity and fragment area and a negative relationship between diversity and the level of isolation. Both of these relationships are consistent with island biogeography theory (MacArthur & Wilson, 1963; 1967). However, these relationships vary in their precise response and degree of significance among and within different taxonomic groups, primarily because of variation in habitat specialism and the level of permeability of the matrix for different groups of organisms (MacArthur & Wilson, 1967; Andrén, 1994; Mazerolle & Villard, 1999; Bennett, 1999, 2003; Lövei et al., 2006). For instance, in a study conducted in the Carpathians (Hungary/Ukraine) on the effects of forest fragmentation, Magura et al. (2001) found that the total number of generalist carabid beetle species decreased with the size of the forest fragments, whereas for specialist carabid diversity this relationship was positive. They further found that the number of generalist species increased with isolation, whereas the number of specialist species decreased.

While the majority of previous investigations have focused on relatively mobile large-bodied species (e.g. vertebrates and birds; (Andrén, 1994)), a substantial body of literature has also developed examining the diversity and abundance of relatively small ground-dwelling woodland invertebrates in fragmented landscapes (e.g. Niemelä et al., 1988; Usher et al., 1993; Margules et al., 1994; Didham, 1997; Mazerolle & Villard, 1999; Lövei & Cartellieri, 2000; Jukes et al., 2001; Magura et al., 2001; Barbaro et al., 2005; Debuse et al., 2007; Bailey, 2007), mainly focussing on woodland carabid assemblages. From these studies, a number of patch characteristics in addition to patch area have been found to influence species diversity, including within-patch habitat availability (Mazerolle & Villard, 1999; Jukes et al., 2001; Barbaro et al., 2005), amount of edge (Didham, 1997; Barbaro et al., 2005), patch shape (Usher et al., 1993; Magura et al., 2001; Barbaro et al., 2005) and patch age (Jukes et al., 2001). In these studies, various combinations of patch variables together with patch area and measures of isolation explained the variation in beetle diversity within woodland fragments.

Relatively few studies have assessed the factors influencing the presence/absence of individual species within fragmented wooded landscapes (Andrén, 1994; Mazerolle & Villard, 1999; Bailey, 2007). In particular, studies on the distribution of invertebrate species at the landscape scale are underrepresented in the literature (Mazerolle & Villard, 1999; Bailey, 2007). However, the available information again indicates the importance of patch area and connectivity as key variables influencing the distribution of individual species at the landscape scale as shown in studies on plants (Grashof-Bokdam, 1997), mammals (Andrén, 1994; Mazerolle & Villard, 1999; Bennett, 1999, 2003) and birds (Andrén, 1994; Mazerolle & Villard, 1999). Studies on relatively immobile woodland specialist beetle species showed differences in area effect and generally no isolation effect on their patterns of distribution (i.e. presence/absence) (Rukke & Midtgaard, 1998; Ranius, 2000a; Rukke, 2000). However, a study on a mobile butterfly species classed as a woodland edge generalist (i.e. common in woody edge habitat) showed a significant negative isolation effect and a positive area effect between habitat locations (Chardon et al., 2003). Furthermore a study on a ground-dwelling non-flying large mobile woodland carabid beetle classed as a woodland generalist (i.e. using both interior and exterior woody habitat) showed a significant negative isolation effect (Petit & Burel, 1998), although the effect of area was not tested. A further factor that appears to influence the distribution of woodland invertebrate species in fragmented landscapes is habitat availability within individual patches. Previous studies on tree associated specialist beetle species all found a positive effect of within-patch habitat availability on patterns of distribution (Rukke & Midtgaard, 1998; Ranius, 2000a; Rukke, 2000). Within-patch habitat availability variables therefore appear to have strong predictive power when considering the distribution of invertebrate species in fragmented landscapes. Together, this suggests that at the landscape scale, woodland species respond differently to fragmentation depending on their mobility, degree of habitat specialism and within-fragment habitat availability.

No previous study has examined the landscape-scale effects of woodland availability together with within-patch habitat availability and fragment age, on the presence/absence of a non-flying ground-dwelling woodland invertebrate species. This investigation therefore examined the effects of patch area, isolation, habitat availability and patch age on the incidence of such a species within woodland fragments in an agricultural landscape. The study was performed on Wood cricket (*Nemobius sylvestris*) on the Isle of Wight, United Kingdom. Wood cricket is a non-flying cricket species that is strongly associated with native broadleaved woodland, typically dominated by oak (*Quercus spp.*) (Richards, 1952). The species is characteristic of relatively open areas, including wooded edges, clearings, tracks and rides (Richards, 1952). The insects live on the ground and prefer a well-developed leaf litter layer which provides shelter, and acts as a primary food source and breeding ground (Richards, 1952; Gabbutt, 1959; Brown, 1978; Proess & Baden, 2000). In Europe the species is widely distributed from the Mediterranean countries through central Europe, reaching its Northern limit in the United Kingdom (UK), Holland, Germany and Poland (Chinery, 1977; Brown, 1978; Marshall & Haes, 1988; Wallaschek, 1997). In the UK populations of the species are only found in the South of England at three main locations, the New Forest (Hampshire), in South Devon and on the Isle of Wight (Marshall & Haes, 1988; NBN Gateway, 2007). In the UK, wood cricket is classified as 'Nationally Scarce' and designated as a 'Species of Conservation Concern' (NBN Gateway, 2007).

In the UK, and throughout Europe, landscape-scale approaches are increasingly becoming the focus of conservation management efforts involving connecting and increasing the extent of natural habitat in order to reverse the negative impacts of habitat loss and fragmentation on biodiversity (e.g. Hobbs, 2002; Humphrey et al., 2005). In Europe a growing number of countries, including the United Kingdom, have committed themselves to a landscape-scale approach to conservation of natural resources under the European Landscape Convention (Council of Europe, 2007) and similar commitments have been made focussing on sustainable management of forests (MCPFE, 2003). This reflects a current trend in conservation focussing on the creation of habitat networks aiming at developing physical links (i.e. corridors) between habitat fragments to increase connectivity and consequently reduce the negative effects of fragmentation (Bennett, 1999, 2003; Hobbs, 2002). In the case of woodland habitat on the Isle of Wight, this has resulted in several initiatives aiming to increase the total woodland cover as well as to increase connectivity between individual fragments (Quine & Watts, 2007). However, the lack of empirical knowledge on the dispersal ability of woodland species (Dolman & Fuller, 2003) and on the effects of increasing connectivity on such species (Bennett, 1999, 2003) raises the question of whether these efforts will deliver their expected benefits for biodiversity.

This study addressed the following aims: (1) to determine the landscape scale distribution of wood cricket on the Isle of Wight (UK), which was largely unknown at the outset of this investigation (NBN Gateway, 2007); (2) to test the relationships between wood cricket presence/absence and (*a*) patch area, (*b*) isolation (i.e. Euclidean distance) (*c*) measures of habitat availability and (*d*) patch age; and (3) to develop a deterministic model for wood cricket presence. Based on the general findings of previous fragmentation research it was hypothesised that wood cricket would be more likely to be present in woodlands that: (*1*) are large rather than small, (*2*) are spatially aggregated rather than isolated, (*3*) have a long outside edge rather than short, (*4*) are more complex shaped than simple, (*5*) provide a high amount of edge habitat, and (*6*) are old (i.e. long-established) rather than young. The results of this study were further used to critically evaluate the principles underpinning current management strategies and to identify the broader implications for landscape-scale conservation efforts.

2.2 Methods

2.2.1 Study area

A survey was carried out in the woodlands of the Isle of Wight (UK) situated between 50° 39' N, 1° 35' W and 50° 40' N, 1° 04' W (Figure 2). The total surface area of the Isle of Wight is 388 km² (estimated in ArcGIS 9.1 (ESRI, Redlands, California, USA)). Total woodland area is currently 51.2 km² (5120 ha) or 13% of the island (Figure 2). The landscape matrix is dominated by urban and agricultural land with woodland patches distributed across the island. Of the total woodland area, 32% is classified as woodland still retaining ancient woodland characteristics of which 17% is classified as ancient semi-natural woodland (ASNW) and the remaining 15% as planted ancient woodland sites (PAWS) (i.e. planted with non-native, mainly coniferous, tree species). The remaining woodlands are secondary in origin or are plantations (English Nature, 1998 - 2006; Smith & Gilbert, 2003).

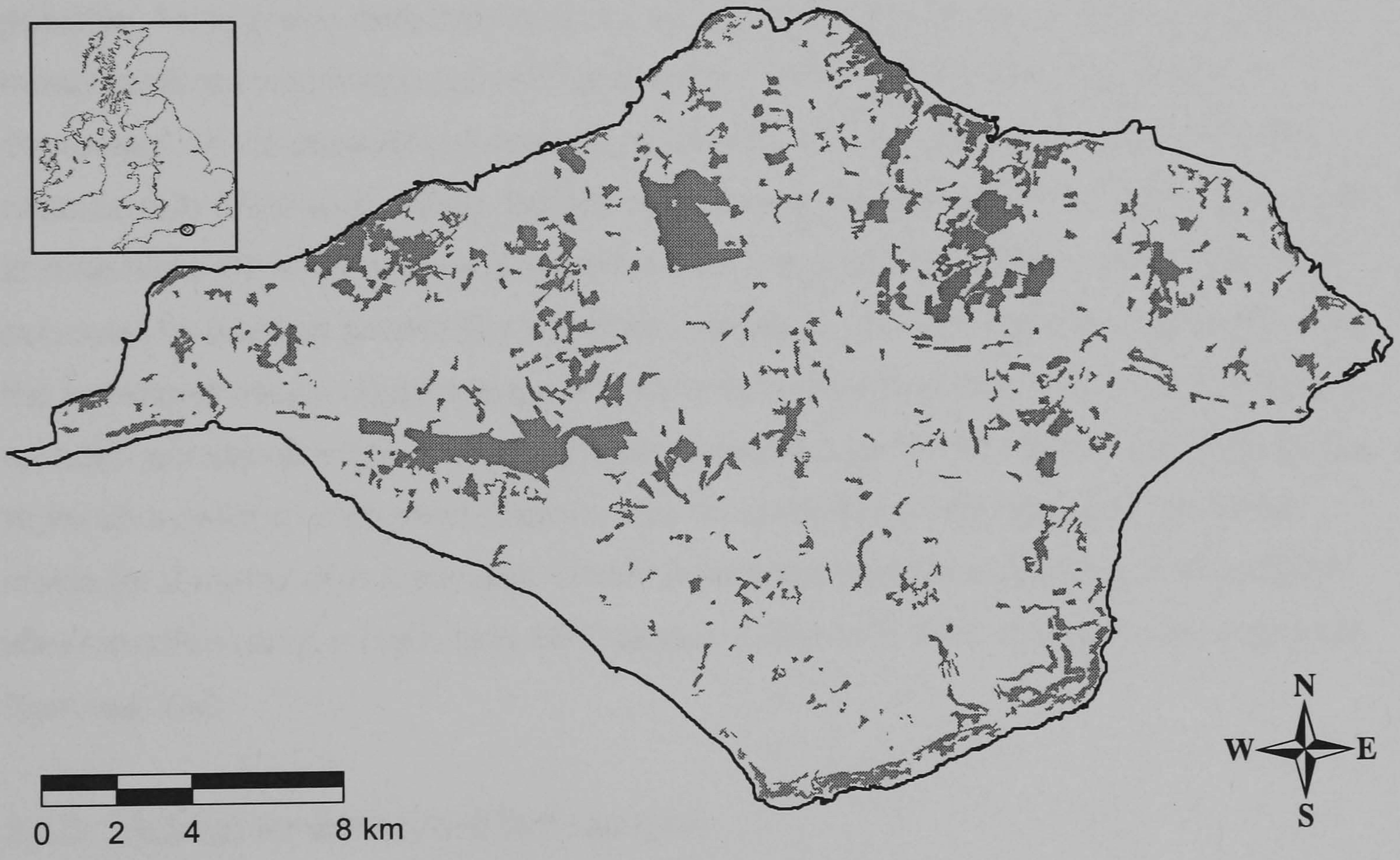


Figure 2: The woodland fragments on the Isle of Wight. Derived from digital maps based on the National Inventory of Woodland and Trees (NIWT) (Smith & Gilbert, 2003).

2.2.2 Survey methods

The survey was carried out between mid-July and mid-September 2005. Wood cricket is known to be associated with deciduous woodlands as its preferred habitat (e.g. Richards, 1952; Gabbutt, 1959; Brown, 1978). Therefore, the focus of the survey was on the northern part of the Isle of Wight where the majority of deciduous woodland fragments are located (Figure 2). All mature deciduous woodlands with at least 50% native species cover in the canopy larger than 5 ha were surveyed. When wood cricket was found in a particular location, all surrounding areas of woodland were also surveyed, regardless of their size and composition.

The survey was carried out focussing on adult wood crickets. The individuals were located by sound recognition of stridulating males, following the survey method of Proess and Baden (2000). Male wood cricket produce a very distinctive sound by stridulation, which is not readily confused with any other species (Proess & Baden, 2000). Presence of wood cricket was confirmed by visual observation wherever possible. To optimise detection success the surveys were carried out on days with a mean daytime temperature of 15°C and above. The volume of the stridulation is dependant on the prevailing temperature. Below 15°C, stridulation volume reduces considerably (Richards, 1952). Before each survey, local weather forecasts were used to determine if this requirement would be met. Individual woodlands were thoroughly surveyed by walking around the woodland periphery and through the woodlands using the woodland tracks. Stops were made at likely habitat locations focussing particularly on open woodland edges typically present along the periphery, tracks and in clearings. At these locations, presence/absence was determined by listening for stridulating males for a period of 2-5 minutes. When individuals were encountered, each location was recorded using a hand-held GPS device (Garmin III GPS V, Garmin (Europe) Ltd, Romsey, UK).

2.2.3 Habitat variables and GIS analysis

A digital map based on the National Inventory of Woodland and Trees (NIWT) (Smith & Gilbert, 2003) was used within the software package ArcGIS 9.1 to create a base map by differentiating between the different woodland habitat types present on the Isle of Wight (Figure 2). Based on the tree species composition, the original map was adapted by including all NIWT classification categories into one of the three main woodland habitat stand type classes, namely “mixed”, “broadleaved” and “coniferous” (see Smith

& Gilbert, 2003). “Mixed” included stands with a mixture of broadleaved and coniferous species with both groups occupying at least 20% of the canopy. “Broadleaved” and “coniferous” stands were defined as each respectively having an overall dominance of at least 80% within the canopy (Smith & Gilbert, 2003).

From the base map two woodland sample maps were constructed, which were used in further analyses. The first sample (Sample 1) included all the woodlands that were surveyed, which were each classified according to three woodland habitat stand type classes. With this classification, a single woodland could therefore be divided in several individual woodland ‘units’, each representing a different stand type. This resulted in a sample including 215 separate woodland “units”, which were each classified as one of three stand type categories namely broadleaved (n_b = 115), coniferous (n_c = 44) and mixed (n_m = 56). For the second sample map (Sample 2), the separate woodland “units” (Sample 1) were aggregated into one within the boundaries of each single woodland fragment. Fragment boundaries were defined either by neighbouring agricultural land (grassland or arable) or by distinct anthropogenic/natural landscape features (urban fringes, roads, railway lines, rivers and steams (> 1 m wide)). This resulted in a sample size of 147 individual woodland fragments. ‘Sample 1’, representing the woodland ‘units’, was used to test for differences in wood cricket presence between the different woodland habitat stand types and ‘Sample 2’, representing the whole woodland fragments, was used for all other analyses. The separate classifications were checked for accuracy against digitised, orthorectified aerial photographs using imagery from The GeoInformation Group (© 2007) available in Google Earth (3.0, Google Inc., Silicon Valley, California, USA) and Getmapping Plc (© 1998, Hartley Wintney, Hampshire, United Kingdom). All further analyses were undertaken using these two samples to represent the individual woodland areas.

The extent of occurrence and the area of occupancy (following IUCN, 2001) were measured using the Hawth's Analysis Tools (for ArcGIS, Version 3.24, (Beyer, 2004)). To measure the extent of occurrence for this species on the Isle of Wight a smallest convex polygon was drawn around the GPS coordinates of the wood cricket locations. By projecting a 200x200 m grid over the extent of occurrence, the area of occupancy was determined for the species, by identifying within how many grid cells the species was located.

Wood cricket presence/absence was related to patch variables that were computed by analysing the sample maps in ArcGIS. ‘Sample 2’ was used to calculate for each individual woodland fragment the total area (ha), perimeter (m) (i.e. circumference), and two shape measures, namely the fractal dimension index (FRAC) and the shape index (SHAPE) using FRAGSTATS 3.3 (McGarigal et al., 2002). These shape metrics are both computed by using the variables woodland area and perimeter to describe woodland shape complexity. FRAC describes the shape of a woodland patch between the values 1 and 2, with values approaching 1 for very simple shapes (e.g. circles), and approaching 2 for shapes with highly convoluted, area-filling perimeters. An increasing FRAC therefore indicates an increase in shape complexity. The shape index can be interpreted in the same way, but here the range of outcomes is from one to infinity. When SHAPE = 1, the patch is maximally compact (i.e. circular) and as values increase patch shape becomes more irregular and convoluted (for more details see McGarigal et al., 2002).

For quantifying the degree of isolation between woodland fragments, an Euclidean distance measure (i.e. nearest occupied neighbour distance) was computed. The distance from the edge of each surveyed woodland to the edge of its nearest occupied neighbour was measured in a straight-line using measurement tools in ArcGIS. This measure was performed separately for both the inhabited and uninhabited woodlands. For the individual woodlands (Sample 2), woodland age was derived using a digital map produced from the inventory of ancient woodland sites for the United Kingdom (Ancient Woodland Inventory; see Spencer & Kirby, 1992; English Nature, 1998 - 2006). This map was used to differentiate between ancient (i.e. woodland established before 1600 AD) and secondary woodland (i.e. woodland established after1600 AD). All woodlands including ancient woodland characteristics within its boundary were classified as 'Ancient'. All other woodlands were classified as 'Secondary'. Only woodland fragments over two hectares in area were included in the analysis, following the original inventory criteria (Spencer & Kirby, 1992).

Finally, for each woodland fragment a measure of habitat availability was computed. This measure was based on the amount of permanent edges present within each fragment. This measure was computed by adding the perimeter distance to the total distance of permanent edges present within the boundaries of the woodland fragments. Permanent edges within woodlands were defined as clearly visible tracks, paths, roads and railways within the boundary of the woodland as detected on orthorectified aerial photographs derived from the GeoInformation Group (© 2007) available in Google Earth (3.0, Google Inc., Silicon Valley, California, USA). The total distance of these features were calculated with measurement tools available in Google Earth and ArcGIS.

2.2.4 Statistical data analysis

The individual habitat variables were tested to identify relationships with wood cricket presence using SPSS 12.0.1 for Windows (SPSS Inc., Chicago, Illinois, USA). The values for the separate variables were first explored using descriptive statistics within SPSS. This included testing for normality (Kolmogorov-Smirnov test) and producing boxplots for the individual variables to visualise the range and variation in values of measurements made for both 'presence' and 'absence' locations. All variables were found to be not normally distributed. To explore the relationships between wood cricket presence and woodland area, woodland perimeter, fractal dimension index (FRAC), shape index (SHAPE), distance to nearest wood cricket inhabited woodland and habitat availability (i.e. permanent edges), Mann-Whitney *U* tests were performed. Additionally, the effect size (r) for each individual variable was calculated (= z / square root n), in this case indicating the strength of association of each variable with wood cricket presence/absence (Pallant, 2007). The z test statistic is given by SPSS when performing a Mann-Whitney *U* test and is used to test for a significant difference between two groups. For exploring the relationships between wood cricket presence and woodland age (using Sample 2) and stand type (using Sample 1), chi-square tests of association were performed. In addition, for woodland age, the odds ratio for wood cricket presence was calculated to examine the likelihood of wood cricket presence in ancient woodland compared to secondary woodland (see Field, 2005 (p.693-4)). Finally, a Spearman rank correlation test was undertaken to examine correlations between the measured variables. Assessment of the correlations and effect size (r) was based on the guidelines of Cohen (1988) where values between $r = 0.10$ and 0.29 indicate a small correlation effect/effect size; $r = 0.30$ to 0.49 a medium effect and values $r = 0.50$ to 1.00 a large effect.

Several logistic regression methods were used to examine the relative influence of the different habitat variables on distribution of wood cricket and to identify the key variables explaining the presence of the species within woodlands at a landscape scale. For these analyses the continuous variables Area, Perimeter, Permanent edge, FRAC, SHAPE, Distance and Age were included. Three outlying cases were excluded from 'Sample 2' ($n = 147$) resulting in a sample size of $n = 144$, with 113 'absent' and 31 'present' woodlands. These three woodland fragments were excluded, because they were situated in areas where the survey of the surrounding woodlands was not completed. Of the excluded woodland fragments, one supported a wood cricket population whereas the other two did not.

First, all individual variable responses were explored in order to determine their individual explanatory power. For this, all variables were used to create individual univariate models using the 'Enter' function within SPSS. This function is used to build regression models by hand. Only the significant variables (Wald test: $P < 0.05$, see below) were used in subsequent analyses. To explore the influence of the individual variables, multivariable models were constructed. First a stepwise logistic regression (Forward: LR in SPSS) was used. This function lets the program build a regression model, step by step including the variables with the highest score statistic and significance, until there are no variables left that significantly add to the model. Particularly when using a large number of variables, this method is useful to provide an indication of the explanatory variables that are most powerful. The outcomes of these automatic logistic regressions and the outcomes from the Spearman rank correlation test were used to inform further exploration of different variable combinations by using the 'Enter' function. This manual method allows correlations between variables and other factors influencing models generated from stepwise methods to be taken into account (Strauss & Biedermann, 2005).

The output that is generated by SPSS when analysing the individual models provides information on the performance of the total model and information on performance of the individual variables used within these models. For total model performance, SPSS produces two 'goodness-of-fit' tests, a 'classification table' and information on 'effect size'. Goodness-of-fit test are designed to test how well the created models perform and fit the data. There is no universally preferred test for this purpose (Tabachnick & Fidell, 2001), so SPSS performs a 'model fit test' and a 'Hosmer & Lemeshow model fit test'. However, in this case the 'Hosmer & Lemeshow model fit test' is considered to be more powerful than the 'model fit test' (Pallant, 2007). The 'classification table' provides information on the percentage of cases (i.e. presence/absence locations) that are correctly classified by the model and the 'effect size' provides information on the amount of variation that is explained by the model. For the performance of the individual variables, SPSS uses the 'Wald test' to test the contribution of the individual variables to the predictive ability of the model. SPSS further generates B values (+ Standard Error) which are used as constants in the probability function (see Equation 1). This equation was further used to construct probability curves to display the relationships between the individual predictor variables and wood cricket presence.

Equation 1: Probability equation for wood cricket presence (from Tabachnick & Fidell, 2001). ‘B’ values are generated by SPSS for the individual variables that are included in the model.

$$P(y) = \frac{e^{a + \sum_{n}^{x=1} b}}{1 + e^{a + \sum_{n}^{x=1} b}}$$

$P(y)$ = probability of wood cricket being present

a = B value for the constant included in the model

b = B value * variable(s) included in the model

The B value further indicates the direction of the relationship between the individual predictor variables and the dependant variable (i.e. wood cricket presence). The final piece of information given is the Exp(B) value (with 95% Confidence Interval) which indicates the odds ratio for wood cricket presence per unit increase of the predictor variable. Further details on SPSS output interpretation for logistic regression analyses are provided by Tabachnick and Fidell (2001), Field (2005) and Pallant (2007).

The following selection criteria were used to choose the most powerful and realistic model: (1) all individual correlations (*r* values) between the variables included had to be less than +/- 0.7 (following Strauss & Biedermann, 2005), (2) all individual tests for significance had to be met (‘model fit test’ ($P < 0.05$), ‘Hosmer & Lemeshow model fit test’ ($P > 0.05$) and ‘Wald test’ ($P < 0.05$)), (3) all B values had to indicate the correct sign of the relationship (+/-), and (4) the 95% confidence interval for Exp(B) was not allowed to include the value of 1, which indicates no effect. The best fitting model was then selected based on the highest scores for ‘effect size’ (R^2_N) and ‘Hosmer & Lemeshow model fit test’ scores.

2.3 Results

2.3.1 Landscape scale distribution

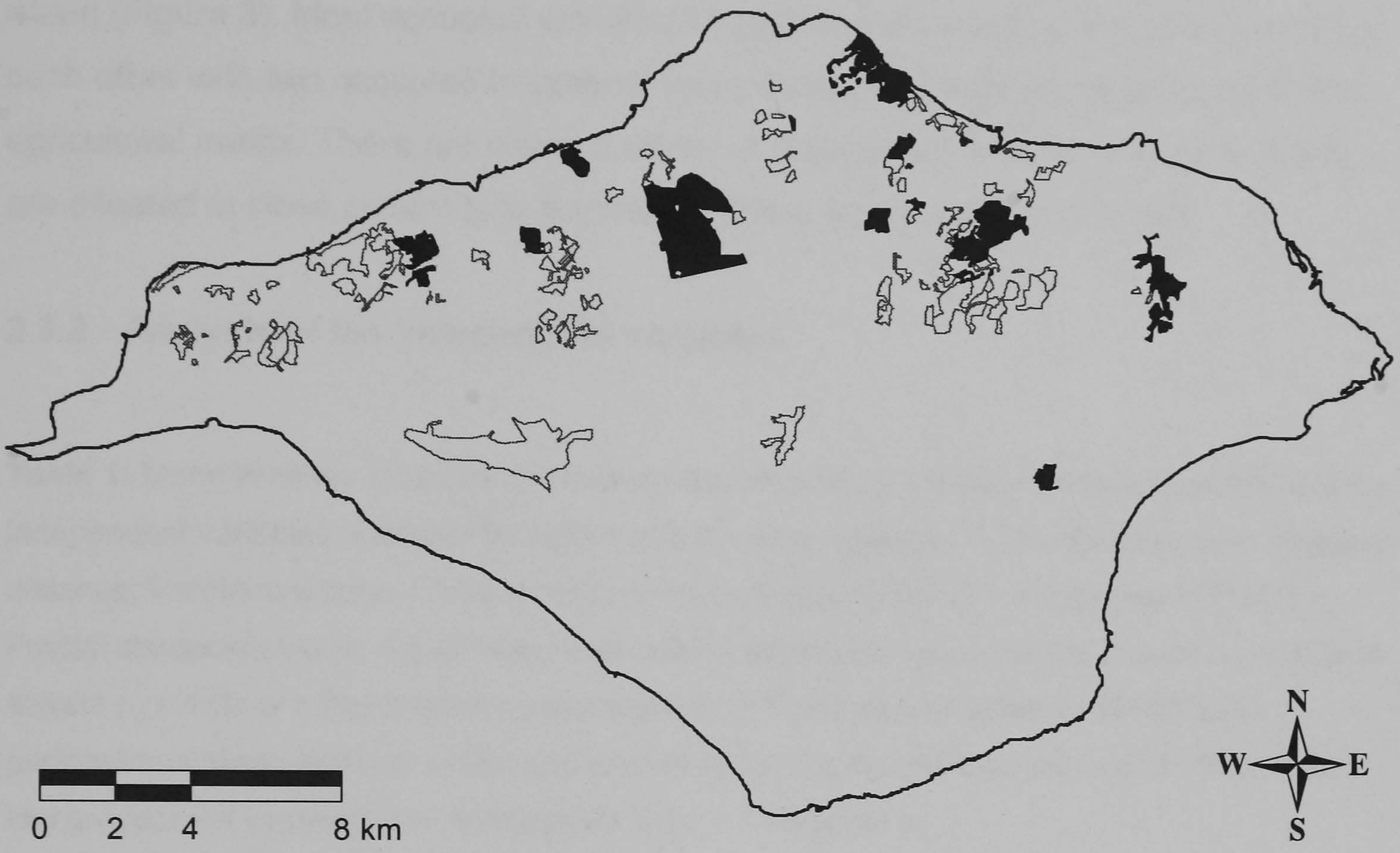


Figure 3: Distribution of wood cricket (*Nemobius sylvestris*) on the Isle of Wight. The black patches represent woodlands where wood cricket was present and the white patches represent woodlands where they were absent. In the survey, the two combined areas represent the total woodland area that was surveyed, covering 6.0% of the island's surface area. Original map derived from digital maps based on the National Inventory of Woodland and Trees (NIWT) (Smith & Gilbert, 2003).

Of the total woodland area (5123 ha) present on the Isle of Wight, 2346 ha (45.8%) was surveyed. Of this surveyed woodland area, 1018 ha (43.4%) sustained wood cricket populations. A total of 147 different woodland fragments were surveyed ranging from 0.13 to 396 ha in surface area with a mean of 15.6 +/- 3.71 ha. Of the 147 woodland fragments that were surveyed, 32 fragments supported wood cricket populations where the remaining 115 fragments did not (Figure 3). The extent of occurrence for wood cricket on the Isle of Wight covered 33.9% of the island's surface area. However, when using a 200x200 m grid covering this extent of occurrence, the area of occupancy was only 2.6% (following IUCN, 2001).

Results from this survey indicate that wood cricket is patchily distributed on the island. Wood cricket shows a wide distribution over the northern part of the island, but the species is absent from several major woodland areas, mainly dominated by mixed stands. Most notable of these is the complex of woodlands on the western part of the island (Figure 3). Most occupied woodland fragments are situated in close proximity to each other with two occupied fragments found that are completely isolated within the agricultural matrix. There are also a number of unoccupied woodland fragments that are situated in close proximity to fragments where wood cricket is present.

2.3.2 Analysis of the independent variables

Table 1: Mann-Whitney *U* test for the relation between wood cricket presence/absence and six independent variables analysed through separate tests. Distance = nearest occupied neighbour distance; Permanent edge = total amount of edge habitat; SHAPE = Shape index; FRAC = Fractal dimension index. n = number of woodland fragments: wood cricket present n_1 = 32 and absent n_2 = 115; U = Mann-Whitney test statistic; z = test statistic given by SPSS when performing a Mann-Whitney *U* test and is used to test for a significant difference (P) between two groups; P = probability or significance level; r = effect size.

Mann-Whitney *U* test	*n*	*U*	*z*	*P*	*r*
Distance	147	714.0	-5.29	<0.001	0.44
Permanent edge	147	1061	-3.65	<0.001	0.30
Perimeter	147	1107	-3.44	0.001	0.28
Area	147	1199	-3.01	0.003	0.25
SHAPE	147	1321	-2.44	0.015	0.20
FRAC	147	1470	-1.74	0.082	0.14

Analysis performed on 'Sample 1' (n = 215) testing for association between wood cricket presence/absence and stand type revealed that there was no significant difference between the three stand type categories (chi-square: χ^2 = 2.283, df = 2, P = 0.319). Therefore, further analyses focused on 'Sample 2' (n = 147). In Table 1, a summary of the independent Mann-Whitney *U* test results are shown. Nearest occupied neighbour distance showed the highest *r* and significance (*P*) values related to wood cricket presence (Table 1), indicating a medium negative effect on wood cricket presence with increasing distance between woodland fragments. Furthermore, the variable indicating the level of habitat availability (Permanent edge) showed a relatively strong relationship with wood cricket presence compared to the other variables (Table 1). Finally, fractal dimension index (FRAC) did not show a significant relationship with wood cricket presence (Table 1).

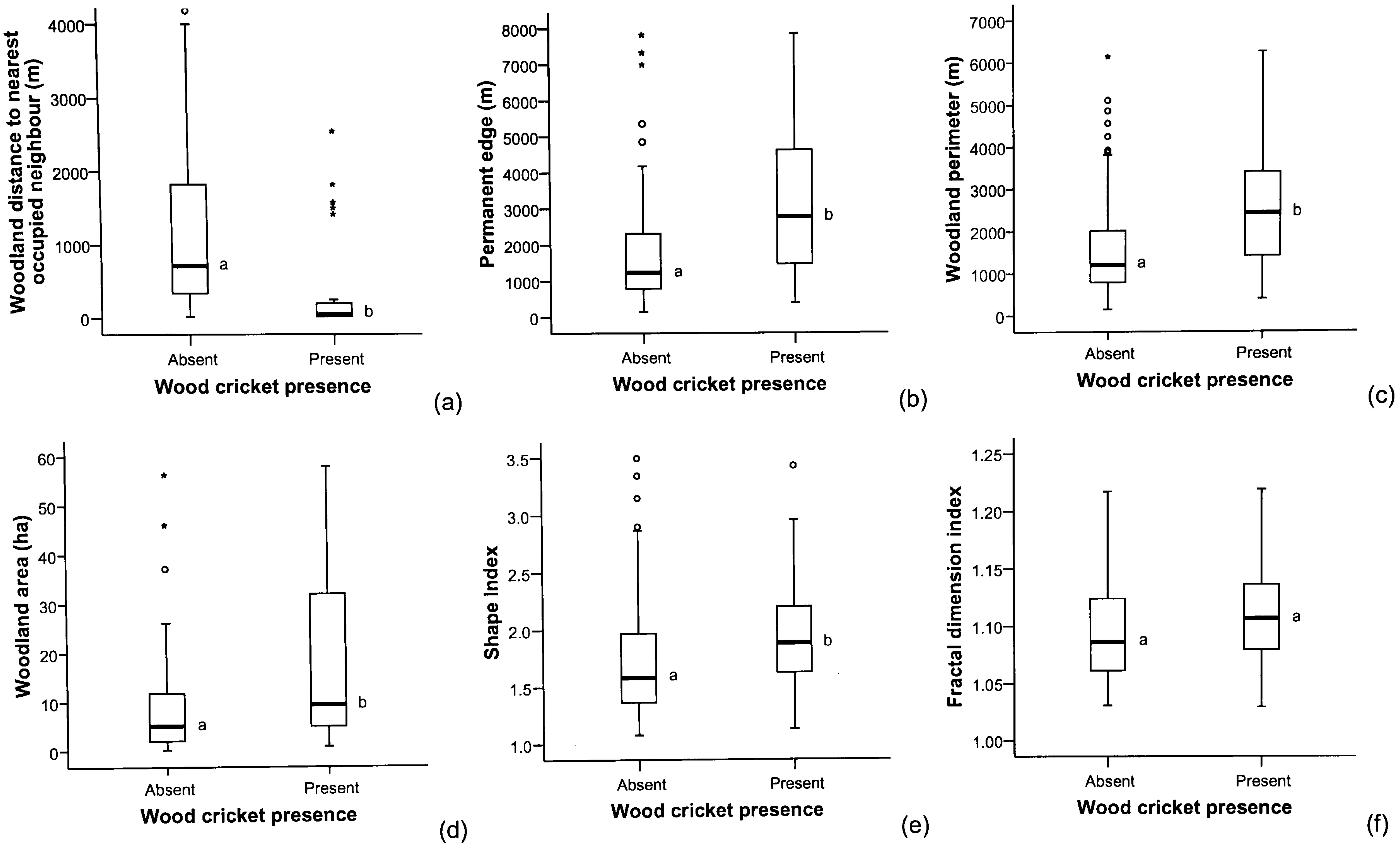

Woodland distance to nearest occupied neighbour (m)
4000
3000
2000
1000
0
a
b
Absent
Present
Wood cricket presence
(a)
Permanent edge (m)
8000
7000
6000
5000
4000
3000
2000
1000
0
a
b
Absent
Present
Wood cricket presence
(b)
Woodland perimeter (m)
7000
6000
5000
4000
3000
2000
1000
0
a
b
Absent
Present
Wood cricket presence
(c)
Woodland area (ha)
60
50
40
30
20
10
0
a
b
Absent
Present
Wood cricket presence
(d)
Shape Index
3.5
3.0
2.5
2.0
1.5
1.0
a
b
Absent
Present
Wood cricket presence
(e)
Fractal dimension index
1.25
1.20
1.15
1.10
1.05
1.00
a
a
Absent
Present
Wood cricket presence
(f)

Figure 4: Boxplots (n = 147, with wood cricket present n_1 = 32 and absent n_2 = 115) illustrating the ranges and median (horizontal black line) for woodland fragments where wood cricket was ‘Absent’ or ‘Present’ in relation to (a) Euclidean distance from each surveyed woodland to its nearest occupied neighbour (medians: 715.0 m, 50.00 m), (b) length of permanent edge (medians:1241 m, 2785 m), (c) length of woodland perimeter (medians: 1202 m, 2418 m), (d) woodland area (medians: 5.138 ha, 9.469 ha), (e) shape index (medians: 1.583, 1.886) and (f) fractal dimension index (medians: 1.086, 1.107). Identical letters indicate a non-significant difference (a – a), different letters indicate a significant difference (a – b) ($P < 0.05$, Mann-Whitney *U* test). The stars and circles indicate extreme values and outliers respectively. The boxes in the plots include 50% of all the cases of the individual groups. The whiskers protruding from the box extend to the smallest and largest values excluding the outliers and extreme values. SPSS defines points as outliers if they extend more than 1.5 times the box-length from the edge of the box. Extreme values extend more than three box-lengths from the edge (information on boxplots from Pallant, 2007). For (a), eleven outliers for the Absent plot (6130 m; 6050 m; 5950 m; 5600 m; 5585 m; 5500 m; 5150 m; 4800 m; 4685 m; 4655 m and 4440 m) were omitted for clarity together with one extreme value for Present (4500 m). For (b), two extreme values for Present (25806 and 10549 m) and one for Absent (27352 m), for (c) one extreme value for Present (12918 m) and one for Absent (15722 m) and for (d) two extreme values for Present (397 ha and 100 ha) and one for Absent (360 ha) were omitted for clarity.

In Figure 4, a series of individual boxplots are presented. The median distance between inhabited woodland fragments ($n_1 = 32$) was found to be significantly less than the median distance between unoccupied woodland fragments ($n_2 = 115$) and their nearest neighbouring woodland inhabited by wood cricket (Figure 4a, Table 1). The median distance between occupied woodlands was 50 m (Figure 4a), indicating that fragments more distant from each other were likely to be effectively isolated. Furthermore, the median value of permanent edge (i.e. habitat availability), woodland perimeter, shape index and woodland area was found to be significantly higher for woodland fragments in which wood cricket was present than for woodland fragments where wood cricket was absent, although this was not the case for the fractal dimension index (FRAC) (Figure 4b – f, Table 1).

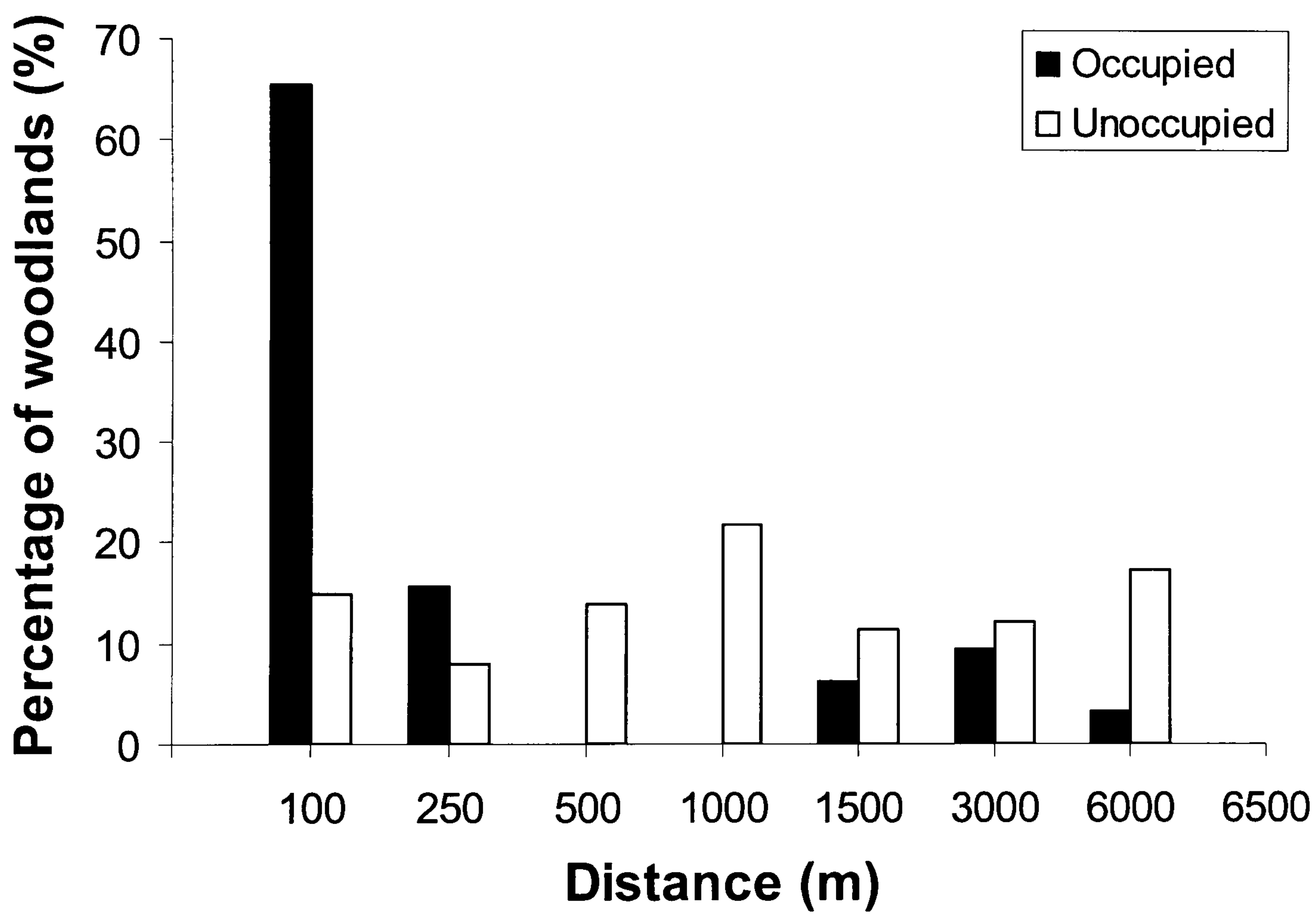


Figure 5: Frequency distribution for Euclidean nearest occupied neighbour distance between the individual woodland fragments. The x-axis represents the distance to the nearest occupied woodland in meters (m) divided in intervals (i.e. interval 100 represents all woodlands between 0-100 m from each other, 250 between 100-250 m etc.). The y-axis indicates the percentage of occupied (n = 32) (black bars) and unoccupied (n = 115) (white bars) woodlands in each interval.

Figure 5 shows the difference between woodlands occupied and unoccupied by wood cricket in relation to the distance from the nearest neighbouring wood cricket location. This figure shows that woodland fragments that are occupied by wood cricket (black bars) are nearly all (82%, n = 26) within a radius of 250 m of another occupied woodland (Figure 5) indicating that occupied fragments tend to be clustered within the landscape. Twelve percent (n = 6) of the occupied woodland fragments are situated more than 1400 m away from another source population, indicating that some populations are isolated.

2.3.3 Woodland age

Table 2: Contingency tables for woodland age related to wood cricket presence and subsequent Pearson Chi-square tests of association. Odds in the contingency table indicate the likelihood for wood cricket being present in secondary (4/36 = 0.1) or ancient woodland. The odds ratio presented with the Pearson's Chi-square test indicate the likelihood for wood cricket being present in ancient woodland compared to presence in secondary woodland (0.4/0.1= 4.0).

Contingency table		Wood cricket			
		Absent	Present	Total	Odds
Age	Secondary	36	4	40	0.1
	Ancient	52	23	75	0.4
	Total	88	27	115	
Pearson χ^2	n	χ^2	df	P	Odds ratio
Age	115	5.10	1	0.024	4.0

Including only woodlands larger than 2 ha resulted in a sample size for 'Sample 2' of n = 115 (40 secondary, 75 ancient) (Table 2). A Chi-square test was performed to determine whether there was an association between the age of woodland and presence/absence of wood cricket. The test showed that wood cricket was significantly more likely to be present in woodland fragments with ancient characteristics than in woodlands of secondary origin (Table 2). Furthermore, the odds ratio indicates that wood cricket is four times more likely to be present in ancient woodland than in secondary woodland (Table 2).

2.3.4 Correlation between the independent variables

Table 3: Spearman rank correlation between the independent variables. n = 147, r = correlation coefficient, P = significance or probability value. SHAPE = Shape index; FRAC = Fractal dimension index. Correlation coefficients r > 0.50 are displayed in bold.

Spearman correlation		Area	Perimeter	SHAPE	FRAC	Distance	Permanent edge
Perimeter	*r*	**0.93**	.				
	P	<0.001	.				
SHAPE	*r*	0.44	**0.71**	.			
	P	<0.001	<0.001	.			
FRAC	*r*	0.24	**0.54**	**0.97**	.		
	P	0.003	<0.001	<0.001	.		
Distance	*r*	-0.03	-0.08	-0.16	-0.17	.	
	P	0.760	0.311	0.048	0.039	.	
Permanent edge	*r*	**0.94**	**0.99**	**0.68**	**0.51**	-0.08	.
	P	<0.001	<0.001	<0.001	<0.001	0.360	.
Age	*r*	0.41	0.29	0.01	-0.09	-0.15	0.30
	P	<0.001	<0.001	0.951	0.302	0.064	<0.001

A Spearman rank correlation test was performed to see if there were any associations between the variables that were examined. Two groups of correlated variables all showing large positive correlations (*r* > 0.50) with each other were identified. The first group included Perimeter, SHAPE, FRAC and Permanent edge (*r* = 0.51 – 0.99; Table 3) and the second group included Area, Perimeter and Permanent edge (*r* = 0.93 – 0.99; Table 3). Both groups included the variables Perimeter and Permanent edge. The main difference between these groups was that Area did not show a large correlation effect with either SHAPE or FRAC (*r* = 0.44 and 0.24, respectively; Table 3). Furthermore, neither Distance nor Age showed large correlation effects with the other variables, nor with each other (Table 3). Distance only showed small negative correlations (*r* = -0.03 – -0.17; Table 3) and Age both small negative as well as small to medium positive correlations (*r* = -0.09 – 0.41; Table 3) with the other variables.

2.3.5 Logistic regression analysis

Several logistic regressions were undertaken to build a predictive model and to identify the key variables explaining the variation in presence/absence of wood cricket between woodlands. In Table 4, a summary of the most realistic models based on the selection criteria as described in the method section are displayed. For these analyses, seven variables were initially included in the logistic regression. From these seven variables, five passed the significance test (Wald test: $P < 0.05$; Table 4). After the exploration of the SPSS output for the separate models, for 'Sample 2' ($n = 144$) (see Methods), the best fitting total model included the variables Distance and Area (Table 4). This model met all selection criteria (see Methods) showing that: (1) all individual correlations (r) between the variables included were less than +/- 0.7 (Table 3); (2) all individual tests for significance were met ('model fit test' ($P < 0.05$), 'Hosmer & Lemeshow Model fit test' ($P > 0.05$) and 'Wald test' ($P < 0.05$)) (Table 4); (3) all B values indicated the correct sign of the relationship (+/-) based on the boxplots presented in Figure 4, and (4) the 95% confidence interval for Exp(B) did not include the value of 1 (Table 4).

Table 4: Summary of the logistic regression analyses. Model: variables included in the logistic regression model. Model performance: summary of model performance tests. Model fit test: tests if the model fits the data (*P* < 0.05 = good model fit). Hosmer & Lemeshow model fit test: tests if the model fits the data (*P* > 0.05 = good model fit). Classification table (%): indicates percentage of cases correctly classified by the model. Effect size: indicates the amount of explained variation by the model (Nagelkerke R^2; range 0 – 1). Variables in the equation: indicates the usefulness of the individual variables included in the model. Wald test: tests contribution of the individual variables to the model (*P* < 0.05 = significant contribution). B (with Standard Error): indicates the direction of the relationship between the individual variables and wood cricket presence (- negative, + positive). Exp. (B) (with 95% Confidence Interval): indicates the odds ratio for wood cricket presence per unit increase of the individual variable (values below 1 indicate a decrease and above 1 an increase).

Logistic Regression Model		Model performance										Variables in the equation							
		Model fit			Hos. & Lem. Model fit test			Classification table (%)			Effect size	Wald test						95% C.I. Exp(B)	
Variables	*n*	χ^2	df	*P*	χ^2	df	*P*	Absent	Present	Total	Nagelkerke R^2	*z*	df	*P*	B	S.E.	Exp (B)	Lower	Upper
Distance	144	36.41	2	<0.001	11.57	8	0.171	96	26	81	0.35	8.506	1	0.004	-0.002	0.001	0.998	0.997	1.000
Area												8.449	1	0.004	0.052	0.018	1.053	1.017	1.091
Constant												8.363	1	0.004	-1.040	0.360	0.353		
Distance	144	19.83	1	<0.001	39.16	8	<0.001	100	0	79	0.20	8.764	1	0.003	-0.001	<0.001	0.999	0.998	1.000
Constant												2.610	1	0.106	-0.450	0.279	0.637		
Area	144	17.39	1	<0.001	14.04	8	0.081	97	23	81	0.18	11.38	1	0.001	0.054	0.016	1.055	1.023	1.089
Constant												44.26	1	<0.001	-1.984	0.298	0.138		
Permanent edge	144	16.58	1	<0.001	4.481	8	0.811	97.3	12.9	79.2	0.17	11.86	1	0.001	<0.001	<0.001	1.000	1.000	1.001
Constant												39.26	1	<0.001	-2.243	0.358	0.106		
Perimeter	144	15.05	1	<0.001	5.032	8	0.754	97.3	16.1	79.9	0.15	11.97	1	0.001	0.001	<0.001	1.001	1.000	1.001
Constant												36.85	1	<0.001	-2.337	0.385	0.097		
SHAPE	144	4.412	1	0.036	9.586	8	0.295	100.0	0.0	78.5	0.05	4.485	1	0.034	0.765	0.361	2.148	1.059	4.359
Constant												14.34	1	<0.001	-2.697	0.712	0.067		

For the woodland fragment sample the 'model fit test' showed that the predictor variables Distance and Area reliably distinguished between woodlands where wood cricket was absent or present (Chi-square: $\chi^2 = 36.41$, df = 2, $P < 0.001$; Table 4). This was furthermore confirmed by the Hosmer & Lemeshow model fit test (Hos. Lem.: $\chi^2 = 11.57$, df = 8, $P = 0.171$; Table 4) (note that here $P > 0.05$ indicates a good model fit). The 'classification table' indicated that the full model correctly classified 81% of all the cases (96% for Absent cases and 26% of the Present cases) (Table 4). The 'effect size' of the model indicated that the total variation explaining wood cricket presence/absence by the model was 35% (Nagelkerke $R^2 = 0.35$; Table 4). The 'Wald test' indicated that both Distance and Area contributed significantly to the total model (Wald: $z = 8.506$, df = 1, $P = 0.004$ and $z = 8.449$, df = 1, $P = 0.004$ respectively; Table 4). The negative B value for Distance and the positive B value for Area respectively indicated the negative and positive relationship with wood cricket presence. The probability of wood cricket being present decreased with an increase in woodland distance to nearest occupied woodland (B = -0.002 +/- 0.001) and increased with woodland area (B = 0.052 +/- 0.018) (Table 4). Furthermore, the Exp (B) value indicated that with an increase in woodland distance from another occupied woodland the odds that wood cricket would be present decreased by a factor of 0.998 (C.I. 0.997 – 1.000). For each ha increase in woodland area, the odds of wood cricket being present increased by a factor of 1.053 (C.I. 1.017 - 1.091) (Table 4). Finally, of the individual predictor variables, woodland distance to the nearest occupied woodland explained most of the total variation (Nagelkerke $R^2 = 0.20$; Table 4). For woodland area the explained variation was slightly less (Nagelkerke $R^2 = 0.18$; Table 4) indicating a similar predictive power of both variables in explaining wood cricket presence. Including woodland area and occupied nearest neighbour distance in one model increased the explained variation by 0.15 to an overall total of 35% explained variation (Table 4).

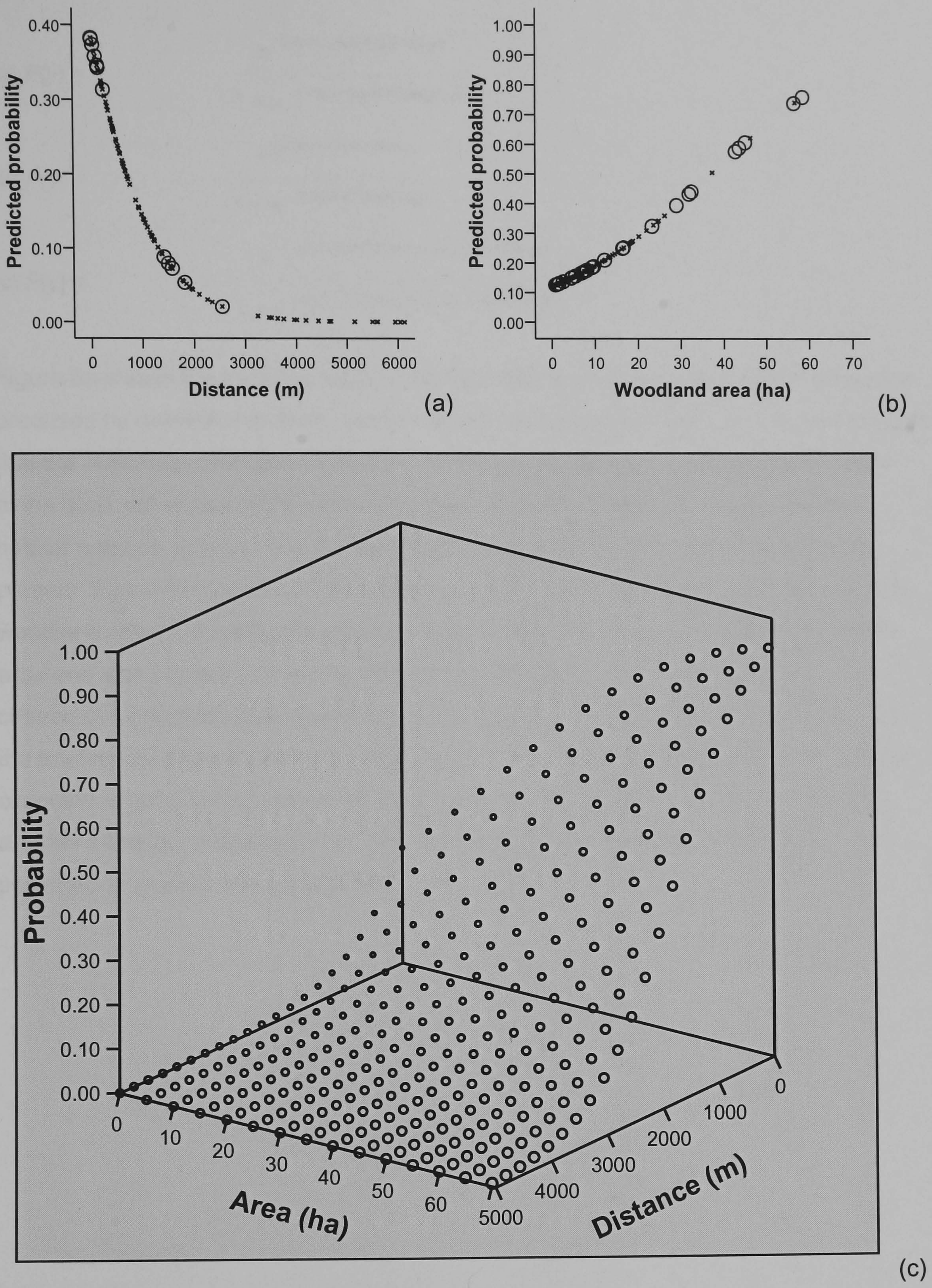


Figure 6: Predicted probability graphs for wood cricket presence in woodland fragments related to (a) distance to the nearest occupied neighbour, (b) woodland area, and (c) for the total model (*n* = 144). For (a) & (b): O indicates sites where wood cricket was present; x indicates sites where wood cricket was absent. For (c): points indicate the predicted probability of wood cricket presence. For figure 5b two cases (397 and 100 ha) were excluded for clarity. The curves were calculated with the following probability equations using the B values from Table 4:

$$(a)\ P(y) = \frac{e^{-0.450+\,(-0.001)(\text{Distance})}}{1 + e^{-0.450.+\,(-0.001)(\text{Distance})}}$$

$$(b)\ P(y) = \frac{e^{-1.984+\,(0.054)(\text{Area})}}{1 + e^{-1.984+\,(0.054)(\text{Area})}}$$

$$(c)\ P(y) = \frac{e^{-1.040+\,(-0.002)(\text{Distance})\,+\,(0.052)(\text{Area})}}{1 + e^{-1.040+\,(-0.002)(\text{Distance})\,+\,(0.052)(\text{Area})}}$$

Figure 6a shows the negative exponential probability curve for wood cricket presence predicted by woodland distance to the nearest occupied woodland. The curve indicates that the maximum probability value for wood cricket presence predicted by distance alone does not exceed 40%, indicating that only small spatial distances between habitat patches already have a considerable negative effect on wood cricket being present. Figure 6b shows the probability curve for wood cricket presence predicted by woodland area, indicating the positive almost linear relationship between woodland area and wood cricket presence, predicting that woodlands > 60 ha have an 80% chance of having wood cricket within them. Figure 6c shows a 3-D representation of the total model showing the probability predicted by woodland distance to the nearest occupied woodland and woodland area together. For woodlands that are close to another inhabited woodland (< 250 m) and are relatively large (60 – 70 ha) the predicted probability lies around 90% (Figure 6c).

2.4 Discussion

The results of this study revealed that wood cricket populations on the Isle of Wight are patchily distributed, and are mainly found in relatively large woodland fragments situated close to each other. Furthermore, the occurrence of wood cricket was related to patch area, isolation, habitat availability and age, in support of all of the initial hypotheses. In addition, the best-fit logistic regression model included isolation and area as the main predictors for wood cricket presence within woodland fragments at the landscape scale. None of these relationships have been defined previously for this species.

Positive relationships between patch area and presence/absence of individual species have been documented in a number of fragmented landscapes. For example, the study by Walker et al. (2003) on a rock-dwelling rodent and that of Kindvall & Ahlén (1992) on a bush cricket revealed positive relationships between habitat fragment size and species occurrence. For wood cricket, a similar relationship was found: with an increase in woodland fragment area, wood cricket was more likely to be present (Table 1 & Figure 4d). However, the importance of this area relationship differs between species. Ranius (2000a) found that for an endangered beetle species associated with old hollow trees, the size of a habitat patch, defined as the number of hollow trees separated < 250 m from each other, was positively correlated with presence of the species. However, in two different studies on beetles living in dead fruiting bodies of fungi growing on trees, this relationship was not always found. Rukke & Midtgaard (1998) found a significant positive relationship for *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae), but in a later study by Rukke (2000) for species dependent on the same fruiting bodies, only three out of five species revealed a positive significant relationship with fragment area. However, compared to wood cricket, these species are more intimately associated with a specific habitat niche.

Studies on ground-dwelling woodland invertebrates that have examined the relationship between fragment size and species occurrence at the landscape scale do not appear to have been undertaken previously. The only study examining the effects of fragmentation on the distribution of a ground-dwelling woodland invertebrate at the landscape scale was on the flightless carabid beetle *Abax parallelepipedus* (Petit & Burel, 1998), which did not test the relationship between the presence of the species in the woodlands that were surveyed (20 occupied, 10 unoccupied) and the size of these fragments. However, as the species was also found in very small woodlots and hedgerow intersections, this relationship was thought unlikely to be significant (S. Petit (INRA, France), personal communication).

One explanation for the variation in response to fragment size found for invertebrate species could be attributable to the level of habitat specialism (Ewers & Didham, 2006). The beetle species studied by Ranius (2000a) was found to be dependent on the presence of old oak trees with hollows, therefore showing a high level of specialism in terms of habitat requirements. The number of trees representing these conditions was highly correlated with fragment size, which consequently was reflected in the positive area relationship found. A similar explanation was given for the fungus species that showed a positive area effect in the studies of Rukke & Midtgaard (1998) and Rukke (2000), where availability of the specific fungus host was strongly related to fragment size. The species that did not show the area response in the study of Rukke (2000) were arguably more generalist in their habitat requirements (i.e. utilising a wider range of fungus host species). This might also be the case for *Abax parallelepipedus,* which is relatively generalist in terms of woodland habitat requirements, utilising both core and edge habitat within woodland fragments (Petit & Burel, 1998; Petit, pers com). Wood cricket, however, are mainly found on the edges of woodlands (Beugnon, 1980; Brouwers, pers obs), indicating a relatively high degree of habitat specialism, which may account for the positive relationship with woodland fragment area. Overall, the results stress the importance of preserving the larger woodlands as habitat for wood cricket in this fragmented landscape.

The effects of habitat fragmentation on biodiversity have been measured in a variety of ways (Pascual-Hortal & Saura, 2006), including impacts on species diversity (e.g. Mazerolle & Villard, 1999) and species occurrence (e.g. Vos & Stumpel, 1995; FitzGibbon et al., 2007). Isolation measures such as Euclidean distance between one habitat fragment and its nearest neighbour have been widely used in this context, mainly because these measures require the least amount of information to obtain them (Calabrese & Fagan, 2004). However, such measures are often found to be poor predictors of species presence (e.g. Ranius, 2000a; Rukke, 2000). For instance in the study of Rukke (2000), the Euclidean distance measure 'distance to the nearest forest island' measured between fifty-eight individual forest fragments did not significantly explain presence/absence patterns of five different fungus beetles. However, in the current study, another Euclidean distance measure was used, measuring the distance between all individual fragments to its nearest occupied neighbour. Here, a strong negative relationship was revealed between wood cricket presence and distance to the nearest inhabited woodland fragment. This measure was used in two similar studies on woodland invertebrate species revealing the same significant relationships. Chardon et al. (2003) found this relationship for a relatively mobile butterfly species associated with woodland edge habitat and Petit & Burel (1998) for a ground-dwelling flightless woodland generalist carabid beetle. Although both these studies found that more complex isolation measures (thus requiring more specific data (Calabrese & Fagan, 2004)) performed better, this isolation measure performed better than measuring distance to any (i.e. either occupied or unoccupied) nearest habitat location. Such results indicate that distance to the nearest occupied neighbour is a useful measure to detect effects of fragmentation and isolation acting on woodland invertebrates at the landscape scale. Furthermore, because fragments sustaining wood cricket populations were mainly found in close proximity to each other, more distant isolated woodlands tended to be uninhabited. A likely explanation for this is that greater isolation may reduce the interactions between individual populations, making isolated populations more prone to extinction (Hanski & Gilpin, 1997).

Patch area can be seen as a measure of potential habitat available to a species. However, it has been shown previously that presence of woodland invertebrates is often better predicted by measures of species-specific habitat availability, informed by the ecology of the species, that is present within a patch compared to total patch area (Rukke & Midtgaard, 1998; Rukke, 2000). In both of these studies, total habitat availability (i.e. volume of fungus fruiting bodies available in the fragments) was found to be a better predictor of species presence than total fragment area. In the current investigation, the amount of edge habitat positively influenced wood cricket presence (Permanent edge: see Table 1, Figure 4b). Based on this result, habitat availability was also found to be a better predictor for wood cricket presence than fragment area. However, both variables were highly correlated (see Table 3), suggesting that both variables can be used in terms of habitat availability explaining wood cricket presence. Additionally, all measures related to edge habitat availability (Perimeter, SHAPE, FRAC and Permanent edge) were highly positively correlated with fragment area (see Table 3). Patch area is often used as a measure of habitat loss in fragmentation studies (Fahrig, 2003). In the case of wood cricket, this is also valid, where a decrease in fragment area will also negatively influence edge habitat availability, consequently decreasing population persistence and the likelihood of wood cricket being present. Therefore, these results indicate that further decreases in habitat/fragment area of the individual woodlands will negatively influence the persistence of wood cricket populations at the landscape scale.

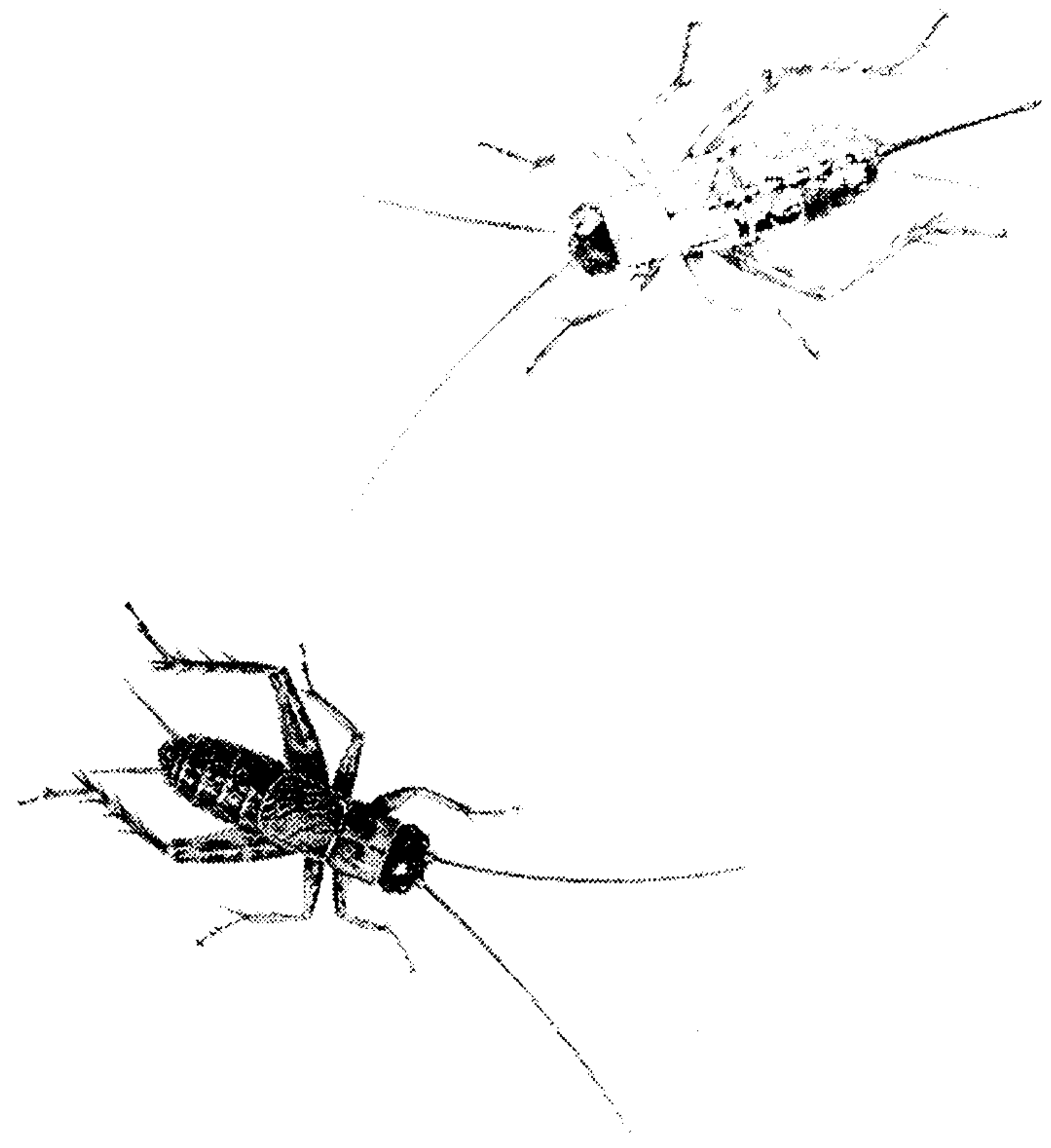
The origin or age of the woodland fragments on the Isle of Wight was also found to be associated with wood cricket presence (Table 2). The origin and age of a habitat patch is thought to have a positive effect on the species diversity it can support and maintain (MacArthur & Wilson, 1967; Forman & Godron, 1981). A number of investigations have documented positive relationships between patch age and species diversity for a wide range of organisms, including plants (e.g. Mikk & Mander, 1995; Grashof-Bokdam, 1997; Jacquemyn et al., 2001), birds (Shochat et al., 2001; Barbaro et al., 2005) and several spider species (Barbaro et al., 2005). For woodland carabid beetles, Magura et al. (2001) highlighted that the historical background of fragments determines current species assemblages. Furthermore, Jukes et al. (2001) found that the occurrence of forest specialists carabid beetles increased and generalist species decreased with an increase in stand age. Both of these studies indicate that older woodlands support different species than younger woodlands, which is mainly driven by the successional development of a woodland (Jukes et al., 2001) and related changes in habitat availability. Some invertebrate species particularly dependent on habitat only occurring in woodlands of a certain maturity (e.g. ancient woodland) can therefore be used as an indicator for woodland age (Peterken, 1981). Wood cricket did occur more often in woodlands with ancient characteristics, but was also found in woodland habitat of secondary origin. It therefore would be unjustified to use this species as a primary ancient woodland indicator. However, within the full range of ancient woodland indicators available (Kirby & Goldberg, 2003), on the Isle of Wight wood cricket occurrence could be used as one of the indications of ancient woodland characteristics.

Simple models using patch characteristics and distance measures have often been used to predict species presence within fragmented landscapes (Fahrig & Jonsen, 1998; Mazerolle & Villard, 1999; Debuse et al., 2007). However, responses often vary between and within different taxa (e.g. Fahrig & Jonsen, 1998; Herrando & Brotons, 2002; Barbaro et al., 2005). For constructing models predicting presence/absence of a species, logistic regression is often used (e.g. Ranius, 2000a; Rukke, 2000). For wood cricket this method produced a predictive model indicating that distance to the nearest occupied neighbouring woodland and woodland area were the most important variables explaining wood cricket presence at the landscape scale. Chardon et al. (2003) found similar results using similar variables for the occurrence of Speckled wood butterfly (*Pararge aegeria*). However, for this species the habitat area was found to be more important than occupied nearest neighbour distance. The difference in outcome between their study and the current investigation is possibly due to the higher mobility of the butterfly species compared to wood cricket. For relatively mobile invertebrate species, distance between habitat patches is probably less important than total habitat area/availability. Additionally, the logistic regression analyses attributed a slightly higher predictive power to fragment area compared to permanent edge (see Table 4). However, a likely explanation for this is the sensitivity of logistic regression analyses to high correlation between variables (Field, 2005) (Table 3), which means that these two variables are exchangeable and both can be used in the model (Vos & Stumpel, 1995).

The similar amount of variance explained by both distance (20%) and area (18%) in the regression analyses indicates the equal importance of habitat availability and fragmentation effects acting on wood cricket presence at the landscape scale. However, the relatively low predictive power of the total model (35%) highlights the importance of further refining the variables used in this model. Previous research has shown that refined methods to measure isolation between habitat fragments can generate a higher predictive power than the simple Euclidean distance measure used in this study (Petit & Burel, 1998; Chardon et al., 2003). Petit & Burel (1998) used an Euclidean (straight-line) nearest occupied neighbour distance measure and a measure of the distance between individual habitat patches via inter-connecting hedgerows. The latter measure was informed by the known ecology of the study species (*Abax parallelepipedus*) and was found to have a higher predictive ability than the simple Euclidean measure. For the Speckled wood butterfly (*Pararge aegeria*) a similar approach, comparing Euclidean nearest occupied neighbour distance with a species informed cost-distance measure, showed that the cost-distance measure performed better than the Euclidean measure (Chardon et al., 2003). Both these examples indicate that including more refined parameters informed by the ecology of the study species can improve model performance. For the model presented here, this might also be true; however, no information on the dispersal ecology of wood cricket was available to inform these more realistic distance measures. Nonetheless, the results show that variable combinations related to habitat amount and isolation together are relatively good predictors of wood cricket presence at the landscape scale.

The predicted probability response curves for the individual variables included in the model (see Figure 6a, b) are similar to those generally found in fragmentation studies. For example, the linear response between the probability of wood cricket being present related to fragment area matches the general response between species diversity and fragment area as shown in Ewers & Didham (2006). However, the generalized linear response between diversity and isolation (Ewers & Didham, 2006) differs from the negative-exponential response curve between the probability of wood cricket being present and nearest occupied neighbour distance found in this study. The negative-exponential response in this study is however similar to dispersal curves often reported for invertebrates (Roslin, 2000; Baguette et al., 2000; Ranius, 2006). For example, Roslin (2000) found a negative-exponential response between the number of dispersers and distance travelled by a dung beetle. Furthermore, for a beetle species living in hollow oaks, Ranius (2006) also found a negative-exponential response between the proportion of dispersing individuals and distance travelled. The apparent match between the response in this and their studies suggests that wood cricket is highly dispersal limited at this scale. This would be a reasonable assumption when considering its physical characteristics, being small and flightless. The curve further suggests that even small spatial distances between habitat fragments have a large effect on the probability of wood cricket being present (median distance between occupied woodlands: 50 m, see Figure 4a and Probability > 40% between 0-100 meter, see Figure 6a). This further strengthens the suggestion that the dispersal ability of wood cricket is highly limited at the landscape scale.

The current structure of the woodland fragments on the Isle of Wight at both the landscape and patch scale has been strongly influenced by past and present human activities. At the landscape scale, past influences are clearly indicated by the current fragmented structure of the woodlands embedded in the human-created urban and agricultural matrix (see Figure 2). However, this pattern is continuously changing, for instance as a result of recent reforestation activities (Quine & Watts, 2007). At the patch scale, most of the woodlands show a long history of management activities often involving coppice practice that have continuously changed woodland structure over time (Pope et al., 2003). New edge habitat at the periphery and within fragments is mainly created and maintained by these ongoing management activities. In previous studies, such edge habitats have been found to favour various groups of woodland invertebrates (e.g. Greatorex-Davies et al., 1994). Based on the strong positive relationship for wood cricket with the availability of permanent edges it therefore can be concluded that ongoing management practice in woodlands has a positive effect on wood cricket population persistence. Re-instatement of traditional coppice rotation and extensive woodland restoration efforts (Defra, 2005; Forestry Commission, 2006b) in woodlands on the Isle of Wight is therefore likely to favour the species within this area. A targeted approach in restoring, connecting and increasing woodland habitat seems highly relevant for the conservation of this and similar species.



3 Habitat requirements for the conservation of wood cricket (*Nemobius sylvestris*) on the Isle of Wight, UK

3.1 Introduction

Much interest has focused recently on the role of landscape-scale factors in maintaining populations of species, particularly as a result of developments in metapopulation theory and landscape ecology (Hanski & Gilpin, 1997; Gutzwiller, 2002a; Crooks & Sanjayan, 2006). However, for the conservation of invertebrate species, factors acting at a local scale may often be equally important for the persistence of individual populations as habitat availability at the landscape scale. Indications for this are found in habitat fragmentation studies that have have been undertaken at a range of different spatial scales, revealing the relative importance of within-patch habitat compared to spatial measures such as patch size and isolation between habitat fragments (e.g. Rukke & Midtgaard, 1998; Ranius, 2000a; Binzenhofer et al., 2005). For example, in a study on a burnet moth species in an abandoned agricultural landscape in Germany, Binzenhofer et al. (2005) found that presence of the species was mainly explained by total nectar plant cover (i.e. habitat availability) within patches, whereas no patch size or isolation effect between habitat patches was found. Two studies on beetles living in dead fungal fruiting bodies on trees revealed similar results, where fragment area and isolation were found to be less important explanatory variables for presence than the total amount of habitat (i.e. fungus fruiting bodies) available within the individual woodland stands (Rukke & Midtgaard, 1998; Rukke, 2000). Furthermore, in a study on an endangered longhorn beetle living on dead trees, Buse et al. (2007) revealed that variables measured at the tree level were better predictors of presence of the species than spatial measurements between trees. These examples indicate the overall importance of within patch (i.e. local scale) habitat availability in determining invertebrate presence and population persistence.

Detailed studies examining habitat factors influencing invertebrate populations are required to be able to determine habitat suitability and species-specific requirements within individual sites. Presence/absence studies are often used to analyse the responses of individual species to habitat variables (e.g. Rukke, 2000; Binzenhofer et al., 2005). Variables often measured include habitat factors related to species-specific food availability, vegetation structure (e.g. canopy cover), abiotic conditions (e.g. sunlight availability) and isolation measures (e.g. nearest neighbour distance). Studies on grassland species have revealed positive relationships with food availability and negative relationships with habitat distance, but differing results for vegetation structure and related abiotic conditions (Binzenhofer et al., 2005; Strauss & Biedermann, 2005; Heller & Gordon, 2006). Studies specifically on woodland species have found similar relationships. Most such studies to date have focused on endangered ground or tree related beetle species (Rukke & Midtgaard, 1998; Siitonen & Saaristo, 2000; Rukke, 2000; Sroka & Finch, 2006; Matern et al., 2007; Buse et al., 2007) and butterfly species (Thomas et al., 1992; Konvicka et al., 2007). These studies have similarly found positive relationships with measures of food availability (Rukke & Midtgaard, 1998; Rukke, 2000; Buse et al., 2007) and negative relationships with occupied nearest neighbour distance between habitat patches (Thomas et al., 1992; Rukke & Midtgaard, 1998; Siitonen & Saaristo, 2000; Rukke, 2000; Buse et al., 2007). For canopy cover in most cases a negative relationship has been found (Rukke & Midtgaard, 1998; Matern et al., 2007; Buse et al., 2007), however the influence of vegetation structure differs widely between species (Siitonen & Saaristo, 2000; Sroka & Finch, 2006; Matern et al., 2007; Konvicka et al., 2007; Buse et al., 2007; Sorvari & Hakkarainen, 2007).

The research described here focused on wood cricket (*Nemobius sylvestris*) on the Isle of Wight, United Kingdom. Although wood cricket is relatively widespread in Europe (Brown, 1978), in the UK it has the national status of a 'Species of Conservation Concern' (NBN Gateway, 2007). In the UK wood cricket reaches the northern limit of its European distribution. Populations of the species are restricted to the South of England at three main locations, the New Forest (Hampshire), South Devon and on the Isle of Wight (NBN Gateway, 2007). On the Isle of Wight, populations are largely restricted to relatively large woodland fragments occurring in the northern half of the island (Chapter 2). The specific habitat requirements of the species are poorly understood, and existing knowledge is largely based on observational and anecdotal information (e.g. Richards, 1952).

Wood cricket is a non-flying cricket species that is strongly associated with native broadleaved woodland, often dominated by oak (*Quercus spp.*) (Richards, 1952). It is typically found in relatively open areas such as woodland clearings and edges of woodland tracks, footpaths, railway lines and woodland peripheries (Richards, 1952; Morvan & Campan, 1976; Beugnon, 1980). Locally the species can reach high population densities (Gabbutt, 1959). The insects live on the ground and prefer a well-developed leaf litter layer, which serves as shelter, a food source and as a breeding ground (Richards, 1952; Brown, 1978; Proess & Baden, 2000). The species is considered to be an omnivorous with the staple diet mainly being composed of dead leaf litter material (Gabbutt, 1959; Koehler & Samietz, 2006). However, to date no detailed study has been undertaken of the specific habitat requirements of the species in relation to its presence or absence within woodland stands.

To address this gap in knowledge the distribution of wood cricket was investigated within three separate woodlands in relation to a range of habitat characteristics. In order to define an appropriate approach to conservation management for this species it is critical to know its precise habitat preferences. Statistical modelling approaches are often used to determine the habitat variables that can be used to predict presence/absence of a species. This method has been implemented in a range of studies (Strauss & Biedermann, 2005; Matern et al., 2007; Buse et al., 2007), however it has been noted that relatively few habitat modelling studies have been undertaken with rare and/or endangered species (Engler et al., 2004). Habitat models have also been identified as highly valuable for informing conservation management (Fleishman et al., 2002). Therefore, in this investigation, habitat suitability models based on logistic regression were developed in order to evaluate the relative importance of different habitat variables to provide a tool for assessing habitat suitability for wood cricket.

This study addressed the following aims: (1) to test the relationships between wood cricket presence/absence within woodlands and (*a*) ground habitat (i.e. leaf litter depth and volume), (*b*) vegetation structure (i.e. ground vegetation cover, vegetation height, canopy closure) and (*c*) isolation measures (i.e. Euclidean distance); and (2) to develop a deterministic habitat suitability model. Based on findings of habitat suitability studies on similar invertebrate species it was hypothesised that a positive relationship would be found between wood cricket presence and ground habitat availability (i.e. leaf litter) and a negative relationship would be found between presence and habitat isolation. Further hypotheses based on findings of previous research were that wood cricket would be more likely to be present when (1) ground vegetation cover was relatively sparse, and (2) canopy closure was relatively low.

3.2 Methods

3.2.1 Study area

A field survey was carried out in 2006 within three different woodlands located on the Isle of Wight, United Kingdom. The selected woodlands were Briddlesford copse (50° 42'40 N, 1° 13'23 W), Borthwood copse (50° 39'21 N, 1° 11'43 W) and Firestone copse (50° 43'00 N, 1° 12'54 W) (Figure 7).

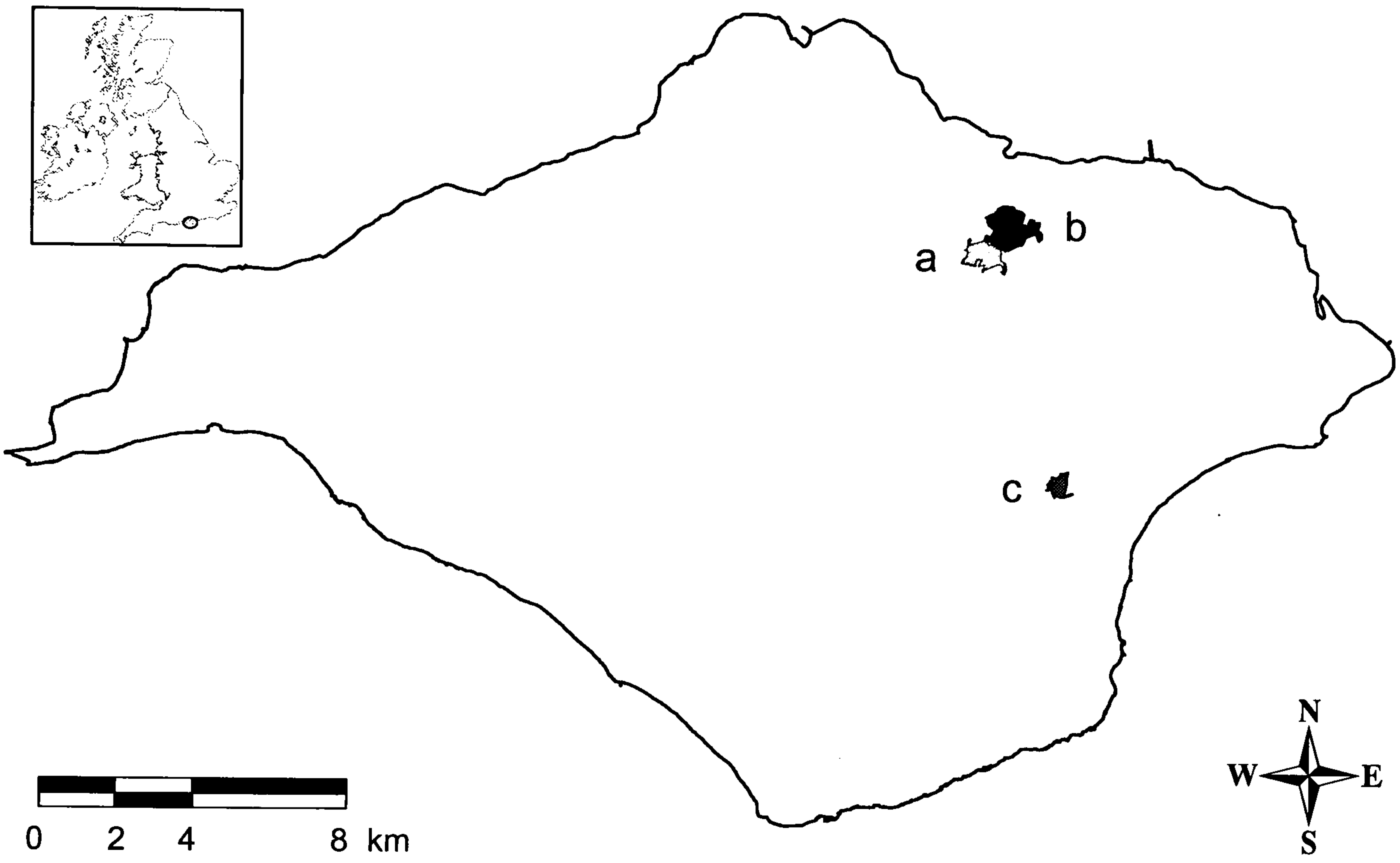


Figure 7: Woodland locations on the Isle of Wight (UK). (a) Briddlesford copse; (b) Firestone copse; (c) Borthwood copse. Derived from digital maps based on the National Inventory of Woodland and Trees (NIWT) (Smith & Gilbert, 2003).

Briddlesford copse was surveyed between 20 - 29 July, Borthwood between 1 - 3 August and Firestone copse between 4 – 9 August. These sites were selected for study based on the fact that they (i) support relative widespread wood cricket communities within them, (ii) are similar in age and origin, (iii) are mainly dominated by broadleaf trees species and (iv) are larger than 20 ha in area.

All three woodlands retain ancient woodland characteristics (i.e. continuous woodland cover since 1600 AD) following the Ancient Woodland Inventory (see Spencer & Kirby, 1992; English Nature, 1998 - 2006). Briddlesford copse and Borthwood copse are predominantly classified as ancient semi-natural woodland sites (English Nature, 1998 - 2006). Firestone copse is predominantly classified as an ancient replanted woodland site (English Nature, 1998 - 2006). This woodland was heavily planted with coniferous tree species but retains its ancient woodland features for 66% of the total woodland area. The individual surface area of the selected woodlands is 49.9 ha for Briddlesford copse, 24.4 ha for Borthwood copse and 99.5 ha for Firestone copse (calculated in ArcGIS 9.1, ESRI, Redlands, California, USA). However, for Firestone copse, the focus of the survey was on the broadleaf-dominated areas that account for 26.2 ha of the total woodland area.

The Forestry Commission (South East England Forest District) manages Firestone copse. The main management aims adopted here are to integrate timber production, recreation and conservation, by restoring the ancient characteristics of the woodland through removal of non-native (coniferous) tree species. Briddlesford copse is managed by the People's Trust for Endangered Species (PTES) (London, UK), a non-governmental conservation organisation (NGO). Their main management strategy aims to maximise biodiversity. The National Trust (Mottistone, Isle of Wight), another conservation NGO, manages Borthwood copse. Here, management focuses on facilitating public access and creating, and maintaining diversity of habitat within the woodland area to maximise visitors' woodland experience.

3.2.2 Survey methods

3.2.2.1 Sample design

The three individual woodlands were each divided into seven different strata. This stratification was based on observations on wood cricket habitat preference recorded during preliminary surveys completed in 2005 and 2006. The strata were: 'Ride' (being woodland tracks and paths), 'Gaps' (being areas without mature trees and/or overhead canopy, situated within the boundaries of a woodland), 'Coppice with standards' (being open coppiced areas with mature trees within them), 'Open canopy' (being areas that were thinned and had an open canopy structure), 'Perimeter' (being the edge of the woodland), 'Understorey' (being a mature undisturbed woodland stand characterised by a closed canopy) and the overlapping strata 'Occupied habitat' (being locations where wood cricket was known to be present). These strata were identified using high-resolution aerial photographs (Google Earth 3.0, Google Inc., Silicon Valley, California, USA), digital OS maps (Ordnance Survey MasterMap, Great Britain) and preliminary field surveys on the ground using a hand-held GPS device (Garmin III GPS V, Garmin (Europe) Ltd, Romsey, UK). These data were then used to produce separate data layers in ArcGIS 9.1 (ESRI, Redlands, California, USA).

In order to obtain a similar sample size for both 'presence' and 'absence' locations, the following strategy was adopted. The six main woodland strata (where wood cricket was absent) were sampled using a stratified random sampling design. Each of the strata were randomly sampled by generating random points using the Hawth's Analysis Tools (for ArcGIS, Version 3.24; (Beyer, 2004). The following criteria were used to establish presence or absence of wood cricket at each measurement site. A five-minute period was used to search and listen for wood cricket in a 3 m radius around the measurement location. When a wood cricket was observed or heard (stridulating males) within these five minutes the location was recorded as being occupied.

The 'Occupied habitat' locations where wood cricket was known to be present based on a preliminary field survey, were thoroughly surveyed by walking through the area in a zigzag pattern. The locations where the individual measurements were taken were separated by a minimum distance of 10 m. If wood cricket was observed, a habitat measurement was taken at that exact location. If wood cricket was only heard (stridulating males), the location of the individual was determined by slowly moving towards it to pinpoint its location. This method is thought to be accurate enough to capture the overall preferred habitat because of the bimodal daily rhythm of movement the species shows during every 24 hour period (see Beugnon, 1980).

The number of sample points was determined proportional to broadleaf dominated woodland area. This resulted in a total sample of $n_{Br} = 180$ with $n_{Br1} = 90$ present and $n_{Br2} = 90$ absent for Briddlesford copse (49.9 ha); $n_{Bo} = 100$ with $n_{Bo1} = 50$ present and $n_{Bo2} = 50$ absent for Borthwood copse (24.4 ha) and $n_F = 122$ with $n_{F1} = 61$ present and $n_{F2} = 61$ absent for Firestone copse (26.2 ha), resulting in a total sample size of $n = 402$ with $n_1 = 201$ present and $n_2 = 201$ absent for all woodlands together.

3.2.2.2 Habitat measurements

The habitat measurements that were obtained were divided into three main groups: ground surface measurements (including all non-living habitat elements on the ground, such as leaf litter), vegetation measurements (including ground vegetation and canopy tree measurement) and isolation measurements (i.e. Euclidean distance measures).

A 1x1 m quadrat was used to perform the vegetation measurements. First, within the quadrat, the total ground vegetation cover was estimated visually (in %). Cover was also estimated for each of the main individual plant species present within the quadrat. Secondly the mean ground vegetation height and the height of the main individual plant species were measured (in cm) using a meter rule. Thirdly, measurements were taken recording leaf litter cover (in %) and leaf litter depth within the quadrat. Leaf litter depth (in cm) was measured by taking four separate measurements with a leaf litter probe in the middle of each of four 0.5 square meter sections within the quadrat. From the centre of the quadrat, canopy closure was measured using a spherical densiometer (Forest Densiometers, Bartlesville, US). This involved taking readings in North, East, South and Westerly direction.

Within ArcGIS, a series of Euclidean distance measurements were made between the individual quadrat measurement locations and different edge habitat within the woodlands. These measurements were made from the individual locations to: the nearest occupied permanent edge (being the perimeter of a woodland or an open ride edge where wood cricket was present); the woodland edge (being the outer edge of a woodland) and any edge (including edges of rides, within clearings and the woodland perimeter).

3.2.3 Statistical data analysis

The individual habitat variables were tested for their relationship with wood cricket presence using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA). The values for the separate variables were first explored using descriptive statistics within SPSS. This included testing for normality (Kolmogorov-Smirnov test) and computing boxplots for the individual variables to visualise the range and variation in values of measurements made for both 'presence' and 'absence' locations. All variables were found not to be normally distributed. For examining the relationships between wood cricket presence and the individual computed habitat variables, Mann-Whitney U tests were performed. Additionally, the effect size (r) for each individual variable was calculated (= z / square root n) in this case indicating the strength of association of each variable with wood cricket presence/absence (Pallant, 2007). The z test statistic is given by SPSS when performing a Mann-Whitney U test and is used to test for a significant difference between two groups. A Spearman rank correlation test was undertaken to examine correlations between these variables. Assessment of the correlations and effect size (r)

was based on the guidelines of Cohen (1988) where values between $r = 0.10$ and 0.29 indicate a small correlation effect/effect size; $r = 0.30$ to 0.49 a medium effect and values $r = 0.50$ to 1.00 a large effect.

Several logistic regression methods were used to examine the relative influence of the different habitat variables for explaining the presence or absence of wood cricket within the woodlands. First, all individual variable responses were explored in order to determine their individual explanatory power. For this, all variables were used to create individual univariate models using the 'Enter' function within SPSS. This function is used to build regression models by hand. Only the significant variables (Wald test: $P < 0.05$, see below) were used in subsequent analyses. To explore the influence of the individual variables, multivariable models were constructed. First a stepwise logistic regression (Forward: LR in SPSS) was used. This function lets the program build a regression model, step by step including the variables with the highest score statistic and significance, until there are no variables left that significantly add to the model. Particularly when using a large number of variables, this method is useful to provide an indication of the explanatory variables that are most powerful. The outcomes of these automatic logistic regressions and the outcomes from the Spearman rank correlation test were used to inform further exploration of different variable combinations by using the 'Enter' function. This manual method allows correlations between variables and other factors influencing models generated from stepwise methods to be taken into account (Strauss & Biedermann, 2005).

The output that is generated by SPSS when analysing the individual models provides information on the performance of the total model and information on performance of the individual variables used within these models. For total model performance, SPSS produces two 'goodness-of-fit' tests, a 'classification table' and information on 'effect size'. 'Goodness-of-fit' tests are designed to test how well the created models perform and fit the data. There is no universally preferred test for this purpose (Tabachnick & Fidell, 2001), so SPSS performs a 'model fit test' and a 'Hosmer & Lemeshow model fit test'. However, in this case the 'Hosmer & Lemeshow model fit test' is considered to be more powerful than the 'model fit test' (Pallant, 2007). The 'classification table' provides information on the percentage of cases (i.e. presence/absence locations) that are correctly classified by the model and the 'effect size' provides information on the amount of variation that is explained by the model. For the performance of the individual variables, SPSS uses the 'Wald test' to test the contribution of the individual variables to the predictive ability of the model. SPSS further generates B values (+

Standard Error) which are used as constants in the probability function (see Equation 2). This equation was further used to construct probability curves to display the relationships between the individual predictor variables and wood cricket presence.

Equation 2: Probability equation for wood cricket presence (from Tabachnick & Fidell, 2001). 'B' values are generated by SPSS for the individual variables that are included in the model.

$$P(y) = \frac{e^{a + \sum_{x=1}^{n} b}}{1 + e^{a + \sum_{x=1}^{n} b}}$$

$P(y)$ = probability of wood cricket being present

a = B value for the constant included in the model

b = B value * variable(s) included in the model

The B value further indicates the direction of the relationship between the individual predictor variables and the dependant variable (i.e. wood cricket presence). The final piece of information given is the Exp(B) (with 95% Confidence Interval) value which indicates the odds ratio for wood cricket presence per unit increase of the predictor variable. Further details on SPSS output interpretation for logistic regression analyses are provided by Tabachnick and Fidell (2001), Field (2005) and Pallant (2007). The following selection criteria were used to choose the most powerful and realistic model: (1) all individual correlations (*r* values) between the variables included had to be less than +/- 0.7 (following Strauss & Biedermann, 2005), (2) all individual tests for significance had to be met ('model fit test' ($P < 0.05$), 'Hosmer & Lemeshow model fit test' ($P > 0.05$) and 'Wald test' ($P < 0.05$)), (3) all B values had to indicate the correct sign of the relationship (+/-), and (4) the 95% confidence interval for Exp(B) was not allowed to include the value of 1, which indicates no effect. The best-fitting model was then selected based on the highest scores for 'effect size' (R^2_N), 'Hosmer & Lemeshow model fit test' scores and the total percentage given in the 'classification table'.

3.3 Results

3.3.1 Analysis of the independent variables

The measurements undertaken in the field were used to compute 26 different variables. Mann-Whitney *U* test were performed to test the relationship between each habitat variable and wood cricket presence. Results of these tests indicated that 14 variables were found to have a significant influence on wood cricket presence (Table 5 and Table 6). The variable showing the strongest relationship with and effect on wood cricket presence was the distance measure 'Euclidean distance to nearest occupied permanent edge', followed by the vegetation variable 'South orientated canopy closure' (Table 5), indicating the importance of a nearby source populations and availability of sunlight at ground level.

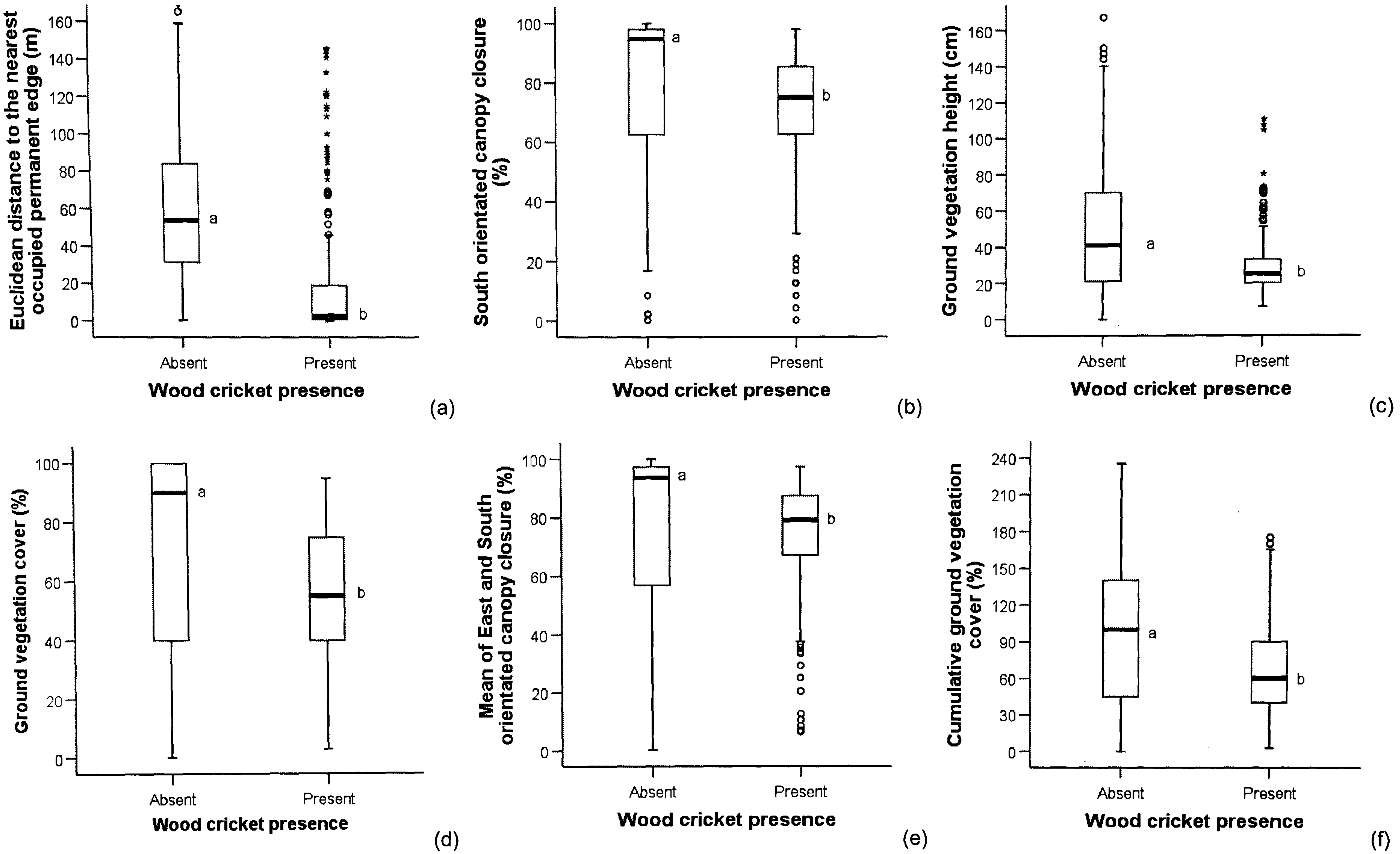
Overall, results indicated that wood cricket is more likely to be present at sites: (1) within a relatively short distance of an occupied permanent edge (Table 5, Figure 8a), (2) with relatively low percentages of South-orientated canopy closure (Table 5, Figure 8b), (3) with relatively low measures of ground vegetation height (Table 5, Figure 8c), (4) with relatively low percentages of ground vegetation cover (Table 5, Figure 8d), (5) with relatively low percentages of East/South orientated canopy closure (Table 5, Figure 8e), and (6) with relatively low values of cumulative ground vegetation cover (Table 5, Figure 8f). Higher values of this latter measure represent a more structured ground vegetation indicating multiple layers and therefore denser undergrowth. This indicates that the structure of the ground vegetation also influences wood cricket presence. Furthermore, wood cricket is more likely to be present at sites (7) with relatively low values of total vegetation cover (Table 5, Figure 8g), (8) within a relatively short distance of a permanent edge (Table 5, Figure 8h), (9) with a relatively thick leaf litter layer (Table 5, Figure 8i), (10) with relatively high volumes of leaf litter (Table 5, Figure 8j), (11) with relatively low percentages of total canopy closure (Table 5, Figure 8k), (12) with relatively low percentages of East orientated canopy closure (Table 5, Figure 8l), (13) within a relatively short distance of an occupied woodland edge (Table 5, Figure 8m) and (14) with relatively low percentages of West-orientated canopy closure (Table 5, Figure 8n).

Table 5: Mann-Whitney *U* test for the relationship between wood cricket presence/absence and fourteen habitat variables analysed through separate tests. n = 402; wood cricket present n_1 = 201 and absent n_2 = 201; *U* = Mann-Whitney test statistic; *z* = test statistic given by SPSS when performing a Mann-Whitney *U* test and is used to test for a significant difference (*P*) between two groups; *P* = probability or significance level; *r* = effect size.

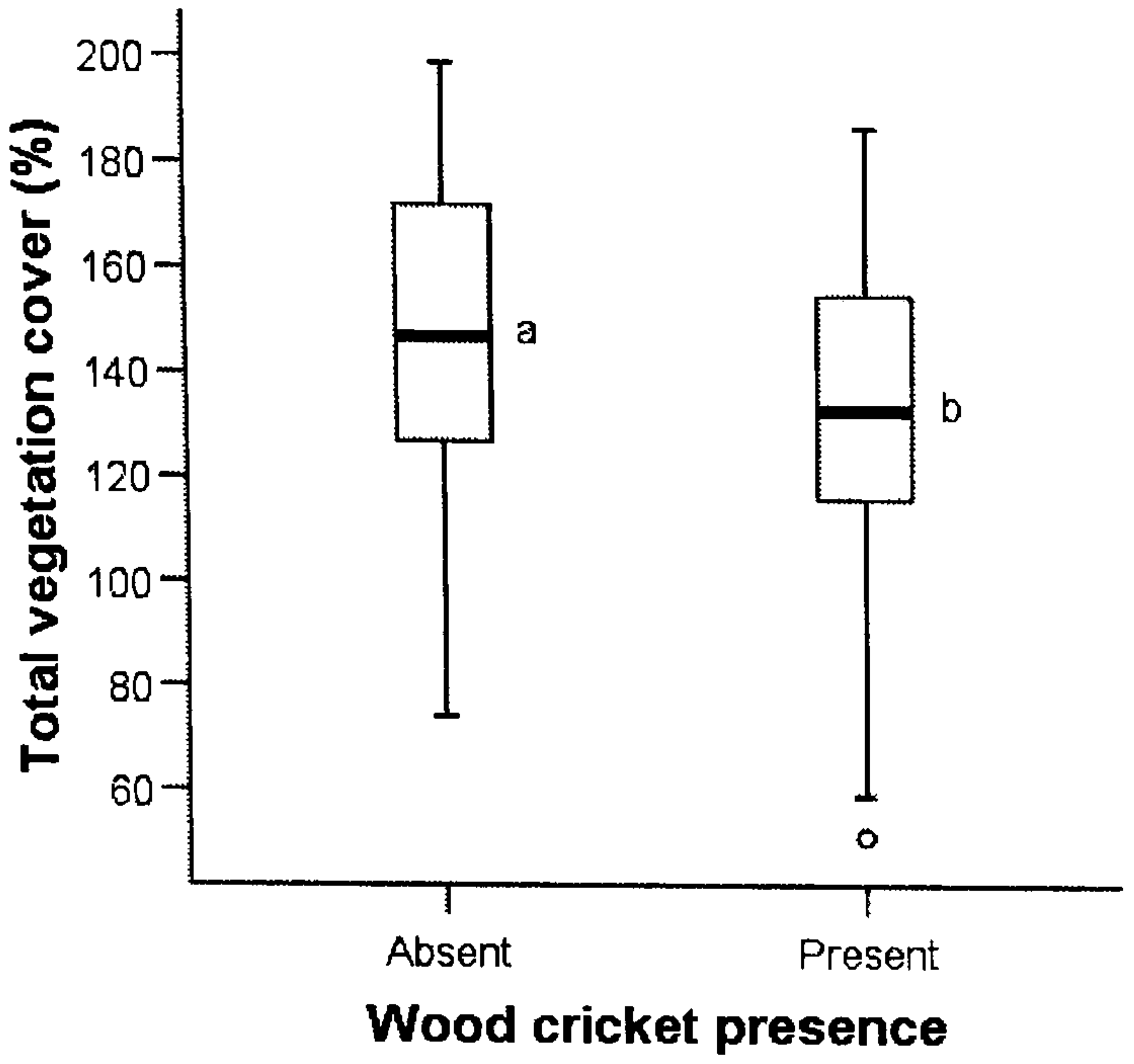
Mann-Whitney *U* test	*U*	*z*	*P*	*r*
Euclidean distance to nearest occupied permanent edge	6778.5	-11.5	<0.001	0.57
South orientated canopy closure	12567	-6.56	<0.001	0.33
Ground vegetation height	12946	-6.24	<0.001	0.31
Ground vegetation cover	12989	-6.22	<0.001	0.31
East/South orientated canopy closure	13920	-5.39	<0.001	0.27
Cumulative ground vegetation cover	14042	-5.29	<0.001	0.26
Total vegetation cover	14774	-4.66	<0.001	0.23
Euclidean distance to nearest permanent edge	14840	-4.60	<0.001	0.23
Leaf litter depth	14883	-4.57	<0.001	0.23
Leaf litter volume	15030	-4.44	<0.001	0.22
Canopy closure	15835	-3.75	<0.001	0.19
East orientated canopy closure	16430	-3.24	0.001	0.16
Euclidean distance to nearest occupied woodland edge	16650	-3.05	0.002	0.15
West orientated canopy closure	17846	-2.02	0.043	0.10

Table 6: Variables that were computed from the field measurements and found to influence wood cricket presence/absence within woodland habitat.

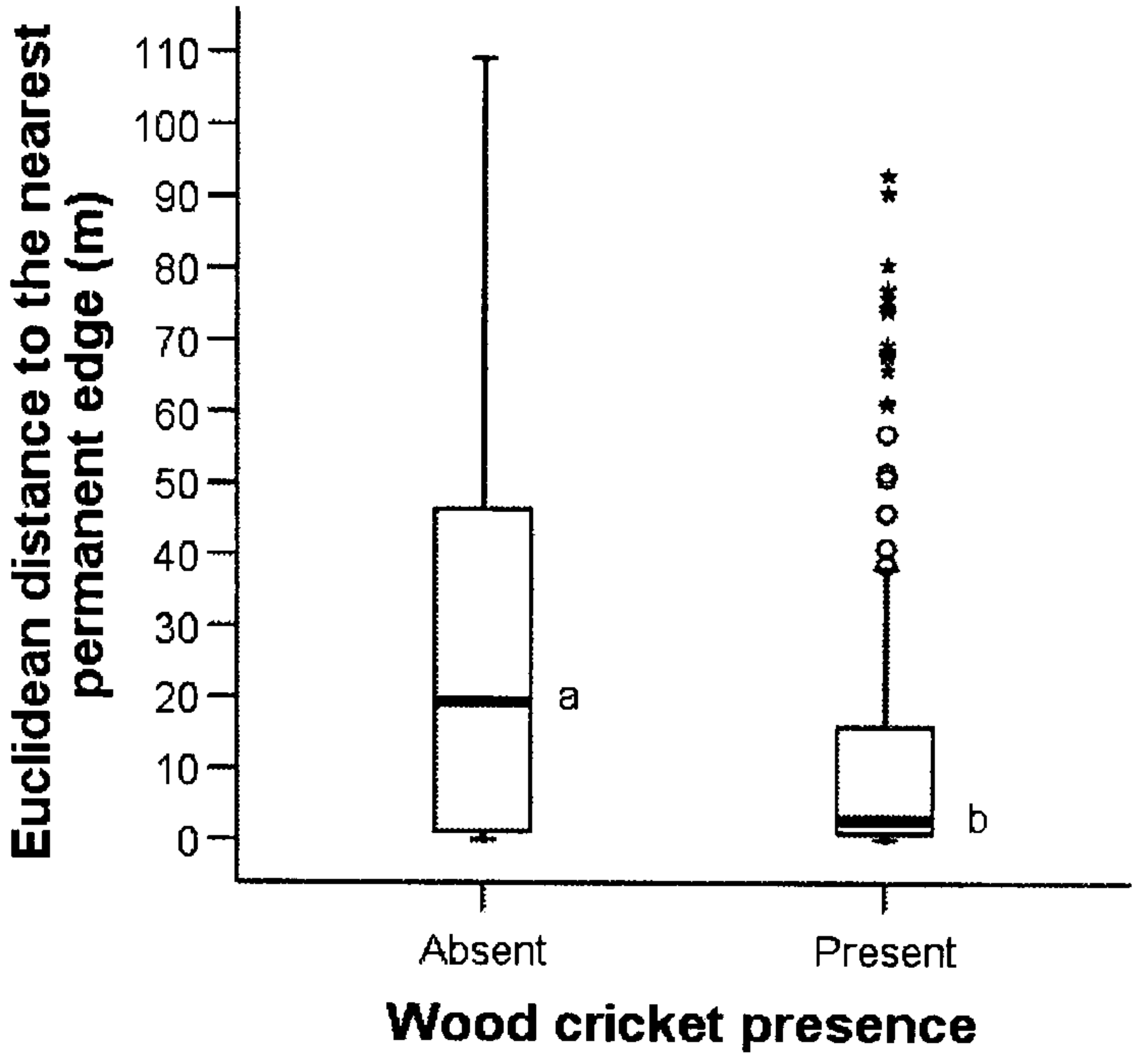
Variable group	Description
Vegetation variables	
Ground vegetation cover	The total area covered by all ground vegetation (in %)
Cumulative ground vegetation cover	The sum of % area covered for each individual species of ground vegetation
Ground vegetation height	Mean ground vegetation height (in cm)
East orientated canopy closure	Densiometer measurement of overhead canopy in Eastern direction (in %)
South orientated canopy closure	Densiometer measurement in Southern direction (in %)
West orientated canopy closure	Densiometer measurement in Western direction (in %)
East/South orientated canopy closure	Mean of East and South densiometer measurements (in %)
Canopy closure	Mean of North, East, South and West measurements (in %)
Total vegetation cover	Ground vegetation cover + Canopy closure (in %)
Leaf litter depth	Mean of four measurements made in the quadrat (in cm)
Leaf litter volume	Leaf litter depth x quadrat area x % leaf litter cover (in cm^3)
Distance measures	Linear distance from quadrat location to:
Euclidean distance to nearest permanent edge	The perimeter of a woodland or an open ride edge (as observed in the field)
Euclidean distance to nearest occupied permanent edge	The perimeter of a woodland or an open ride edge occupied by wood cricket
Euclidean distance to nearest occupied woodland edge	The perimeter of a woodland occupied by wood cricket


Euclidean distance to the nearest occupied permanent edge (m)
160
140
120
100
80
60
40
20
0
a
b
Absent
Present
Wood cricket presence
(a)
South orientated canopy closure (%)
100
80
60
40
20
0
a
b
Absent
Present
Wood cricket presence
(b)
Ground vegetation height (cm)
160
140
120
100
80
60
40
20
0
a
b
Absent
Present
Wood cricket presence
(c)
Ground vegetation cover (%)
100
80
60
40
20
0
a
b
Absent
Present
Wood cricket presence
(d)
Mean of East and South orientated canopy closure (%)
100
80
60
40
20
0
a
b
Absent
Present
Wood cricket presence
(e)
Cumulative ground vegetation cover (%)
240
210
180
150
120
90
60
30
0
a
b
Absent
Present
Wood cricket presence
(f)

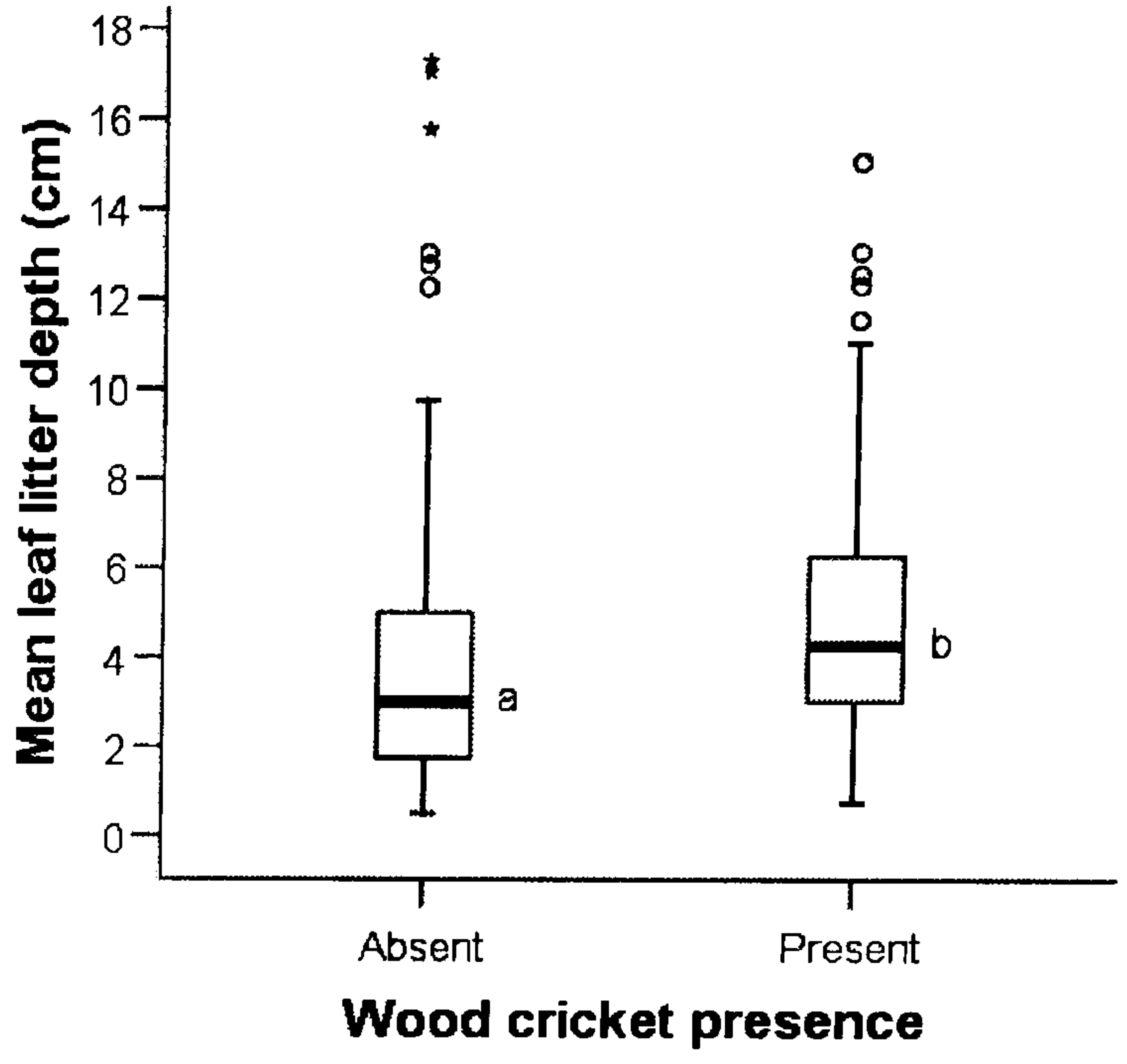
Continued



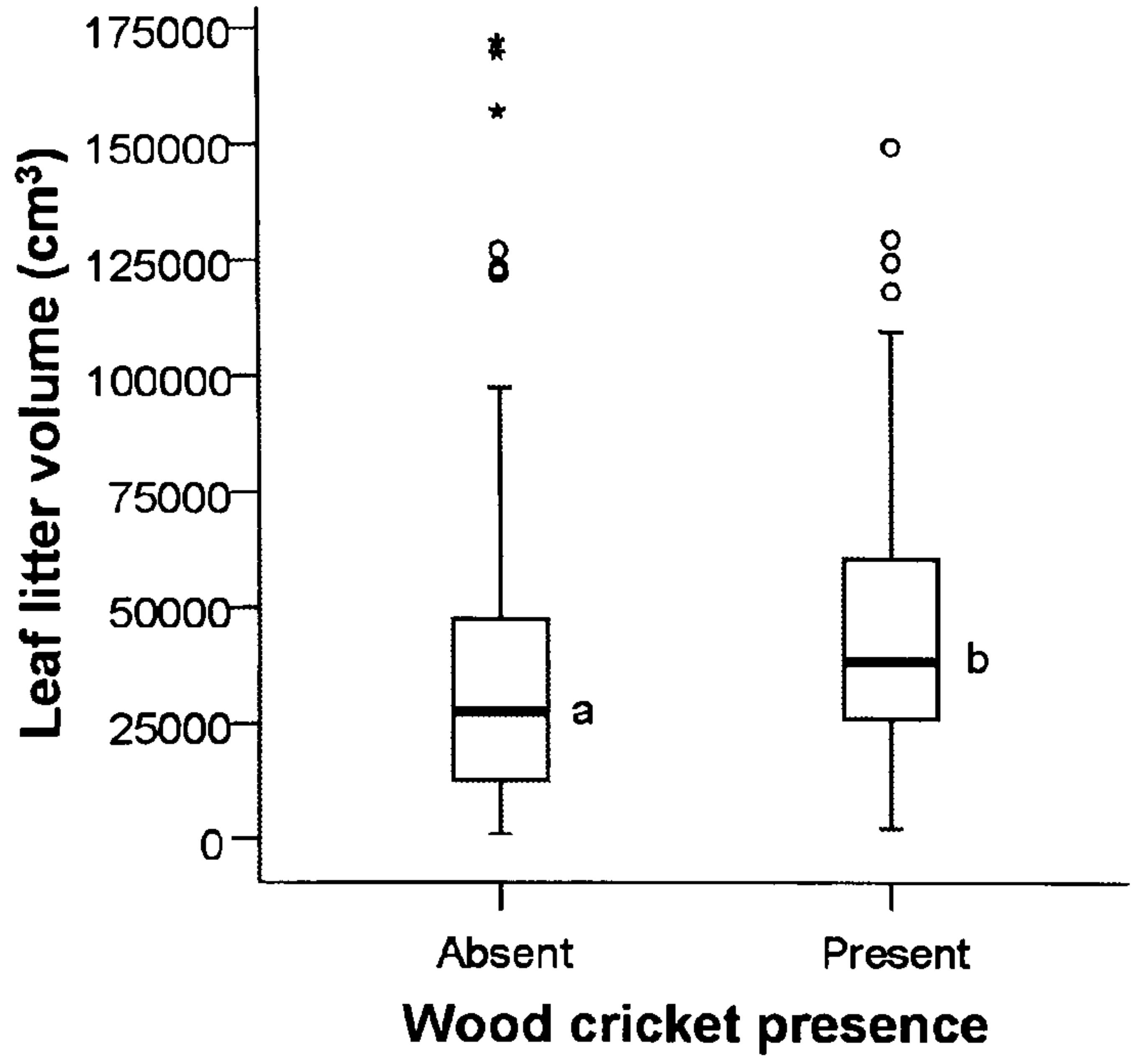
(g)



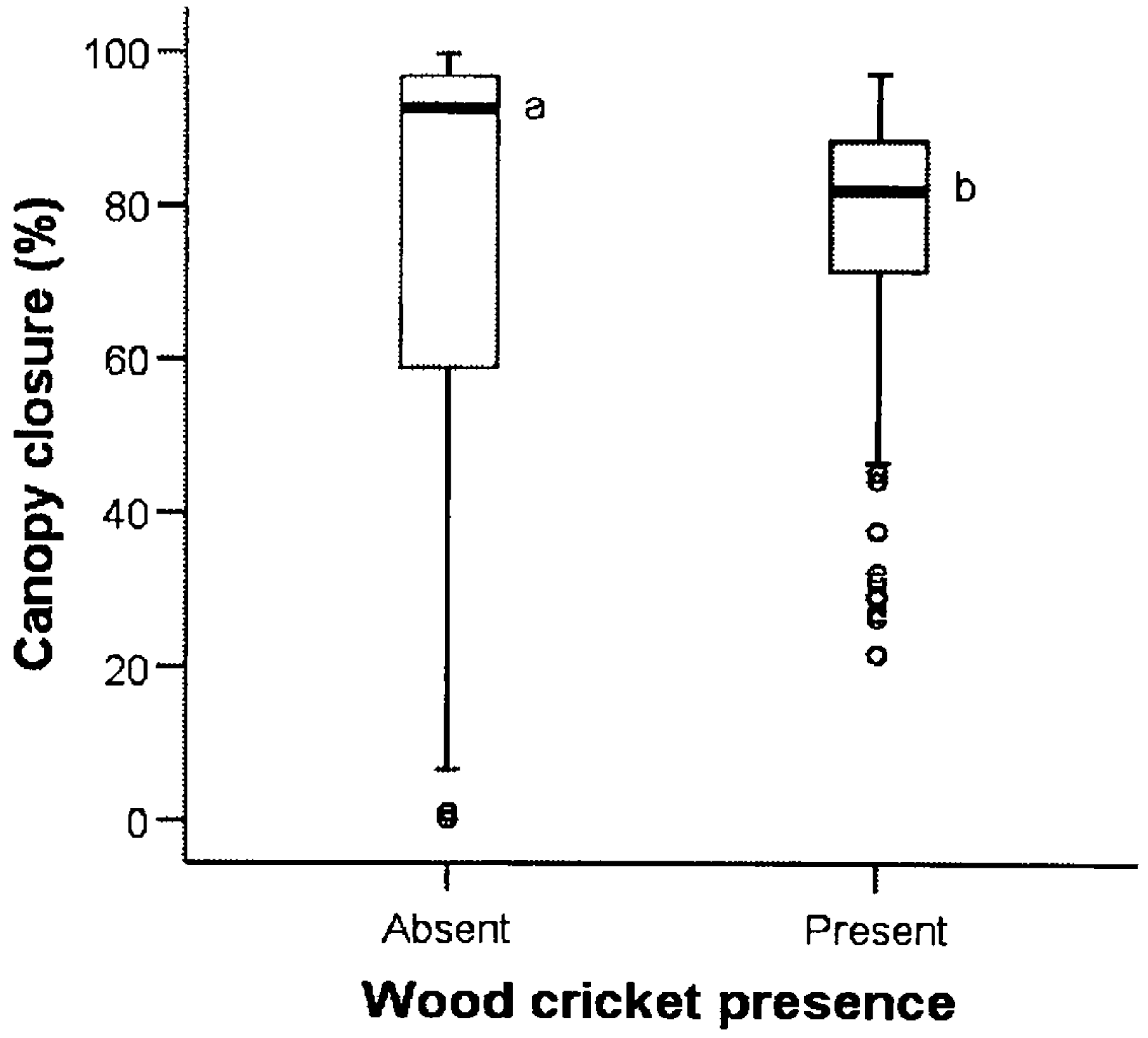
(h)



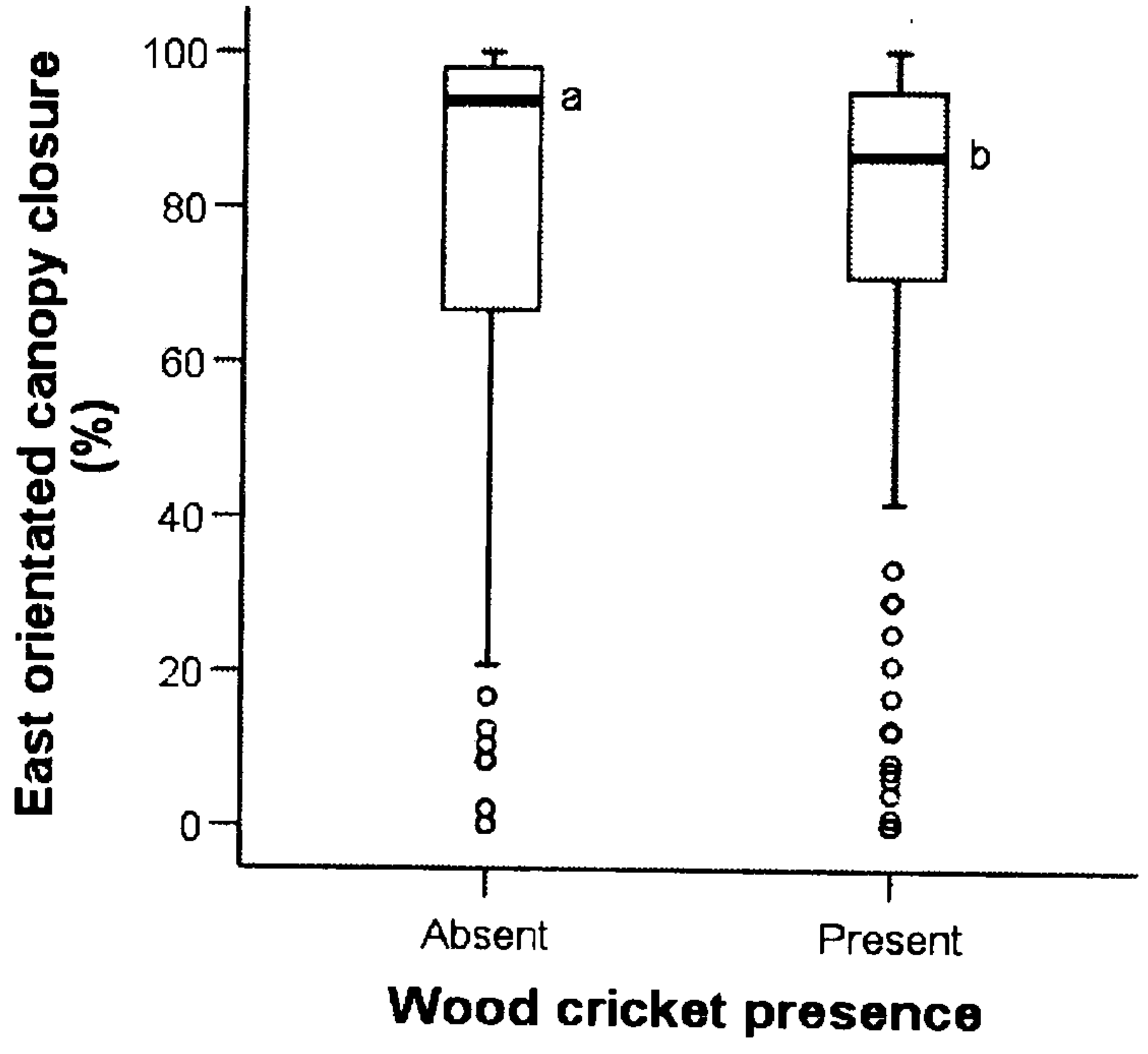
(i)



(j)

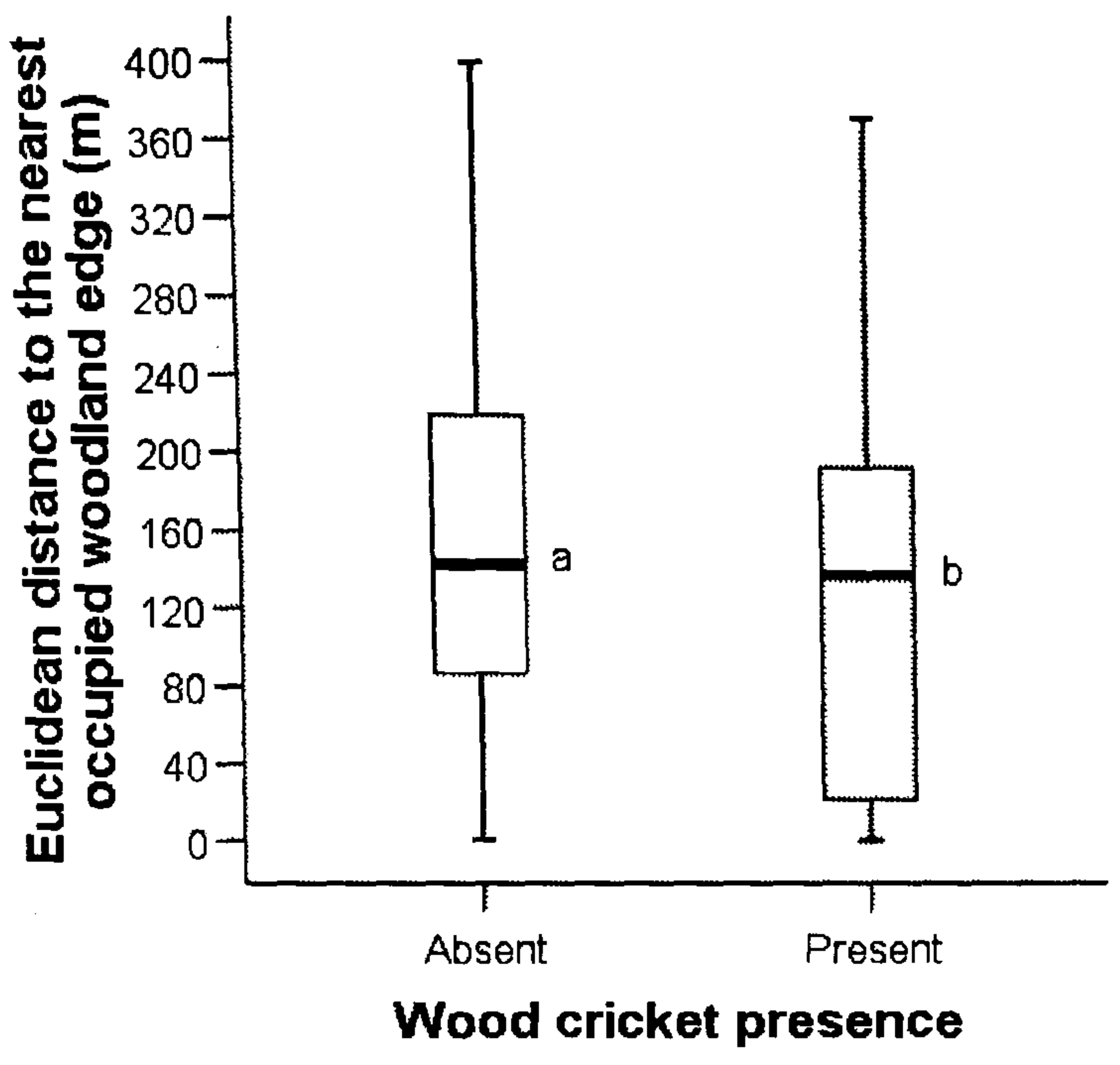


(k)

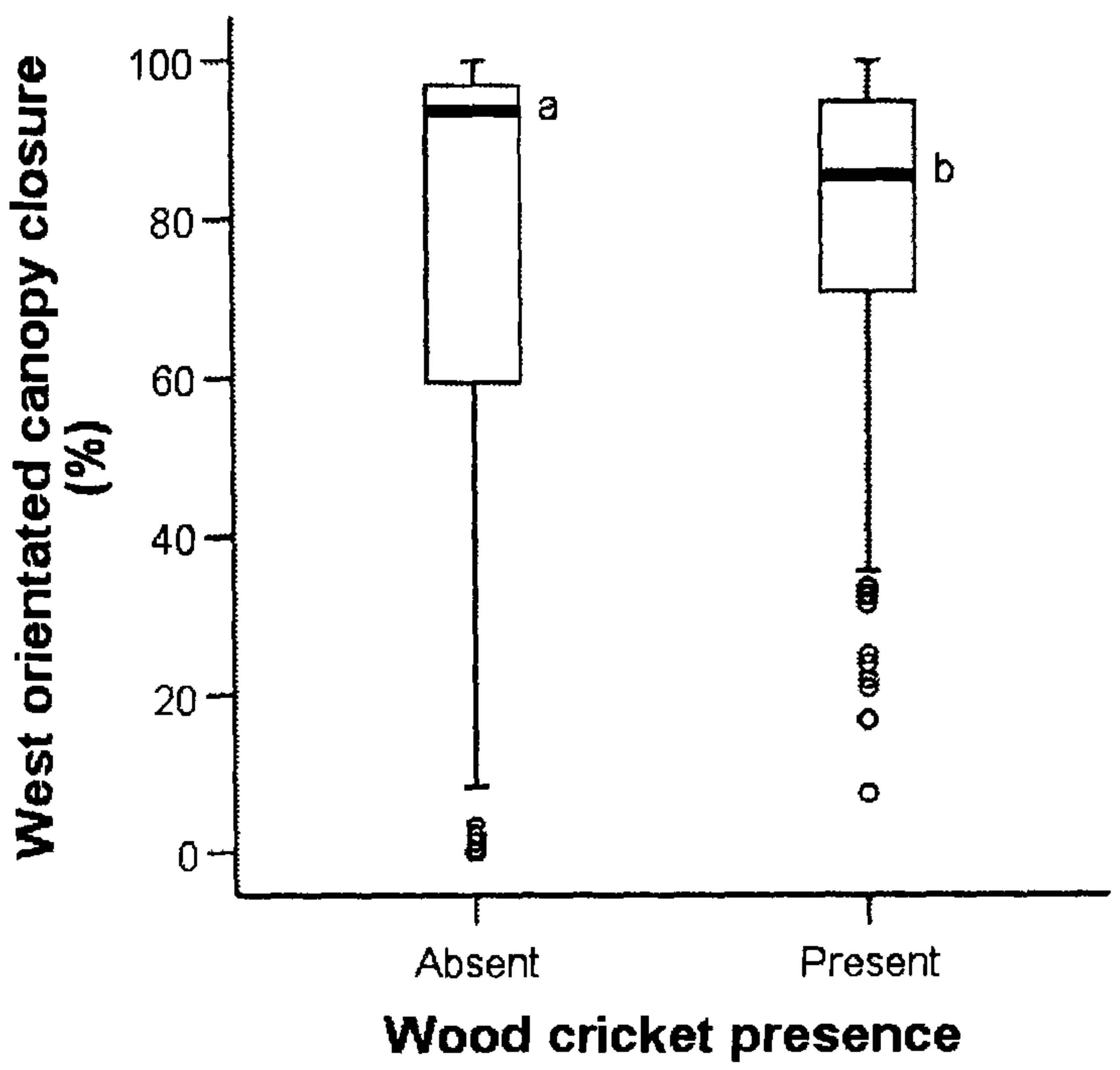


(l)

Continued



(m)



(n)

Figure 8: Boxplots ($n = 402$; wood cricket present $n_1 = 201$ and absent $n_2 = 201$) illustrating the median (horizontal black line) and ranges for locations where wood cricket was 'Absent' or 'Present' in relation to (a) Euclidean distance to the nearest occupied permanent edge (medians: 53.90 m, 2.700 m), (b) South orientated canopy closure (medians: 94.8%, 75.0%), (c) Ground vegetation height (medians: 41.0 cm, 25.0 cm), (d) Ground vegetation cover (medians: 90.0%, 55.0%), (e) East/South orientated canopy closure (medians: 93.8%, 79.2%), (f) Cumulative ground vegetation cover (medians: 100%, 60.0%), (g) Total vegetation cover (medians: 147%, 133%), (h) Euclidean distance to nearest permanent edge (medians: 19.30 m, 2.700 m), (i) Leaf litter depth (medians: 3.00 cm, 4.25 cm), (j) Leaf litter volume (medians: 27500 cm^3, 38400 cm^3), (k) Canopy closure (medians: 92.7%, 82.1%), (l) East orientated canopy closure (medians: 93.8%, 86.5%), (m) Euclidean distance to nearest occupied woodland edge (medians: 142.8 m, 136.8 m), and (n) West orientated canopy closure (medians: 93.8%, 85.4%). Identical letters indicate a non-significant difference (a – a), different letters indicate a significant difference (a – b) ($P < 0.05$, Mann-Whitney *U* test). The stars and circles indicate extreme values and outliers respectively. The boxes in the plots include 50% of all the cases of the individual groups. The whiskers protruding from the box extend to the smallest and largest values excluding the outliers and extreme values. SPSS defines points as outliers if they extend more than 1.5 times the box-length from the edge of the box. Extreme values extend more than three box-lengths from the edge (information on boxplots from Pallant, 2007). For the 'Absent' boxplot, three extreme values for graph (a) (170.5; 186.3; 273.1 m) and two for graph (m) (468.6 and 478.8 m) were omitted for clarity.

Table 7: Spearman rank correlation between the individual habitat variables. $n = 402$, r = correlation coefficient, P = significance or probability value. Bold figures indicate correlation coefficients (r) values > 0.50.

	Spearman rank correlation		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Ground vegetation cover	*r*	.													
		P	.													
2	Cumulative ground vegetation cover	*r*	**0.94**	.												
		P	<0.001	.												
3	Ground vegetation height	*r*	**0.68**	**0.64**	.											
		P	<0.001	<0.001	.											
4	East orientated canopy closure	*r*	-0.38	-0.34	-0.32	.										
		P	<0.001	<0.001	<0.001	.										
5	South orientated canopy closure	*r*	-0.35	-0.34	-0.33	**0.74**	.									
		P	<0.001	<0.001	<0.001	<0.001	.									
6	West orientated canopy closure	*r*	-0.44	-0.42	-0.30	**0.54**	**0.66**	.								
		P	<0.001	<0.001	<0.001	<0.001	<0.001	.								
7	East/South orientated canopy closure	*r*	-0.40	-0.37	-0.35	**0.91**	**0.94**	**0.65**	.							
		P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	.							
8	Canopy closure	*r*	-0.48	-0.46	-0.37	**0.87**	**0.87**	**0.82**	**0.94**	.						
		P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	.						
9	Total vegetation cover	*r*	**0.68**	**0.66**	0.37	0.21	0.22	0.13	0.22	0.18	.					
		P	<0.001	<0.001	<0.001	<0.001	<0.001	0.011	<0.001	<0.001	.					
10	Leaf litter depth	*r*	-0.39	-0.36	-0.14	0.26	0.21	0.26	0.26	0.32	-0.11	.				
		P	<0.001	<0.001	0.006	<0.001	<0.001	<0.001	<0.001	<0.001	0.028	.				
11	Leaf litter volume	*r*	-0.41	-0.38	-0.15	0.27	0.23	0.29	0.27	0.34	-0.11	**0.97**	.			
		P	<0.001	<0.001	0.002	<0.001	<0.001	<0.001	<0.001	<0.001	0.026	<0.001	.			
12	Euclidean distance to nearest permanent edge	*r*	-0.09	-0.16	0.00	-0.07	0.00	-0.01	-0.03	0.00	-0.22	-0.04	0.01	.		
		P	0.059	0.001	0.926	0.138	0.933	0.881	0.564	0.992	<0.001	0.447	0.857	.		
13	Euclidean distance to nearest occupied permanent edge	*r*	0.08	0.04	0.06	0.04	0.15	0.00	0.10	0.03	-0.03	-0.21	-0.19	**0.53**	.	
		P	0.127	0.450	0.215	0.474	0.002	0.956	0.037	0.510	0.541	<0.001	<0.001	<0.001	.	
14	Euclidean distance to nearest occupied woodland edge	*r*	0.01	-0.01	0.07	0.03	0.06	-0.03	0.05	0.02	0.05	-0.03	0.00	0.18	0.21	.
		P	0.849	0.801	0.184	0.556	0.197	0.558	0.319	0.672	0.298	0.562	0.923	<0.001	<0.001	.

A Spearman rank correlation test was performed to see if there were any associations between the variables that were examined. Four distinct correlated groups could be recognised based on a large effect size (*r* > 0.50) between all of the individual variables included. The first group included the 'Ground vegetation height', 'Cumulative ground vegetation cover', 'Ground vegetation cover' and 'Total vegetation cover' showing a high positive correlation with each other (range *r* = 0.64 – 0.94; Table 7). An exception in this group was the medium correlation between 'Total vegetation cover' and 'Ground vegetation height' (*r* = 0.37; Table 7). The second group included 'East-, South-, West-, East/South orientated canopy closure' and 'Canopy closure'. These five variables all showed a high positive correlation with each other (*r* = 0.54 – 0.94; Table 7). The third group included 'Leaf litter depth' and 'Leaf litter volume' that showed a very high positive correlation with each other (*r* = 0.94; Table 7). Finally the fourth group included 'Euclidean distance to nearest occupied permanent edge' and 'Euclidean distance to nearest permanent edge', which also showed a high positive correlation with each other (*r* = 0.53; Table 7). Euclidean distance to nearest occupied woodland edge was the only variable not correlated with any of the other variables.

Between these groups all canopy closure variables showed a medium negative correlation with 'Ground vegetation height', 'Cumulative ground vegetation cover' and 'Ground vegetation cover' (*r* = - 0.30 – -0.48; Table 7). This indicated the negative influence of canopy closure on ground vegetation development. The leaf litter variables both showed a moderate negative correlation with 'Ground vegetation cover' and 'Cumulative ground vegetation cover' (*r* = -0.36 – - 0.41; Table 7) and a moderate positive correlation with 'Canopy closure' (*r* = 0.32 – 0.34; Table 7). This indicated the positive influence of canopy closure on leaf litter presence.

Table 8: Summary of the logistic regression analyses. Model: variables included in the logistic regression model. Model performance: summary of model performance tests. Model fit test: tests if the model fits the data ($P < 0.05$ = good model fit). Hosmer & Lemeshow Model fit test: tests if the model fits the data ($P > 0.05$ = good model fit). Classification table (%): indicates percentage of cases correctly classified by the model. Effect size: indicates the amount of explained variation by the model (Nagelkerke R^2; range 0 – 1). Variables in the equation: indicates the usefulness of the individual variables included in the model. Wald test: tests contribution to the model for the individual variables ($P < 0.05$ = significant). B (with Standard Error): indicates the direction of the relationship between the individual variables and wood cricket presence (- indicates a negative and + a positive relationship). Exp. (B) (with 95% Confidence Interval): indicates the odds ratio for wood cricket presence per unit increase of the individual variable (below 1 indicates a decrease above 1 an increase).

Logistic Regression					Model performance							Variables in the equation							
Model		Model fit test			Hos. & Lem. Model fit test			Classification table (%)			Effect size	Wald test						95% C.I. Exp(B)	
Variables	*n*	χ^2	df	*P*	χ^2	df	*P*	Absent	Present	Total	Nagelkerke R^2	*z*	df	*P*	B	S.E.	Exp (B)	Lower	Upper
Euclidean distance to nearest occupied permanent edge	402	225.3	4	<0.001	6.608	8	0.579	80	85	82	0.57	64.21	1	<0.001	-0.032	0.004	0.968	0.961	0.976
Ground vegetation height												35.82	1	<0.001	-0.048	0.008	0.954	0.939	0.969
South orientated canopy closure												46.94	1	<0.001	-0.053	0.008	0.949	0.934	0.963
Cumulative ground vegetation cover												15.14	1	<0.001	-0.014	0.004	0.986	0.979	0.993
Constant												78.63	1	<0.001	8.009	0.903	3007		
Euclidean distance to nearest occupied permanent edge	402	208.6	3	<0.001	7.968	8	0.437	77	83	80	0.54	63.89	1	<0.001	-0.031	0.004	0.970	0.963	0.977
Ground vegetation height												59.50	1	<0.001	-0.059	0.008	0.942	0.928	0.957
South orientated canopy closure												42.01	1	<0.001	-0.047	0.007	0.955	0.941	0.968
Constant												73.28	1	<0.001	6.826	0.797	921.8		
Euclidean distance to nearest occupied permanent edge	402	152.8	2	<0.001	18.42	8	0.018	73	81	77	0.42	65.70	1	<0.001	-0.029	0.004	0.972	0.965	0.978
Ground vegetation height												37.23	1	<0.001	-0.034	0.006	0.966	0.956	0.977
Constant												75.27	1	<0.001	2.358	0.272	10.57		
Euclidean distance to nearest occupied permanent edge	402	101.2	1	<0.001	97.48	8	<0.001	70	82	76	0.30	69.92	1	<0.001	-0.029	0.003	0.971	0.965	0.978
Constant												45.64	1	<0.001	1.085	0.161	2.959		
Ground vegetation height	402	58.50	1	<0.001	29.85	8	<0.001	54	83	68	0.18	42.05	1	<0.001	-0.032	0.005	0.969	0.959	0.978
Constant												34.99	1	<0.001	1.177	0.199	3.245		
Cumulative ground vegetation cover	402	37.83	1	<0.001	55.81	8	<0.001	62	71	66	0.12	33.16	1	<0.001	-0.013	0.002	0.987	0.983	0.992
Constant												25.46	1	<0.001	1.025	0.203	2.788		
Euclidean distance to nearest permanent edge	402	32.79	1	<0.001	30.39	8	<0.001	51	79	65	0.10	28.34	1	<0.001	-0.026	0.005	0.975	0.965	0.984
Constant												12.95	1	<0.001	0.478	0.133	1.612		
Ground vegetation cover	402	24.71	1	<0.001	120.5	7	<0.001	65	56	60	0.08	23.30	1	<0.001	-0.017	0.004	0.983	0.976	0.990
Constant												19.05	1	<0.001	1.081	0.248	2.948		
Total vegetation cover	402	24.18	1	<0.001	15.75	8	0.046	59	58	59	0.08	22.44	1	<0.001	-0.018	0.004	0.982	0.975	0.989
Constant												21.61	1	<0.001	2.561	0.551	12.95		
Euclidean distance to nearest occupied woodland edge	402	11.62	1	0.001	46.87	8	<0.001	49	53	51	0.04	11.18	1	0.001	-0.003	0.001	0.997	0.995	0.999
Constant												7.670	1	0.006	0.494	0.178	1.639		
Leaf litter depth	402	11.17	1	0.001	14.42	8	0.071	67	50	59	0.04	10.39	1	0.001	0.122	0.038	1.130	1.049	1.217
Constant												7.608	1	0.006	-0.518	0.188	0.596		
South orientated canopy closure	402	10.56	1	0.001	108.2	8	<0.001	70	48	59	0.03	10.07	1	0.002	-0.013	0.004	0.987	0.979	0.995
Constant												8.983	1	0.003	0.977	0.326	2.658		
Leaf litter volume	402	9.928	1	0.002	16.31	8	0.038	68	49	59	0.03	9.308	1	0.002	<0.001	<0.001	1.000	1.000	1.000
Constant												6.319	1	0.012	-0.435	0.173	0.647		

3.3.2 Logistic regression analysis

Several logistic regressions analyses were undertaken to build a predictive habitat model and identify the key variables explaining presence/absence of wood cricket within woodlands. For these analyses, twenty-six variables were initially included in the logistic regression. From these twenty-six variables, ten passed the significance test (Wald test: $P < 0.05$; Table 8) excluding one variable based on a false negative response (see Strauss & Biedermann, 2005). After the exploration of the SPSS output for the separate models, the best fitting (full) model explaining the highest amount of variation within the data included the variables 'Euclidean distance to nearest occupied permanent edge', 'Ground vegetation height', 'South orientated canopy closure' and 'Cumulative ground vegetation cover' (Table 8). This model met all selection criteria (see Methods) showing that: (1) all individual correlations (r) between the variables included were less than +/- 0.7 (Table 7); (2) all individual tests for significance were met ('model fit test' ($P < 0.05$), 'Hosmer & Lemeshow Model fit test' ($P > 0.05$) and 'Wald test' ($P < 0.05$)) (Table 8); (3) all B values indicated the right sign of the relationship (+/-) based on the boxplots presented in (Figure 8) and (4) the 95% confidence interval for Exp(B) did not include the value of 1 (Table 8). The best-fitting alternative model included the variables 'Euclidean distance to nearest occupied permanent edge', 'Ground vegetation height', 'South orientated canopy closure', which also met all initial selection criteria (Table 8). The univariate analyses revealed that the only single variable model meeting all of the selection criteria included 'Leaf litter depth', however only explaining a very small amount of the variation in the in the data (Nagelkerke R^2: see Table 8).

The model fit test showed that the predictor variable combination in the full four-variable model reliably distinguished between habitat locations where wood cricket was present or absent (chi-square: $\chi^2 = 225.3$, df = 4, $P < 0.001$; Table 8). This was furthermore confirmed by the Hosmer & Lemeshow model fit test (Hos. Lem.: $\chi^2 = 6.608$, df = 8, $P = 0.579$; Table 8) (note that $P > 0.05$ indicates a good model fit). The classification table indicated that the full model correctly classified 82% of all of the cases (80% for Absent cases and 85% of the Present cases) (Table 8). The effect size of the model indicated that the total variation explaining wood cricket presence/absence by the full model was 57% (Nagelkerke $R^2 = 0.57$) and 54% for the alternative model (Table 8).

The Wald test indicated that all of the individual variables contributed significantly to the model (Euclidean distance to nearest occupied permanent edge, Wald: $z = 64.21$, df = 1, $P < 0.001$; Ground vegetation height, Wald: $z = 35.82$, df = 1, $P < 0.001$; South orientated canopy closure, Wald: $z = 46.94$, df = 1, $P < 0.001$; Cumulative ground vegetation cover, Wald: $z = 15.14$, df = 1, $P < 0.001$; Table 8). The negative B values indicated that all of the variables within the model had a negative relationship with wood cricket presence. The probability of wood cricket being present decreased with an increase in 'Euclidean distance to nearest occupied permanent edge' (B = -0.032 +/- 0.004); increase in 'Ground vegetation height' (B = -0.048 +/- 0.008); increase in 'South orientated canopy closure' (B = -0.053 +/- 0.008) and increase in 'Cumulative ground vegetation cover' (B = -0.014 +/- 0.004) (Table 8). Furthermore, the Exp (B) value indicated a similar relationship. This indicated that with an increase in distance from an occupied permanent edge the odds that wood cricket would be present decreased by a factor of 0.968 (C.I. 0.961 - 0.976). Moreover, for each centimetre increase in vegetation height the odds dropped by a factor of 0.954 (C.I. 0.939 - 0.969) and with one percent increase in canopy closure and vegetation cover the odds also dropped by a factor of 0.949 (C.I. 0.934 - 0.963) and 0.986 (C.I. 0.979 - 0.993) respectively (Table 8). Finally, of the individual predictor variables, 'Euclidean distance to nearest occupied permanent edge' explained most of the total variation (Nagelkerke $R^2 = 0.30$; Table 8). Adding 'Ground vegetation height' to the model increased this value by 0.12 to an overall percentage of 42% (Table 8), however the model including only these two variables did not significantly fit the data (Hos. & Lem.: $P < 0.05$; Table 8). A further 12% was added by including 'South orientated canopy closure'. Including 'Cumulative ground vegetation cover' only added a further 3% making the total model explain 57% of the variation within the data (Table 8, Nagelkerke R^2). It should be noted here that 'Ground vegetation height' and 'Cumulative ground vegetation cover' were highly correlated with each other ($r = 0.64$; Table 7), which could have influenced the outcomes in this analysis.

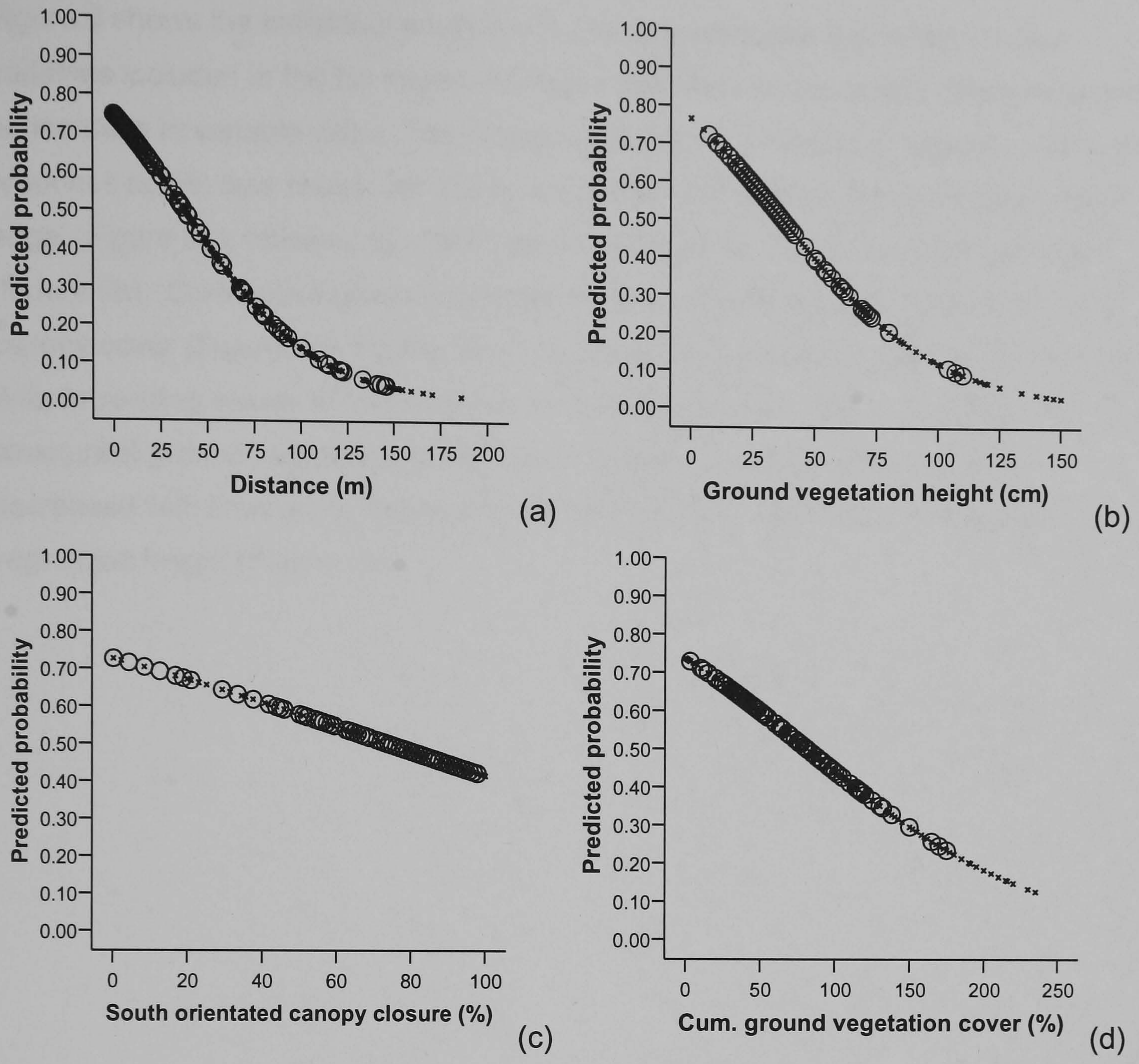


Figure 9: Predicted probability of wood cricket being present related to the main explanatory variables. O indicates sites where wood cricket was present; x indicates sites where wood cricket was absent. Two outliers (167 cm for vegetation height and 273 m for distance) were omitted from Figure a & b. The curves were calculated with the following probability equations using the B values from Table 8:

$$\text{(a) } P(\text{y}) = \frac{e^{1.085 + (-0.029)(\text{Distance})}}{1 + e^{1.085 + (-0.029)(\text{Distance})}}$$

$$\text{(b) } P(\text{y}) = \frac{e^{1.177 + (-0.032)(\text{Ground vegetation height})}}{1 + e^{1.177 + (-0.032)(\text{Ground vegetation height})}}$$

$$\text{(c) } P(\text{y}) = \frac{e^{0.977 + (-0.013)(\text{South orientated canopy closure})}}{1 + e^{0.977 + (-0.013)(\text{South orientated canopy closure})}}$$

$$\text{(d) } P(\text{y}) = \frac{e^{1.025 + (-0.013)(\text{Cum. ground vegetation cover})}}{1 + e^{1.025 + (-0.013)(\text{ Cum. ground vegetation cover})}}$$

Figure 9 shows the individual predictive probability response curves for the four variables included in the full model. All responses showed a negative relationship with an increase in variable value. The strongest response, similar to a negative-exponential response curve, was shown for 'Euclidean distance to nearest occupied permanent edge' (Figure 9a), followed by more linear responses for 'Ground vegetation height' (Figure 9b), 'Cumulative ground vegetation cover' (Figure 9d) and 'South orientated canopy cover (Figure 9c). Figure 10 shows bivariate response curves for the full model. With increasing values of 'South orientated canopy closure' and 'Cumulative (i.e. structured) ground vegetation cover', the probability of wood cricket presence decreased with increasing distance to the nearest occupied location and ground vegetation height (Figure 10).

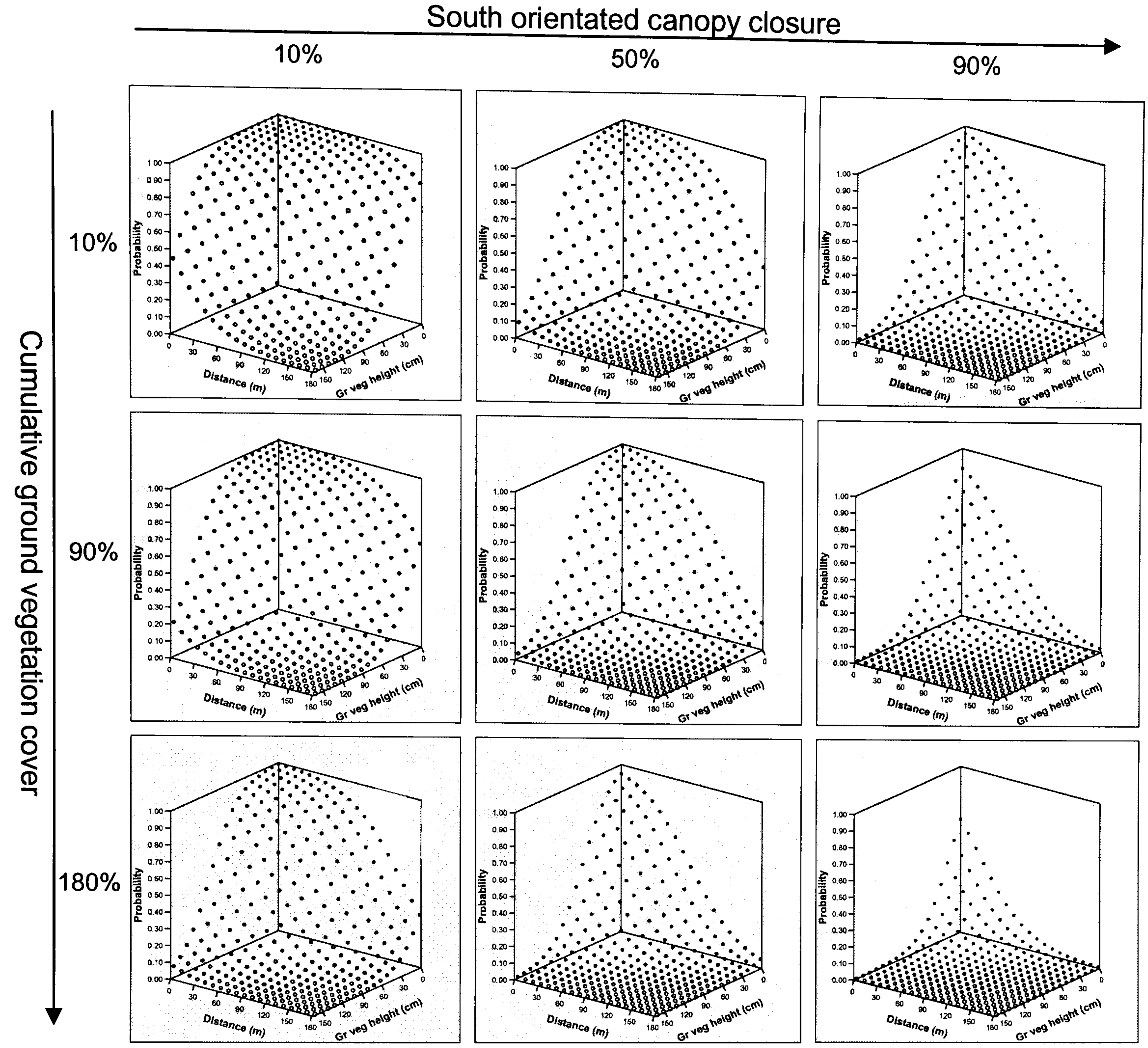


Figure 10: Predictive probability of the full model represented in 3-D. In each figure probability of wood cricket presence (y-axis) is plotted against occupied nearest neighbour distance (x-axis) and ground vegetation height (z-axis). Columns represent different levels of South orientated canopy cover and rows represent different values of cumulative ground vegetation cover.

$$P(y) = \frac{e^{8.009 + (-0.032)(\text{Distance}) + (-0.048)(\text{Gr vegetation height}) + (-0.053)(\text{S orientated canopy closure}) + (-0.014)(\text{Cum ground vegetation cover})}}{1 + e^{8.009 + (-0.032)(\text{Distance}) + (-0.048)(\text{Gr vegetation height}) + (-0.053)(\text{S orientated canopy closure}) + (-0.014)(\text{Cum ground vegetation cover})}}$$

3.4 Discussion

The results of this study confirmed earlier observations indicating the preference of wood cricket for open wooded edges. Factors positively influencing wood cricket presence within woodland included the presence of a well-developed leaf litter layer, relatively low ground vegetation cover and height and relatively short distances between individual populations, supporting all of the initial hypotheses. Furthermore, the logistic regression model identified the distance from inhabited habitat patches and variables describing habitat structure as the main predictors for wood cricket presence within woodland fragments. None of these relationships have been defined previously for this species.

For invertebrates, habitat factors linked with different stages of development in their life-cycle have often been found to be positively related with species presence (e.g. Rukke & Midtgaard, 1998; Binzenhofer et al., 2005; Strauss & Biedermann, 2005). For example, Rukke & Midtgaard (1998) found a strong positive relationship across three different spatial scales for presence of a fungus beetle and its specific breeding habitat. Wood cricket is known to pass most of its life-cycle in leaf litter, which is related to its breeding requirements (Brown, 1978). Furthermore, although omnivorous, the staple diet of wood cricket was found to be components of dead leaf litter material (Gabbutt, 1959; Koehler & Samietz, 2006). Information available at the onset of this study indicated that leaf litter could therefore be assumed as one of the primary factors determining wood cricket presence. Results of the current analyses revealed positive relationships between wood cricket presence and both leaf litter depth and volume. However, both variables only showed a small effect size in terms of predicting wood cricket presence (see Table 5). This might be due to the fact that wood cricket is omnivorous (Gabbutt, 1959), which indicates that it is not entirely dependant on the presence of leaf litter as a food source over the course of its life-cycle. Furthermore, although the univariate model including ‘Leaf litter depth’ as its predictor variable performed relatively well compared to the other univariate models, it only explained a very small proportion of the variation within the data (Nagelkerke R^2, see Table 8). Therefore, leaf litter as a sole variable was found to be a poor predictor of wood cricket presence.

In general, sunlight availability has been shown to have a positive influence on diversity of a number of invertebrate groups (Greatorex-Davies et al., 1994; Rieske & Buss, 2001). Ground-dwelling invertebrates generally favour sunlit conditions because of their thermophilic nature (e.g. Rieske & Buss, 2001; Buse et al., 2007). The main vegetation variables influencing wood cricket presence were 'South orientated canopy closure', 'Ground vegetation height' and 'Ground vegetation cover'. These factors are often linked with sunlight availability, which has a strong effect on microclimatic conditions (e.g. Matern et al., 2007). Canopy closure and vegetation cover influence sunlight availability at ground level, and therefore air temperature and humidity. Ground vegetation height appeared to be another successful predictor of wood cricket presence. Where ground vegetation was relatively high, wood cricket was less likely to be present. Relatively high measures of vegetation height were associated with an increase in the number of vegetation layers, which again would negatively influence sunlight availability at ground level, resulting in relatively low air temperatures. For wood cricket, these results indicate their preference for relatively open habitat conditions, also confirming the thermophilic nature of the species (Proess & Baden, 2000).

The factor most strongly influencing wood cricket presence within woodlands was distance to the nearest occupied permanent edge. Locations where wood cricket was found tended to be relatively close to a source population, which indicated that more isolated habitat locations were more likely to be uninhabited. Similar results were found for three related beetle species (Rukke & Midtgaard, 1998; Rukke, 2000; Buse et al., 2007). Buse et al. (2007) found that host trees supporting a longhorn beetle community were more likely to be situated in close proximity of each other and isolated host trees were more likely to be uninhabited. Furthermore, in a study on a beetle species (*Bolitophagus reticulates*) living in dead fungus fruiting bodies found on old/dying trees, again isolation had a negative influence on presence of the species in distinct habitat locations within woodlands (Rukke & Midtgaard, 1998). On the basis of this relationship, Rukke & Midtgaard (1998) argued that this species demonstrates a habitat-tracking metapopulation structure (Harrison & Taylor, 1997). Because of the successional dynamics of the habitat locations (host trees within a continuous woodland stand) for *B. reticulates*, extinction was assumed more likely to be a consequence of the environment becoming permanently unsuitable than stochastic population fluctuations within a permanent stable habitat location (see Thomas, 1994). The same was observed for wood cricket habitat locations within the woodlands surveyed in this study. Habitat locations where wood cricket was found were observed to change from year to year, making a successional shift from open to overgrown conditions, because of growth of the forest understorey (Brouwers, pers obs). Results of this study (e.g. the negative responses for the vegetation variables in Table 5 & Figure 8) suggest that wood cricket presence varied in parallel with these changes, being continuously present only in permanently open edge habitat (Brouwers, pers obs). For wood cricket, therefore the same metapopulation structure might apply, where the rate of habitat turnover determines the dynamics of the populations within woodland.

The most powerful habitat suitability model identified here included an isolation measure and vegetation structure variables as the main predictors for wood cricket presence within woodland fragments. The best-fitting model included four variables: 'Euclidean distance to nearest occupied permanent edge', 'Ground vegetation height', 'South orientated canopy closure' and 'Cumulative ground vegetation cover'. Because of the low explanatory power revealed by the univariate analyses, 'South orientated canopy cover' could have been excluded from the multivariate analyses, following Strauss & Biedermann (2005). However, in this case 'South orientated canopy closure' did prove to be a strong and important indicator for wood cricket presence, contributing a significant proportion to the explained variation of the model. Furthermore, the model could arguably be reduced to include three explanatory variables by excluding 'Cumulative ground vegetation cover'. Including this variable only added a minimal amount to the explanatory power of the model, mainly because of the high correlation with 'Ground vegetation height'. Additionally, the logistic regression model for a longhorn beetle living on oak trees developed by Buse et al. (2007) included similar variables as were found for wood cricket. This model also included nearest occupied neighbour distance and variables related to sunlight availability, indicating the potential importance of these factors for woodland invertebrates more generally. In the case of longhorn beetle (Buse et al., 2007), however, specific habitat factors related to life-cycle requirements were also influential, whereas for wood cricket these variables (i.e. leaf litter availability) did not add to the overall performance of the model.

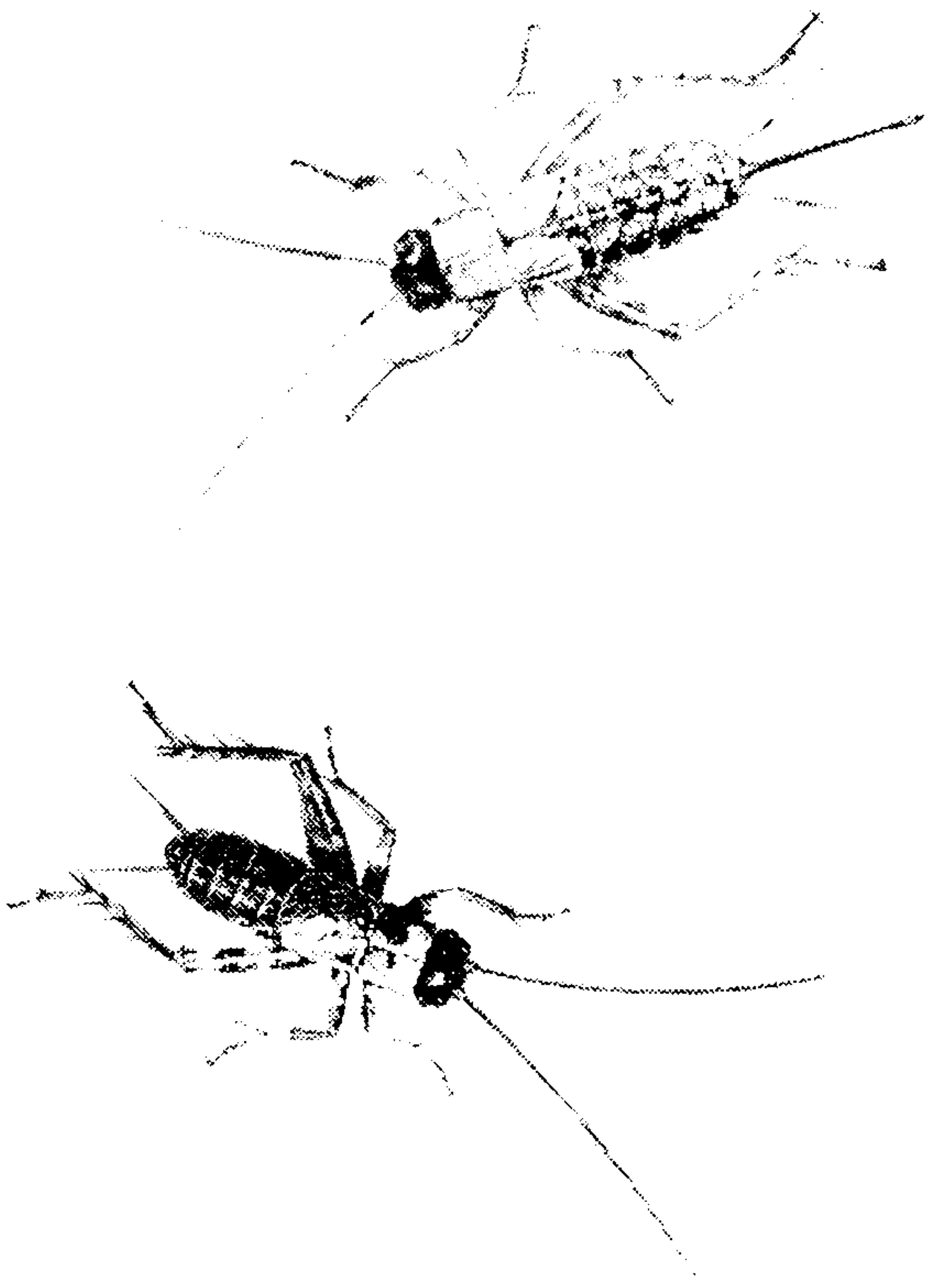
Overall, both models for predicting wood cricket presence performed relatively well, explaining 54 - 57% of the variation in the data (Pallant, 2007). These results are comparable with model performance values found for invertebrates living in grasslands and brown fields (Strauss & Biedermann, 2005). Furthermore, the logistic regression model for a longhorn beetle living on oak trees (Buse et al., 2007) performed slightly less well than the models presented here. For a semi-aquatic woodland carabid beetle, a substantially better model performance was found (Matern et al., 2007). However, compared to the current study, these authors were less rigorous in excluding non-significant response variables from the total model. Still, the best-fit model for wood cricket revealed a substantial proportion of unaccounted variation when using the set of predictor variables described in this study. Including more precise measures of, for example, humidity, light availability at ground level and wind exposure might improve the model performance. The fit could also potentially be improved by adopting a different sampling method. Measurements were taken over a relatively small spatial area (1 m^2) at one moment in time. However, it has been shown that wood cricket displays a daily rhythm of movement between more open and closed vegetation at different times of the day (Beugnon, 1980). The sampling method therefore might have resulted in over- and/or underestimations of presence locations, that negatively influenced the discriminative power of the individual variables used within the model.

Results suggested that the dispersal ability of the species is limited. Regression analyses indicated that the measurement locations where wood cricket was present were aggregated around occupied permanent edges that were recognised as source locations. The locations where wood cricket was not found were more isolated (i.e. further away) from these source populations. In such locations, either wood cricket was not present because of the lack of suitable habitat or because of their limited dispersal ability, or possibly because of the presence of internal barriers to dispersal within the woodlands. Another indication of the limited dispersal ability of the species was absence of the species at apparently suitable locations at certain moments in time (Proess & Baden, 2000; Brouwers, pers obs). In some locations, wood cricket was observed to colonise areas of suitable habitat such as new clearings or coppice coups over a period of 1-3 years, presumably from adjacent source populations (Brouwers, pers obs). This suggests that because of their dispersal limitations, the species demonstrated a time lag in occupying suitable habitat. This might have accounted for part of the unexplained variation in the regression models. Altogether, the dispersal ability of this species is therefore a factor that needs to be considered in order to predict their presence with more accuracy than based on habitat suitability alone. This further highlights the need to obtain species-specific parameters relating to dispersal ability in order to improve and inform future modelling approaches.

To ensure that the model is generally applicable to the study area, the data used to construct the model were collected at three individual isolated woodland sites that are representative of the majority of inhabited woodland fragments found on the Isle of Wight (Brouwers, pers obs). However, for more widespread application, for example in conservation management, it would be desirable to test the robustness and transferability of the model both with data sets from other inhabited woodlands on the island as well as data sets collected from populated areas on the mainland (Strauss &

Biedermann, 2005). Binzenhofer et al. (2005) showed that their model developed for a burnet moth was transferable in space when testing it with a data set from another topographic region. However, in the case of a nymphalid butterfly species the model developed was not found to be transferable between different locations (Binzenhofer et al., 2005). This indicates the importance of performing these tests of model robustness, which were not carried out in this current study. For other invertebrates, however, transfer of habitat models that were based on data collected from just one topographic location have been found to be successful (e.g. Binzenhofer et al., 2005; Matern et al., 2007; Buse et al., 2007). For instance, both Matern et al. (2007) (for a rare ground beetle) and Buse et al. (2007) (for an endangered longhorn beetle) found that models constructed with data collected from only one topographic region performed well when transferred to another region. Therefore, because the model for wood cricket was constructed with data collected from three different topographic locations, it is possible that this predictive habitat model can also be used for other areas in the UK, and possibly for mainland Europe.

Presence of permanent edge habitat within fragments was found to be a strong indicator for wood cricket presence. Locally very high population abundances have been recorded at permanent edges along railway lines and wide rides (Gabbutt, 1959; Brouwers, pers obs), indicating the importance of this particular habitat for wood cricket. Maintenance of these permanent 'source' locations therefore might be critical to secure a viable wood cricket population within individual fragments. However, these conditions are often only present in woodlands or woodland areas that are under some sort of management regime. Re-instatement of traditional coppice rotation in woodlands on the Isle of Wight is likely to favour persistence of the species within these areas. Furthermore, the Isle of Wight has been the focus of extensive woodland restoration efforts including the restoration of planted ancient woodland sites by removing non-native tree species (Defra, 2005; Forestry Commission, 2006b). These activities, which involve opening up the canopy, could potentially have a positive effect on wood cricket populations by increasing habitat availability in these woodlands. Furthermore, when clearings are created, these should preferably be adjacent to inhabited locations (e.g. permanent ride edges) in order to increase the potential of dispersal of the species into these newly created habitat areas. Ride edges and open areas (e.g. coppice coups) have been found to be generally important for woodland invertebrate diversity (Warren & Key, 1991; Greatorex-Davies et al., 1994), and particularly for butterfly species dependant on host and nectar plants only found in woodland habitat. Management activities promoting the continuity of these habitats will promote and maintain viable wood cricket populations as well as other woodland species (Bratton & Andrews, 1991). Therefore, a wider adoption of traditional management practices such as coppice rotation and yearly mowing of ride and track edges will be favourable for this and similar species.



4 Movement rates of woodland invertebrates: a systematic review of empirical evidence

4.1 Introduction

The lack of knowledge regarding the dispersal ability of species living in fragmented landscapes has repeatedly been emphasised in the scientific literature (e.g. Tscharntke et al., 2002; Dolman & Fuller, 2003; Bowne & Bowers, 2004). Woodlands are one of many natural habitats that have in many areas become increasingly fragmented as a result of human activities, such as expansion of agricultural land and over-harvesting (e.g. Andrén, 1994; Fahrig, 2003; Newton, 2007). The negative effects of habitat loss and fragmentation on the persistence of species have been widely documented (e.g. Freemark et al., 2002; Fahrig, 2003). Research has suggested that those species that are of a relatively small size, with limited dispersal abilities, are particularly vulnerable to fragmentation impacts (Niemela, 2001; Tscharntke et al., 2002; Bailey, 2007). An understanding of the dispersal abilities of individual species is important in order to predict the impacts of habitat fragmentation on species persistence (Tscharntke et al., 2002; Ranius, 2006), metapopulation viability (Hanski & Gilpin, 1997; Hanski, 1998) and extinction thresholds (Fahrig, 2001).

Within the group of woodland invertebrates, habitat-specialist species have been found to be more vulnerable to habitat loss (Tscharntke et al., 2002) and fragmentation effects (Niemela, 2001) than more generalist species. This might indicate that habitat specialist species are more prone to extinction because of a lower dispersal ability compared to generalist species. However, even within these groups, the effects of fragmentation and habitat loss on dispersal ability will be highly species dependent (Niemela, 1997). Variation in dispersal ability is likely to be reflected in the movement rate observed at different scales. Measurements of movement rate and range are often difficult to obtain (Bullock et al., 2002), and consequently very little information is available for woodland invertebrates (Niemela, 1997), especially for relatively rare and endangered habitat-specialist species (Ranius, 2006). For invertebrates in general, but mainly for relatively mobile non-woodland butterfly or fly species, Bowne & Bowers (2004) found that the estimated movement rate per generation (mean: 45%, range 0.16 – 100%) between distinct habitat patches was relatively high compared to other species groups (mean: amphibians (2%), birds (1%), mammals (6%) and reptiles (12%)). Yet, for two non-flying woodland-associated ground beetle species (*Abax ater* and *Pterostichus niger*), movement rates were found to be much lower (mean: 0.16% and 0.92% respectively) (Bowne & Bowers, 2004). This occurrence of limited dispersal ability in woodland invertebrates is supported by other research. For example, for a woodland specialist beetle species living on trees, the dispersal rate between trees within a forest stand was estimated to be 15% per generation (Ranius & Hedin, 2001). Furthermore, because of its limited dispersal ability and level of habitat specialism, dispersal between woodland stands was assumed to be very rare for this species (Ranius, 2006). This suggests that woodland-specialist invertebrates might be particularly vulnerable to habitat fragmentation effects (Ranius & Hedin, 2001).

The review presented here was designed to summarize the current state of knowledge regarding the movement rates of woodland invertebrates. A particular focus was given to ground-dwelling woodland species, which are considered to be a group likely to be affected by habitat loss and fragmentation (Niemela, 1997), because of their limited dispersal ability. The aim was to identify direct measures of movement made in the field in order to quantify dispersal rates, which is not possible with studies based on spatial occupancy or patterns of genetic variation (Ranius, 2006). The most commonly used methods to obtain rates of this kind include a wide range of capture-recapture techniques and experiments (e.g. Vermeulen, 1994; Barton & Bach, 2005; Ranius, 2006), and direct observation (e.g. Haddad, 1999; Ross et al., 2005). However, recent developments of methods such as telemetry (Ranius, 2006) and harmonic radar (e.g. O'Neal et al., 2004) are helping to provide improved measurements of invertebrate movement (Ranius, 2006).

Measurements of movement rate provide a valuable indication of how rapidly a species can potentially move within a given area of habitat and across a landscape, enabling predictions to be made regarding the colonisation of habitat patches within habitat networks and the potential functioning of habitat corridors (Bailey, 2007). Furthermore, species-specific movement rates are important parameters of models used to explore the impacts of environmental change, including land cover and climate change, on the pattern of distribution of individual species (e.g. Fahrig, 2001; Vos et al., 2001; Watts et al., 2005; del Barrio et al., 2006; Walters et al., 2006). The current review was also designed to examine the factors influencing movement rate, with the aim of developing generalisations regarding the dispersal behaviour of different groups of woodland invertebrates. Previous research has suggested that factors influencing dispersal ability (including movement rates) of invertebrates include the habitat type with which a species is generally associated (den Boer, 1990b) and physical traits such as flight capacity (den Boer, 1990a; b; Thomas, 2000) and body size (Drach & Cancela da Fonseca, 1990; den Boer, 1990b). However, for woodland invertebrates, these relationships have not been thoroughly explored previously.

To conduct this study, a systematic review approach was adopted following the guidelines developed by Pullin & Stewart (2006). The need for systematic reviews originates from the field of medicine where, as in conservation, a framework for firm evidence-based decision making processes has been lacking (Pullin & Knight, 2001). The advantage of conducting a systematic review over a conventional literature review lies in the fact that it is largely unbiased and repeatable, by pre-defining search strategies and criteria at the onset of each study. This allows any other party to add new results over time by applying the same search strategy. A number of systematic reviews of conservation evidence have recently been undertaken including studies on the effectiveness of hedgerow corridor functioning between woodland fragments (Davies & Pullin, 2007) and the effectiveness of current management approaches for saproxylic invertebrates (Davies et al., 2008) (for more examples and further details see: www.cebc.bangor.ac.uk).

The specific aims of the current review were: (1) to systematically identify studies within the published scientific literature providing direct measures of movement for woodland invertebrate species; and (2) to examine whether ground-dwelling woodland invertebrates could be grouped based on movement rate (m day^{-1}) (i.e. dispersal ability) and habitat specialism, and (3) to examine the relationships between movement rate, body size and habitat specialism. From the reported lack of studies on species-specific dispersal ability, it was hypothesised that relatively few studies would be identified reporting a direct measure of movement for woodland invertebrates. Furthermore, it was hypothesised that woodland specialist species would be less mobile than generalist species, and a positive relationship would exist between body size and movement rate.

4.2 Methods

4.2.1 Phase 1: Database search

For identifying relevant studies, the following electronic databases were searched: EBSCO Research databases (including Academic Search Premier; EJS E-Journals and Library, Information Science & Technology Abstracts), JSTOR (including Arts & Sciences I; Arts & Sciences II; Arts & Sciences III; Biological Sciences), AGRICOLA (1970-2006), AGRIS (1975-2006), Biological abstracts (1969-2006), CAB abstracts (1910-2006), Current Content (1996-2007/2/22), Scopus (1960-2006), ISI Web of Science (including Science Citation Index Expanded (SCI-EXPANDED) (1945-2006); Social Sciences Citation Index (SSCI) (1956-2006); Arts & Humanities Citation Index (A&HCI) (1975-2006)).

The search term combinations used to search the individual databases were combinations of relevant words related to invertebrates (invertebrat*, arthropod*, insect*, beetle* and butterfl*) and words related to dispersal (dispers*, migrat*, colon*, spread* and scat*) resulting in (5 x 5) 25 search term combinations. Using '*' within a search engine increases the number of matching references; the character '*' is referred to as a "wildcard", and in this case stands for any number of characters. Within the databases, these 25 combinations were used to identify articles that included these word combinations either within the title or within the abstract. All references that matched any one of these combinations were exported into a baseline library (1) using the reference database program EndNote 9 (Thomson ResearchSoft, San Francisco, USA).

Further selections were applied using the "references" options available in the EndNote program. First, duplicate references within the baseline library 1 were deleted based on an exact match of author, title and year (using "find duplicates" option in Endnote). Then the following selection procedure was used to filter out the most relevant articles within the baseline library 1, using the "search references" option. Selection criteria were used to identify all studies referring to woodland habitat and measures of movement. References were selected when including a combination of one of each of the following three word groups in the abstract: *ability* or *capacity*; *wood* or *forest*; *move* or *pattern* or *measure*, resulting in (2 x 2 x 3) 12 selection combinations. Furthermore, articles were selected when including a combination of: *wood* or *forest*; *measure* or *determin* or *assess* or *quantif* or *estimat*;

move or *distribut* in the abstract, resulting in an additional (2 x 5 x 2) 20 selection combinations. Finally, two separate selection words were used to find references with either *corridor* or *hedge* in the title or in the keywords. All matching references were combined in a separate (EndNote) library (2).

Within library 2, duplicates were deleted using the “find duplicates” option and sorting the references on title only. To include studies only undertaken on animals in temperate regions, references including *tropica* or *rain forest* or *seed* in either the journal title, title, keywords or abstract, were deleted after checking the title of the selected references. From this point, all remaining references were examined individually. First, the titles of all remaining references were scanned visually, enabling references that did not refer to an invertebrate-related study to be excluded. The second examination involved scanning the abstracts of the remaining references to select those studies referring to direct measures of movement. Finally, all remaining studies were entered into the full text review stage. This stage involved reading the complete article and selecting those that included a direct measure of movement.

4.2.2 Phase 2: Additional search

Additionally, relevant references cited in the articles that were entered in the full text review stage of ‘Phase 1’ were visually examined, and when found relevant, were included in the review process.

4.2.3 Data extraction and analyses

For each study the following information was recorded: (1) the source location of the reference, (2) the search phase in which the study was found, which for ‘Phase 2’ references included whether or not it was present in library 1 (determined by cross-referencing), (3) the country the study was conducted in, (4) species name and taxonomic group, (5) whether or not the species was associated with woodland habitat, (6) method used to estimate the reported rate, (7) the number of observations used to estimate the rate, and (8) details of the reported rate including the habitat where the rate was measured.

The habitat associations of the species encountered during the review process were determined by consulting the publications identified during the search. Further verification was undertaken by searching relevant literature using the internet search engine 'Google' (www.google.com) and the Bugs Coleopteran Ecology Package (BugsCEP) (Buckland & Buckland, 2006). The BugsCEP database integrates compiled historic and current scientific data on the Coleopteran fauna found in Europe, making it a valuable reference source (for more details see Buckland (2007)). The same sources were used to extract additional ecological information (e.g. on flight capability and body size of the individual species), where available. The methods used in the individual studies to estimate the rates were: 'Capture-Recapture'; 'Enclosure experiment'; 'Radioactive marker/Enclosure experiment'; 'Observing/following'; 'Telemetry'; 'Harmonic radar'; and 'Monitor invasion front'. 'Capture-Recapture' included capture-recapture methods with multiple recapture performed under field conditions; 'Enclosure experiment' included capture-recapture methods with multiple recapture performed within an enclosure; 'Radioactive marker/Enclosure experiment' included capture-recapture methods with multiple recapture performed within an enclosure with specimens that were marked with radioactive isotopes; 'Observing/following' included methods where the species was caught no more than once and/or actively observed over time under field conditions; 'Telemetry' included methods where the species was caught no more than once and followed over time under field conditions using transmitter equipment; 'Harmonic radar' included methods where the species was caught no more than once and followed over time under field conditions using harmonic radar equipment; and 'Monitor invasion front' included methods estimating range expansion of the study species under field conditions using annual monitoring data (for more details on the individual methods see Sutherland (2006)).

Studies providing straight-line movement rates for species moving over the ground that could be standardised in m day^{-1} were selected and used for further analyses. Each species in this selection was assigned to a habitat group based on the 'Bugs ecology codes' as presented in the BugsCEP database (Buckland & Buckland, 2006). These codes are based on referenced data available in BugsCEP and existing published classifications (Buckland, 2007), and indicate in which habitat type a species can typically be found. The following habitat codes were used: 'Wood and trees' (WT), indicating species associated with either forest, woodland, or individual trees; 'Heathland & moorland' (HM), indicating species found in heathland and moorland, but also in the under-story of Boreal forests; 'Meadowland' (M), indicating species found in open landscapes such as natural grassland or near equivalents; and 'Sandy/dry disturbed/arable' (SD), indicating species typically found on open/disturbed ground on poor sandy soils such as ploughed fields in beach, dune and Aeolian landscapes (see Buckland, 2007). These habitat codes were further used to group the species in terms of habitat specialism (Group 1 – 3). 'Group 1' included species that were present in WT or WT/M habitat and were considered to be the most specialised associates of woodland habitat; 'Group 2' included species present in either HM or HM/SD habitat; and 'Group 3' included species present in WT, HM and M habitat and were considered to be generalist in terms of dependency on woodland habitat. Species associated with 'Group 2' were not directly associated with woodland environments (i.e. did not include habitat code WT), and were considered to be primarily heathland specialist species.

4.2.4 Quality assessment

A tentative quality assessment was performed for the studies that reported straight-line movement rates made over the ground, using the following method. Studies were weighted based on the accuracy of the rate estimate, which was evaluated by assessing the robustness of method used, combined with the number of observations (N) made. First, the methods that were used to make the rate estimations were categorised into three classes. Weights were awarded based on the level of accuracy that could be obtained with the method used for the estimated straight-line distance travelled over time. Rates obtained by using the methods 'Telemetry' and 'Harmonic radar' were awarded the highest weight (3), because these methods can obtain the most accurate distance measures in a given time interval, followed in descending order by 'Enclosure studies' (weight 2) and 'Capture-Recapture' methods (weight 1). Furthermore, rate estimates based on a high number of observations were considered more accurate than estimates based on relatively few observations. Therefore, within each method group the rate estimates were ordered from high to low by the number of observations used and the rates within each group weighted accordingly (value 1 for the rate with the lowest number of observations, 2 for the second lowest etc.).

4.2.5 Statistical analysis

Statistical tests were performed to investigate whether movement rate (with and without the individual weights) differed between the habitat specialism groups (Kruskal-Wallis and Mann-Whitney *U* tests), if body size differed between the specialism groups (Kruskal-Wallis and Mann-Whitney *U* tests) and if there was a relationship between body size and movement rate (Spearman rank correlation). Non-parametric tests were used because the variables were not normally distributed (Shapiro-Wilk tests). Analyses were performed using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA). The individual weights as described in the quality assessment (see above) were included in the analyses by using the 'Weight Cases' option available in SPSS. The 'Weight Cases' option assigns weights to cases through simulated replication. In this case the weights assigned to the rates corresponded to the number of times the rate was used in the statistical analysis.

4.3 Results

4.3.1 Search statistics

Applying the 25 search term combinations to the individual databases resulted in a baseline library 1 including a total of 70682 references (after deleting duplicates). After the first selection procedure, library 2 contained a total of 1241 references (after deleting duplicates). After the final selection procedure a total of 48 articles were entered into the full text review stage. Of the 48 full text references, one could not be obtained. From the 47 full text articles that were reviewed an additional 45 relevant references were extracted from the bibliographies. Of these 45 additional references, 8 could not be obtained, leaving an additional 36 full text articles that were reviewed.

After reviewing the total of 83 full text articles, all articles providing a rate of movement (i.e. distance moved measured over time) were included in the final analyses. This resulted in a total of 25 relevant studies of which 10 were identified using the systematic search method as described in 'Phase 1' and 15 using the additional search as described in 'Phase 2' (see Methods and Table 9). Cross-referencing of the additional 15 studies in library 1 revealed that nine of these studies were present in this library, indicating that these studies were excluded by following the selection procedure used in 'Phase 1'. From the studies that met the selection criteria, two summary tables were created. The first table summarises all of the studies that were found that provided rates for invertebrate species associated with woodland habitat (Table 9). The second table presents standardised straight-line movement rates for woodland invertebrate species that moved over the ground (Table 10). The studies that were found were conducted in the period 1964 – 2005, and mainly undertaken in Europe (16), including four studies from the UK, with an additional seven studies from North America and two from Asia (Table 9). The majority of the 25 studies involved ground beetle studies (15), with another two studies on bark beetle, two on ant species, five on butterflies and one on a moth species (Table 9). Within the 25 studies, rates were reported for 34 separate invertebrate species of which 30 were associated with woodland habitat (Table 9). Of these 30 'woodland' species, seventeen ground beetles and eight butterfly species were investigated relating to their natural occurrence and conservation (i.e. non-pest species); and two bark beetle, two ant, and one moth species were investigated relating to their negative impacts on the woodland environment (i.e. they were considered as forestry pests).

4.3.2 Factors influencing rate

All studies included in Table 9 mentioned some factor influencing the rate of movement found for the species involved. The most common factors that were referred to were habitat, weather and physiological traits. Additionally a majority (16) of the 25 'woodland' studies referred to different movement strategies/patterns observed for the individual species (e.g. random vs. directed walk/flight or diffusion/distribution). Furthermore, six studies tested linear features in the landscape (e.g. hedges) for their role as a potential corridor and a further four studies referred to a possible corridor effect regarding habitat features in the study area.

Table 9: Summary table for articles including a rate of movement that were found in this study. Reference: includes the reference source; in which search phase the reference was found (P1: Phase 1; P2: Phase 2; P2 (1): found in 'Phase 2' and present in baseline library 1); and the site of study (SS). Taxon: represents species taxa i.e. Ground beetle (Gb), Bark beetle (Bb), Butterfly (Bf), Spider (Sp), Moth and Ant. Wood: W indicates the species affiliated with woodland. Method: represents the methods used to infer the rate of movement mentioned in the articles. N: represents the number of observations (individuals or years (y)) used to estimate the rate of movement mentioned in the articles. Rate summary: gives the main results regarding the rate as mentioned in the articles.

Reference	Species	Taxon	Wood	Method	N	Rate summary
Hagvar, 2001	*Boreus westwoodi*	Gb	W	Observing/following		Mean migration rate
Nor. J. Entomology 48(1): 51-60						On snow in coniferous woodland:
P1, SS: Norway					5	0.3 m min^{-1}
Riecken & Raths, 1996	*Carabus coriaceus*	Gb	W	Telemetry		Average direct distance
Ann. Zoologici Fennici 33(1): 109-116					64	1.59 - 9.26 m day^{-1} (in river valley)
P2 (1), SS: Germany					55	2.01 - 22.16 m day^{-1} (in beech/pine woodland)
					70	2.26 - 7.32 m day^{-1} (in meadow)
Charrier et al., 1997	*Abax parallelepipedus*	Gb	W	Harmonic radar		Mean distance
Agr., Ecol. & Env. 61(2-3): 133-144	*(Abax ater)*				132	0.77+/- 0.31 m 48hr^{-1} (in a hedgerow)
P1, SS: France					109	0.45 +/- 0.16 m 48hr^{-1} (in a hedgerow)
					135	1.05 +/- 0.75 m 48hr^{-1} (along a lane)
					138	1.25 +/- 0.46 m 48hr^{-1} (in a woodlot)
Wallin & Ekbom, 1988				Harmonic radar		Mean movement rate
Oecologia 77(1): 39-43	*Pterostichus melanarius*	Gb	.		64	2.4+/-0.4 m hr^{-1} (in a field)
P2 (1), SS: Sweden					20	2.0+/-0.5 m hr^{-1} (in woodland)
	Pterostichus niger	Gb	W		42	6.5+/-0.9 m hr^{-1} (in a field)
					13	3.4+/-0.8 m hr^{-1} (in woodland)
	Harpalus rufipes	Gb	.		7	3.0+/-1.0 m hr^{-1} (in a field)
	Carabus nemoralis	Gb	W		8	2.3+/-0.7 m hr^{-1} (in woodland)
Kennedy, 1994	*Carabus nemoralis*	Gb	W	Harmonic radar		Mean distance covered
In: Carabid Beetles: Ecol. and Evol.					14	55.16 +/- 20.41 m night^{-1} (in arable matrix)
Desender et al. (Ed.): pp. 439-444						Mean velocity
P2, SS: Scotland					171	6.0 m hr^{-1} (in semi-natural grassland)
				Capture-Recapture	15	5 +/- 2 m night^{-1} (in arable matrix)

Continued

Reference	Species	Taxon	Wood	Method	N	Rate summary
Baars, 1979						Average movement rate
Oecologia 44(1): 125-140	*Pterostichus versicolor*	Gb	.	Radioactive marker/	488	7.0 m day^{-1} (in heathland)
P2 (1), SS: The Netherlands	*(Poecilus versicolor)*			Enclosure experiment	161	9.2 m day-1 (average)
	Calathus melanocephalus	Gb	W	Radioactive marker/	399	4.2 m day^{-1} (in heathland)
				Enclosure experiment	156	2.2 m day^{-1} (average)
Nelemans, 1988	*Nebria brevicollis*	Gb	W	Enclosure experiment	598	Average distance covered
Neth. J. Zoology 38(1): 74-95						3 m per 2.3 days (in broadleaf woodland)
P1, SS: The Netherlands						
Vermeulen, 1994a	*Pterostichus lepidus*	Gb	W	Capture-Recapture		Average movement rate
Biol. Conservation 69(3): 339-349	*(Poecilus lepidus)*				58	3.08 m day^{-1} (in open driftsand area)
P2 (1), SS: The Netherlands					33	2.85 m day^{-1} (in heathland)
					21	2.57 m day^{-1} (in broad grass roadside verge)
					6	2.05 m day^{-1} (in narrow grass roadside verge)
Vermeulen, 1994b				Enclosure experiment		Velocity rate
In: Carabid Beetles: Ecol. and Evol.	*Calathus erratus*	Gb	W		55	1.85 m day^{-1} (in woodland)
Desender et al. (Ed.): pp. 387-392	*Calathus ambiguus*	Gb	W		18	1.54 m day^{-1} (in woodland)
P2, SS: The Netherlands	*Pterostichus lepidus*	Gb	W		46	1.78 m day^{-1} (in woodland)
	Amara equestris	Gb	W		37	1.58 m day^{-1} (in woodland)
	Cymindis macularis	Gb	.		3	0.81 m day^{-1} (in woodland)
	Harpalus servus	Gb	W		46	1.00 m day^{-1} (in woodland)
Joyce et al. 1999	*Nebria brevicollis*	Gb	W	Capture-Recapture		Mean movement rate
Bul. Ent. Research 89(6): 523-531						For all beetles:
P1, SS: UK					83	1.50 m day^{-1} (in a hedgerow)
						For beetles that made long distance journey:
					13	6.42 m day^{-1} (in a hedgerow)
Rijnsdorp, 1980	*Carabus problematicus*	Gb	W	Capture-Recapture		Mean displacement velocity
Oecologia 45(2): 274-281						Within woodland:
P2, SS: The Netherlands					42	12.8 m day^{-1} (for male)
					7	11.0 m day^{-1} (for female)
						From woodland into heathland:
					9	24.0 m day^{-1} (for male)
					5	13.7 m day^{-1} (for female)
						For long distance (directed) dispersal events:
					13	25.0 m day^{-1} (for male)
					6	15.0 m day^{-1} (for female)

Continued

Reference	Species	Taxon	Wood	Method	N	Rate summary
Loreau & Nolf, 1993	*Abax ater*	Gb	W	Capture-Recapture		Mean distance covered
Acta Oecologica 14(2): 247-258						In beech woodland:
P1, SS: Belgium					420	1.8 m day^{-1} (for male)
Greenslade, 1964	*Nebria brevicollis*	Gb	W	Capture-Recapture		Mean rate of movement
J. Animal Ecology 33(2): 311-333						In woodland:
P1, SS: UK					218	2.3 m day^{-1} (for male)
					83	1.8 m day^{-1} (for female)
Drach & Cancela da Fonseca, 1990				Capture-Recapture		Diffusion coefficient (i.e. degree of activity)
Rev. Ecol. Biol. Sol 27(1): 61-71	*Abax ater*	Gb	W		50	36 m^{2} week $^{-1}$ (in beech woodland) (average)
P2, SS: France	*Orinocarabus nemoralis*	Gb	W		8	312 m^{2} week $^{-1}$ (in beech woodland)
	Procrustes purpurascens	Gb	W		11	500 m^{2} week $^{-1}$ (in beech woodland)
Petit, 1994	*Abax ater*	Gb	W	Capture-Recapture		Diffusion coefficient (i.e. degree of activity)
In: Carabid Beetles: Ecol. and Evol.					85	38 m^{2} week $^{-1}$ (in woodland)
Desender et al. (Ed.): pp. 337-341					62	143 m^{2} week $^{-1}$ (in a hedgerow)
P2, SS: France						
Williams et al., 2004	*Anoplophora glabripennis*	Bb	W	Harmonic radar		Average movement rate
Envi. Entomology 33(3): 644-649					43	2.8 m day^{-1} (on road verge willow strip)
P2 (1), SS: China						
Togashi, 1990	*Monochamus alternatus*	Bb	W	Capture-Recapture		Average distance traversed
Res. Pop. Ecol. 32(1): 1-13					33	10-20 m week^{-1} (in coniferous woodland)
P2 (1), SS: Japan						Equation estimate
						7.1 -37.8 m week^{-1} (in coniferous woodland)
Holway, 1998	*Linepithema humile*	Ant	W	Monitor invasion front	4 y	Mean rate of spread
Oecologia 115(1): 206-212						Along a stream in woodland:
P2, SS: USA					13	16.3 m year^{-1} (with permanent stream flow)
					7	- 5.9 m year^{-1} (with intermittent stream flow)
Porter et al., 1988	*Solenopsis invicta*	Ant	W	Monitor invasion front	4 y	Mean rate of spread (in woodland matrix)
Ann. Ent. Soc. Am. 81(6): 913-918						35 m year^{-1} (along open sunny roads)
P2 (1), SS: USA						18 m year^{-1} (in cooler wooded areas)
Barton & Bach, 2005	*Neonympha mitchellii mitchellii*	Bf	W	Capture-Recapture		Mean daily distance moved
Am. Midland Naturalist 153(1): 41-51						In wetland/fen area:
P1, SS: USA					50	35.2 m day^{-1} (for male)

Continued

Reference	Species	Taxon	Wood	Method	N	Rate summary
Haddad, 1999a				Capture-Recapture		Mean net displacement
Ecological Applications 9(2): 612-622						Within conifer woodland matrix:
P2 (1), SS: USA	*Junonia coenia*	Bf	W		1530	58.08 m day^{-1} (for male)
						55.16 m day^{-1} (for female)
	Euptoieta claudia	Bf	W		165	48.17 m day^{-1} (for male)
						65.57 m day^{-1} (for female)
					45	32.9 m day^{-1} (for female)
Haddad, 1999b				Observing/following		Average movement path distance
American Naturalist 153(2): 215-227						Within open conifer woodland habitat:
P1, SS: USA	*Eurema nicippe*	Bf	W		141	21.88 m per path
	Papilio troilus	Bf	W		1075	19.82 m per path (for female)
						23.90 m per path (for male)
	Phoebis sennae	Bf	W		1306	36.37 m per path (for migrant)
						24.77 m per path (for non-migrant)
						Average speed for three habitats together
	Eurema nicippe	Bf	W		592	2.17 m sec^{-1} (within conifer woodland matrix)
	Papilio troilus	Bf	W		4515	2.16 m sec^{-1} (within conifer woodland matrix)
	Phoebis sennae	Bf	W		5485	3.16 m sec^{-1} (within conifer woodland matrix)
Warren, 1987	*Mellicta athalia*	Bf	W	Capture-Recapture		Mean daily range
J. Applied Ecology 24(2): 483-498						In semi-natural grassland:
P1, SS: UK					56	46 m day^{-1} (for male)
					14	32 m day^{-1} (for female)
						In a woodland matrix:
					42	83 m day^{-1} (for male)
					12	30 m day^{-1} (for female)
Ross et al., 2005	*Parnassius smintheus*	Bf	W	Observing/following	28	Rate of movement
Landscape Ecology 20(2): 127-135						14.25 +/- 1.98 m min^{-1} (in meadow)
P2 (1), SS: Canada						2.50 +/- 3.26 m min^{-1} (in forest)
Liebhold et al., 1993	*Lymantria dispar*	Moth	W	Monitor invasion front	90 y	Estimated range expansion
J. General Virology 74(1): 513-520						2.5 km year^{-1} (in broadleaf dominated stands)
P1, SS: USA						

Table 10: Summary table for rates of ground-dwelling woodland invertebrate species (all ground beetles). Rate: indicates the overall mean rate for the individual species converted in m day-1 inferred from the original data. N: number of observations used to derive the rate estimate. Method: method used to extract the rate of movement. Habitat: habitat combinations where the species can be found; (WT) Wood and trees, (HM) Heathland & moorland, (M) Meadowland, (SD) Sandy/dry disturbed/arable. Group: indicates the group for each species based on habitat specialism; (1) includes species found in WT or WT/M habitat, (2) in HM or HM/SD and (3) includes species found in WT/HM/M habitat. Size: mean body size (mm) of the individual species. Habitat and Size information were extracted primarily from information available in the scientific literature (see Methods).

Species	Rate	N	Method	Habitat	Group	Size	Reference
Abax ater	0.6	138	Harmonic radar	WT	1	20	Charrier et al., 1997
Abax ater	1.8	420	Capture-Recapture	WT	1	20	Loreau and Nolf, 1993
Abax ater	2.3	50	Capture-Recapture	WT	1	20	Drach and Cancela da Fonseca, 1990
Abax ater	2.3	85	Capture-Recapture	WT	1	20	Petit, 1994
Amara equestris	1.8	259	Enclosure experiment	HM	2	9.3	Vermeulen, 1994b
Calathus ambiguous	2.4	116	Enclosure experiment	HM	2	10	Vermeulen, 1994b
Calathus erratus	2.3	263	Enclosure experiment	HM	2	10.2	Vermeulen, 1994b
Calathus melanocephalus	2.2	156	Enclosure experiment	HM	2	7.5	Baars, 1979
Carabus coriaceus	6.2	189	Telemetry	WT/M	1	36	Riecken and Raths, 1996
Carabus nemoralis	5.0	15	Capture-Recapture	WT/HM/M	3	24	Kennedy, 1994
Carabus nemoralis	18.4	14	Harmonic radar	WT/HM/M	3	24	Kennedy, 1994
Carabus problematicus	15.4	63	Capture-Recapture	WT/HM/M	3	24	Rijnsdorp, 1980
Harpalus servus	1.0	360	Enclosure experiment	HM	2	8	Vermeulen, 1994b
Nebria brevicollis	1.3	598	Enclosure experiment	WT/M	1	12	Nelemans, 1988
Nebria brevicollis	1.5	83	Capture-Recapture	WT/M	1	12	Joyce et al. 1999
Nebria brevicollis	2.1	301	Capture-Recapture	WT/M	1	12	Greenslade, 1964
Orinocarabus nemoralis	6.7	8	Capture-Recapture	WT/HM/M	3	24	Drach and Cancela da Fonseca, 1990
Procrustes purpurascens	8.5	11	Capture-Recapture	WT/M	1	25	Drach and Cancela da Fonseca, 1990
Pterostichus lepidus	1.9	408	Enclosure experiment	HM/SD	2	12	Vermeulen, 1994b
Pterostichus lepidus	2.6	118	Capture-Recapture	HM/SD	2	12	Vermeulen, 1994a

4.3.3 Standardised rate analyses

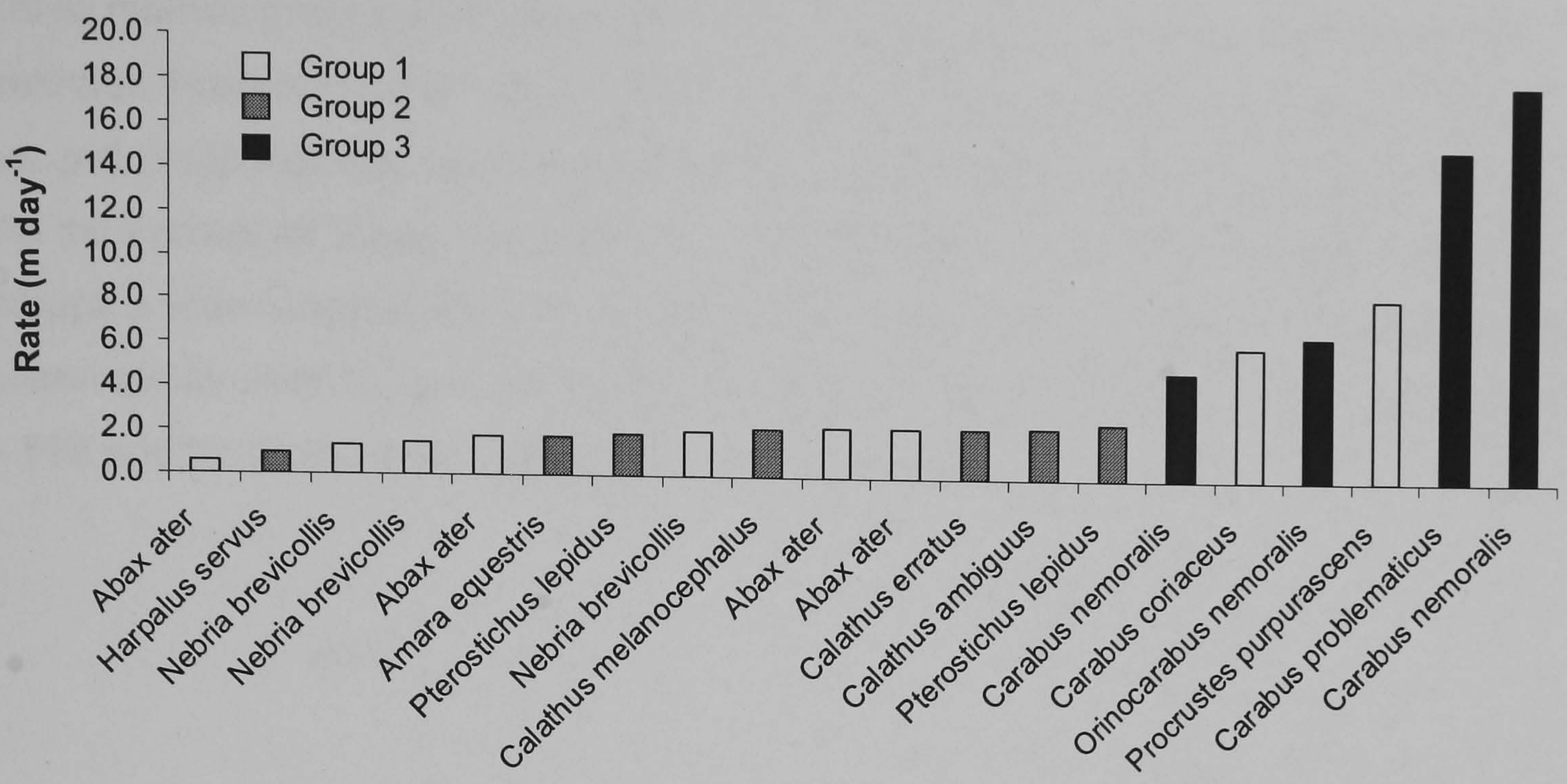


Figure 11: Frequency distribution for the mean movement rates of ground-dwelling woodland invertebrate species as presented in Table 10. The different shading of the bars indicates to what habitat specialism group the species belongs. Group: indicates the group for each species based on habitat specialism; 'Group 1' includes species found in WT or WT/M habitat, (2) in HM or HM/SD and (3) includes species found in WT/HM/M habitat. (WT) Wood and trees, (HM) Heathland & moorland, (M) Meadowland, (SD) Sandy/dry disturbed/arable (see further Methods).

Thirteen studies presenting twenty rates for thirteen ground-dwelling woodland invertebrate species were found that provided estimates of straight-line movement rates in m day^{-1} (Table 9). All rates that were found were for ground beetles. The majority of the rates were obtained using 'Capture-recapture' methods (10) with another seven using 'Enclosure experiments', two using 'Harmonic radar' and one using 'Telemetry' (Table 10). Rates found for the woodland species varied between 0.6 and 18.4 m day^{-1} (Table 10, Figure 11). Based on habitat preference, 'Group 1' included nine rates for four species (body size: range 12.0 – 36.0 mm, mean = 22.6, SD = 8.8) with rates varying between 0.6 and 8.5 m day^{-1} (Table 10, Figure 11) with a mean rate of 3.0 (SD = 2.6) m day^{-1}. 'Group 2' included seven rates for six species (body size: range 7.5 – 12.0 mm, mean = 9.5, SD = 1.6) ranging from 1.0 to 2.6 m day^{-1} (Table 10, Figure 11) with a mean rate of 2.0 (SD = 0.6) m day^{-1}. 'Group 3' included four rates for three species (body size: all three species 24.0 mm) ranging from 5.0 to 18.4 m day^{-1} (Table 10, Figure 11) with a mean rate of 11.4 (SD = 6.5) m day^{-1}.

4.3.4 Quality assessment

Three method groups were identified. The first group included rates obtained by the methods 'Harmonic radar' (2) and 'Telemetry' (1) and were awarded weight 3. The second group included all rates obtained by 'Enclosure experiment' (7) (weight 2) and the third group all 'Capture-recapture' (10) rates (weight 1) (Table 10). Within these groups a wide range of observations (N) were used to calculate the rate estimates. The observations used for group one ranged between 14 – 189, for group two between 116 – 598 and for group three between 8 – 420 (Table 10).

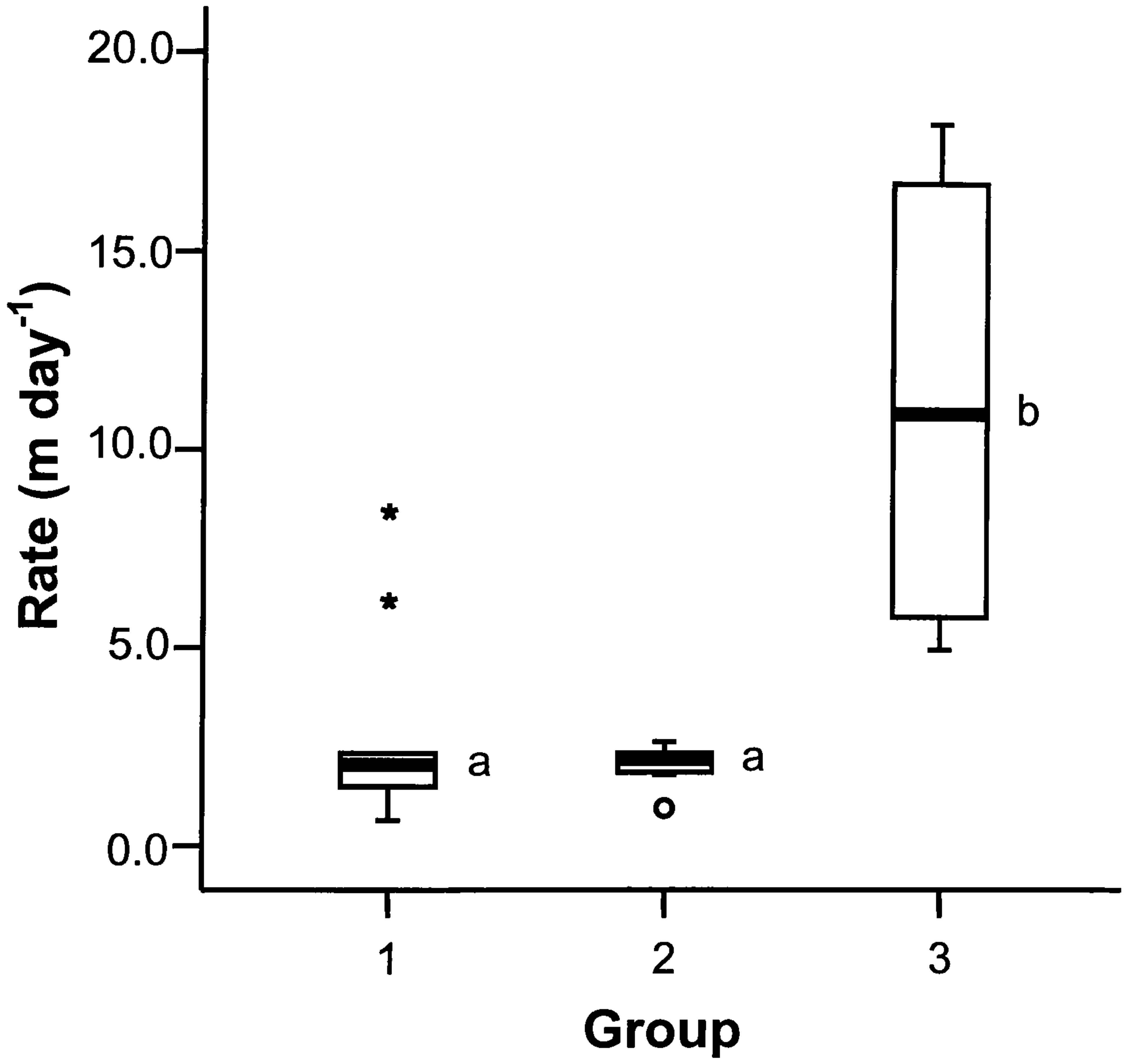


Figure 12: Boxplot illustrating the ranges and median (black line) for all rates found for the individual ground-dwelling woodland invertebrates groups. Group: indicates the group for each species based on habitat specialism; 'Group 1' includes species found in WT or WT/M habitat, (2) in HM or HM/SD and (3) includes species found in WT/HM/M habitat. (WT) Wood and trees, (HM) Heathland & moorland, (M) Meadowland, (SD) Sandy/dry disturbed/arable (see further Methods). 'Group 1': median 2.1 m day^{-1} (inter-quartile: 2.9), 'Group 2': median 2.2 m day^{-1} (inter-quartile: 0.6) 'Group 3': median 11.0 m day^{-1} (inter-quartile: 12.2). Identical letters indicate a non-significant difference (a – a), different letters indicate a significant difference (a – b) ($P <$ 0.05, Mann-Whitney *U* test) between the individual habitat specialism groups. The stars and circles indicate extreme values and outliers respectively. The boxes in the plots include 50% of all the cases of the individual groups. The whiskers protruding from the box extend to the

smallest and largest values excluding the outliers and extreme values. SPSS defines points as outliers if they extend more than 1.5 times the box-length from the edge of the box. Extreme values extend more than three box-lengths from the edge (information on boxplots from Pallant, 2007).

A significant difference was found for median rate between the individual habitat specialism groups (Kruskal-Wallis: $\chi^2 = 7.54$, $df = 2$, $P = 0.023$). 'Group 1 & 2' both revealed lower median movement rates compared to 'Group 3' (Mann-Whitney: $n_1 = 9$, $n_3 = 4$, $z = -2.31$, $P = 0.021$ and $n_2 = 7$, $n_3 = 4$, $z = -2.65$, $P = 0.008$, respectively; Figure 12). Adding the individual weights to the rates did not change this outcome. Further differences between the individual groups were found for median body size (mm) (Kruskal-Wallis: $\chi^2 = 12.96$, $df = 2$, $P = 0.002$). The median body size for 'Group 1' was 20.0 mm (inter-quartile: 10.5); 'Group 2', 10.0 mm (inter-quartile: 4.0); and 'Group 3', 24.0 mm (inter-quartile: 0.0). 'Group 1 & 3' both were associated with higher median body size compared to 'Group 2' (Mann-Whitney: $n_1 = 9$, $n_2 = 7$, $z = -3.09$, $P = 0.002$ and $n_3 = 4$, $n_2 = 7$, $z = -2.71$, $P = 0.007$, respectively), but no difference was found between 'Group 1 & 3'. Together this indicates that the difference found between 'Group 1 & 3' in terms of rate (see Figure 12) was not associated with a body size difference between these groups. However, a strong positive correlation was revealed between body size and movement rate of all individual beetles together (Spearman: $r = 0.606$, $n = 20$, $P = 0.005$), indicating an increase in movement rate with an increase in body size. Additionally, as expected, median ground movement rates were lower than movement rates recorded for flying species (Ground beetle rates Table 10: $n_{\mathrm{Gb}} = 20$, median = 2.32 (inter-quartile: 4.1) vs. Woodland butterfly species with straight-line movement rates in m day^{-1} Table 9: $n_{\mathrm{Bf}} = 4$, median = 52.2 (inter-quartile: 19.3); Mann-Whitney: $z = -3.10$, $P = 0.002$).

4.4 Discussion

The systematic review revealed only a limited number of studies that provided a direct measurement of movement for woodland invertebrates. The majority of the studies found (18) were conducted between 1985 and 2000, mainly focussing on carabid beetles. Interestingly, for the last seven years only four studies were identified. This highlights the general lack of information on movement for woodland invertebrates. Relatively few of the studies used advanced techniques such as telemetry (1) and harmonic radar (4). In the last decade, technological advances have been rapid in these techniques and substantial improvements have been made, for instance in reducing the weight of the tags used (O'Neal et al., 2004). However, after initial popularity especially in the field of harmonic radar (Riley et al., 1996; O'Neal et al., 2004), relatively few studies have used such methods to obtain movement rates for woodland species. Despite ongoing technological development (O'Neal et al., 2004; Szyszko et al., 2004), the relatively high costs and limited availability of these techniques are such that more traditional approaches like mark-recapture are still generally preferred.

This review revealed a bias in the literature toward studies of woodland species living on the forest floor, as most studies focused on ground beetle species (i.e. carabids). Furthermore, the non-pest species that were studied included only carabid and butterfly species, and considering this particular group, the majority were studies on carabid beetles (15 out of 20). This bias is due to the fact that carabid species are relatively easy to study compared to more mobile flying species. This can further be related to the relative ease and availability of techniques to study movement rates for such species. Carabid beetle species mainly disperse by walking (Lövei & Sunderland, 1996), making their movement distances relatively short and therefore the spatial scale at which they move on a daily basis relatively limited. This favours the use of technically undemanding methods such as pitfall traps to measure movement rates (Sutherland, 2006). The more mobile species such as butterflies are harder to study, as they move more rapidly and over larger distances within a given time period. Furthermore, butterflies move through a three dimensional space making them more elusive and harder to catch and/or track over time, especially within a woodland environment. Absolute distances travelled over time for woodland species are therefore easier to obtain for ground-dwelling species.

In this study the absolute distance travelled per day within habitat (i.e. intra-patch) was found to be twenty-two times higher for woodland butterflies (median: 52.2 m day^{-1}) than for woodland carabid beetles (median: 2.32 m day^{-1}). The review study by Bowne & Bowers (2004) found similar differences between movement rates of butterfly and carabid species moving between habitat patches (i.e. inter-patch). Their aim was to provide basic statistics on movement of species between habitat patches. They calculated rates of inter-patch movement as the proportion (%) of the population moving per generation. However, unlike the study presented here, Bowne & Bowers (2004) considered relatively large spatial and temporal scale movement rates of invertebrates. For all carabid and butterfly species that were included in their review, the percentage of the population moving between habitat patches was two times higher for butterflies than for carabid beetles. However, when only considering woodland species, the percentage of the butterfly population moving was twenty-four times higher than that of woodland carabid beetles (butterfly: $n = 2$, mean: 12.9%; carabid: $n = 2$, mean = 0.54%, calculated from data provided by Bowne & Bowers (2004)). The similarity in results for these two woodland invertebrate species groups between this study and that of Bowne & Bowers (2004) might indicate that differences in rates of movement within patches are similar to movement rates between patches. This could have potential implications in terms of 'scaling up' results obtained at a local spatial scale to a larger spatial scale.

In the current review, measures of movement for woodland species were mainly obtained for carabid beetles. The majority of this group of beetles have limited flight capability and mainly move through the environment by walking (Lövei & Sunderland, 1996). Therefore, for this group, the straight-line movement rate (m day^{-1}) made over the ground was analysed further. Specifically, these species were used to explore potential relationships between straight-line ground-movement rates and habitat specialism and with physical attributes such as body size. Body size is often assumed to be positively related with dispersal ability. For instance, home/foraging range for different groups of insects was found to be positively correlated with body size (Tscharntke et al., 2002). A similar relationship was found for heathland carabid beetles (den Boer, 1990b) as well as for woodland carabids (Drach & Cancela da Fonseca, 1990). The study of Drach & Cancela da Fonseca (1990), however, only included data for three beetle species differing in body size. In the current review, a significant relationship between body size and rate of movement was recorded for thirteen carabid species, supporting previous results (Drach & Cancela da Fonseca, 1990). The fact that larger carabid species were found to cover more ground on a daily basis than smaller species can be explained by their higher daily food requirement, which is linked to higher body mass (Lövei & Sunderland, 1996), or simply to their higher movement capability attributable to their larger size.

Identification of species groups is often performed to identify generalisations about the ecological behaviour of invertebrates, or to provide general guidance regarding conservation management (e.g. Lambeck, 1997). Standard approaches to grouping species include the degree of habitat specialism/occurrence and/or physical traits such as dispersal ability. Grouping invertebrates based on their mobility/dispersal ability has been undertaken for butterflies (Thomas, 2000) and for carabid beetles associated with heathland habitat (den Boer, 1990a; b). Thomas (2000) defined three broad classes of mobility based on experimental data describing average distances moved and the proportion of the population demonstrating movement. He used this mobility classification in relation to temporal declines in the occurrence of these different species groups. Responses of these groups were correlated with processes of habitat loss and fragmentation. Den Boer (1990a; 1990b) identified two groups based on the turnover rate (time between extinctions vs. colonisations) for individual carabid species found within a heathland area in The Netherlands. He found that these groups were distinct in terms of dispersal ability (den Boer, 1990a) and habitat occurrence (den Boer, 1990b). These groups could be categorised as species with low dispersal power inhabiting stable habitat vs. species with high powers of dispersal inhabiting unstable habitat (den Boer, 1990a; b). The species of stable habitat were mainly found in woodland and heathland environments (i.e. habitat specialists) (den Boer, 1990b). Species of unstable habitat were mainly found in more open sites such as arable land and meadows, but also within more wooded habitat such as woodland edges (i.e. habitat generalists) (den Boer, 1990b).

In the current study, ground-dwelling woodland invertebrates (i.e. carabid beetles) were grouped according to the degree of habitat specialism based on an existing habitat classification system (Buckland, 2007). Here, dispersal ability based on the daily straight-line rate of movement of woodland carabid beetles was found to be associated with a difference in habitat specialism, with habitat specialists displaying lower movement rates than more generalist species. The results therefore support those obtained by Den Boer (1990b) for carabid species of heathland environments. This suggests that movement rate can be used as an indicator of the degree of habitat specialism for ground-dwelling woodland carabid species (i.e. 'Group 1 & 3', this study), and *vice versa*. Additionally, the difference in movement rate between woodland specialist and generalist species was not influenced by the relationship observed between rate and body size, as body size was not found to be significantly different between the two groups. However, the difference in movement rates between these two groups may be attributable to differences in movement strategy (random vs. directed) (Baars, 1979; Rijnsdorp, 1980). The lower straight-line movement rates for woodland specialist species suggests a more random walk strategy (e.g. Charrier et al., 1997) and the higher rates found for woodland generalists indicate a more directed walk. The generalist species can be found in multiple habitats and are likely to be less bound to these environments, for instance in terms of food availability and microclimatic factors. These characteristics make them more flexible in their requirements, which might be reflected in a more directed movement strategy and pattern than more specialised species. This is illustrated by *Carabus problematicus,* which showed a more directed walk when dispersing between different habitats compared to more random movement when moving within one habitat type (Rijnsdorp, 1980).

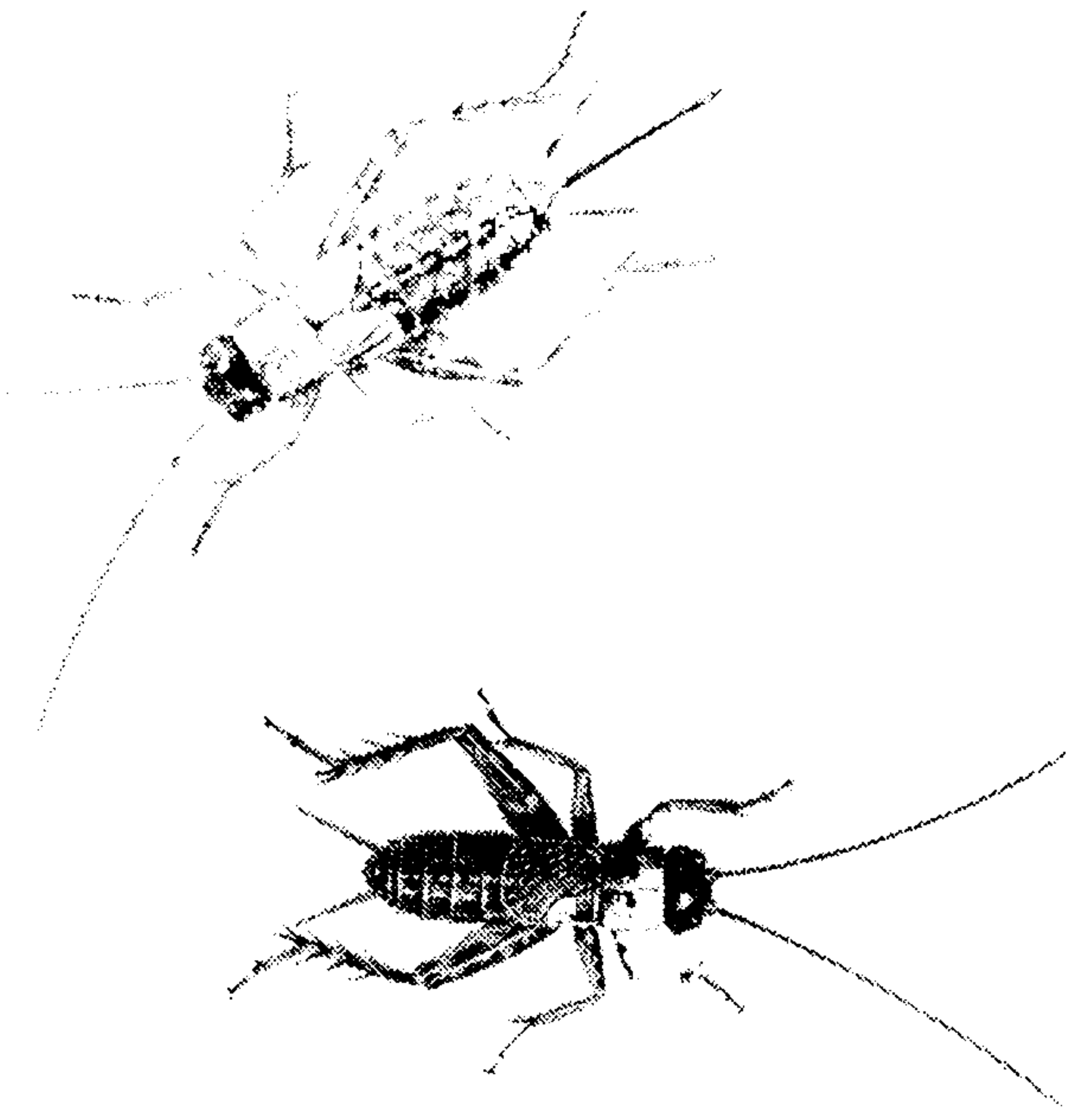
Care needs to be taken in developing generalisations when different methods are used to estimate the movement rate of a species. The rate estimates that were used in this study were obtained using four different methods. When different techniques were used to estimate movement rate for the same species, differences in results were shown (see Table 10). The most striking example is the considerable difference in movement rates for *Carabus nemoralis* obtained using two different techniques (Capture-Recapture vs. Harmonic radar) with equal sample sizes (Kennedy, 1994) (see Table 10). However, in the study of Williams et al. (2004) on a bark beetle, rates obtained using harmonic radar were generally similar to those obtained using mark-recapture techniques. A great advantage of harmonic radar and telemetry techniques over standard capture-recapture techniques is that during the period of study, marked specimens can move continuously through the environment and be traced at any moment in time (e.g. with fixed time lags) without interruption (Charrier et al., 1997). Therefore, exact distances over time can be measured between locations, allowing more accurate rate estimates to be obtained, compared with rates calculated from specimens that are caught randomly without precise time lags. On the other hand, compared to standard capture-recapture techniques, these techniques generally involve application of relatively large and often heavy external tags (Riecken & Raths, 1996; Turchin, 1998; Williams et al., 2004). This might influence the behaviour and dispersal ability of the individuals used, consequently reducing the accuracy of the rate estimates (Riecken & Raths, 1996). Sample size was another consideration when evaluating the results reviewed here. However, studies employing the same species and methodology, but differing in the number of observations used, did not demonstrate major variation in the mean rates obtained (e.g. *Abax ater* and *Nebria brevicollis*, Table 10). However, the relationships found here for woodland-associated carabid beetles were based on only a limited number of species, highlighting the need for more research on movement rates in order to strengthen the findings of this study.

The systematic review approach was designed to synthesize published and unpublished data (Pullin & Stewart, 2006). However, in this study only information from published data was collected. Although using conventional review techniques, for a wide range of animal species, Bowne & Bowers (2004) similarly used a two-stage search strategy, one using fixed search terms and a range of *ad hoc* search strategies. Similarly to this study, they found an equal number of relevant studies in both stages indicating the importance of including intuitive and less stringent search strategies when conducting a literature review. In the study presented here, the additional inclusion of cited references (Phase 2, see Methods) added another fifteen relevant studies to the original ten found in the 'Phase 1' search, underlining the importance of including *ad hoc* search strategies when reviewing the literature. Furthermore, nine of these studies were listed within the library 1 assembled during the initial stages of the systematic review ('Phase 1'). This highlights the limitation of using only fixed search term combinations, which resulted in some relevant studies being deleted during the selection process. This emphasises the care that should be taken in formulating and translating the selection criteria into objective search terms when undertaking a systematic review, in order to detect all relevant studies that need to be included (Pullin & Stewart, 2006).

To date, systematic reviews in ecology have generally been applied to evaluate the impacts of different conservation management interventions (e.g. Davies & Pullin, 2007; Davies et al., 2008). Here, we demonstrate that the approach can also be applied to measurements of species behaviour (e.g. to find movement parameters). Such measurements could potentially be used to inform and validate the parameter estimations used in spatial modelling approaches that focus on responses of species to land cover and climate change. Parameterisation of dispersal ability in such models is often based on estimations and/or expert opinion (e.g. Fahrig, 2001; Watts et al., 2005) rather than values found using a systematic review of the direct measurements that have been made. For instance the metapopulation model developed by Vos et al. (2001) used arbitrary generalised values as species-specific dispersal parameters.

Refining these parameters with measurements of movement rate might prove beneficial in terms of validating the model outcomes. Furthermore, in terms of making useful generalisations for conservation purposes, the average movement rate for the individual groups identified in this study could potentially be used as 'model values' to represent the wider group of species with similar habitat preferences and dispersal characteristics.

In terms of species dynamics in a fragmented landscape (e.g. metapopulation functioning (Hanski & Gilpin, 1997)), and woodland habitat network functioning, Bailey (2007) suggests that different groups of woodland species require different degrees of habitat connectivity based on their relative dispersal ability. For woodland invertebrates in this study, because of the lack of measurements for other woodland species groups, only carabid beetles and butterflies could be compared in this respect. As noted in this study, butterfly species typically demonstrate relatively high dispersal ability, and because they mostly disperse through the air, they tend to be less influenced by obstacles at ground level (Tscharntke et al., 2002). Physical links of suitable habitat (i.e. corridors) are thought to be more important for species that are more specialised in their habitat requirements, and that demonstrate lower dispersal ability (Bailey, 2007). Woodland carabid beetles are possibly one such species group, because they mainly move over the ground and may require woodland habitat conditions to be able to do so. The group of species identified in this investigation, which were particularly specialised in terms of habitat requirements, might therefore be expected to benefit most from increased habitat connectivity. For example *Abax ater* (i.e. *Abax parallelepipedus*) ('Group 1', this study) is known to prefer dispersing through hedgerows rather than over agricultural land (Petit, 1994; Petit & Burel, 1998; Pichancourt et al., 2006; Petit, pers. comm.), indicating the importance of wooded corridor features for this species. However, a much wider range of woodland invertebrate groups needs to be studied to broaden our understanding of such requirements. The lack of field measurements of movement rate for all but a tiny minority of invertebrate groups indicates a substantial knowledge gap that should be addressed by future research.



5 Movement strategy of wood cricket (*Nemobius sylvestris*) through different ground surface habitats

5.1 Introduction

The movement strategies of organisms are of fundamental importance for understanding the dispersal ability and distribution of species within landscapes (Levin, 1992; Turchin, 1998; Morales & Ellner, 2002). Analysis of movement can improve the understanding of patterns of species presence at multiple scales (Turchin, 1991; Crist et al., 1992; Johnson et al., 1992; Morales & Ellner, 2002; Samu et al., 2003). At coarse scales, landscape elements typically display a high level of heterogeneity, which can influence the movement ability of species (Johnson et al., 1992; Doak, 2000; Hein et al., 2003; Schtickzelle et al., 2007) and therefore their pattern of distribution within a landscape. Analysis of the movement strategies displayed at finer scales can help explain the patterns observed at coarser scales (Turchin, 1991; Wiens et al., 1993; Samu et al., 2003).

A range of approaches is available for studying the discrete movements of species. A particular powerful way to quantify movement is directly observing and following individuals when moving through the environment (Turchin, 1998). By recording movement paths and behaviour, possible strategies that may account for the movement pattern can be quickly analysed and tested (Turchin, 1998). However, it is often difficult and highly time consuming to obtain detailed information on continuous movements of individuals (Turchin, 1998), especially for highly specialised sedentary species. None the less, individual movement paths have been recorded and analysed for a variety of species across a range of spatial scales (Benhamou, 1990; Cain, 1990; Bergman et al., 2000; Vernes & Haydon, 2001; Lauzon-Guay et al., 2006; Hapca et al., 2007; Bowlby et al., 2007; Dai et al., 2007; Smith et al., 2007).

Movement data in such studies are often compared with uncorrelated random walk (i.e. simple diffusion) and/or correlated random walk models (Turchin, 1998). Testing the applicability of these models to observational data is relatively straightforward, and where these models are intuitive in terms of population spread (Crist et al., 1992; Turchin, 1998), they prove useful in interpreting ecological relevant processes. For invertebrates, these types of analyses have been used for relatively mobile species such as butterflies and for species that move by walking, such as carabid beetles. In these studies movement strategies were related to a range of physical and ecological characteristics of the individual species, including dispersal ability (Doak, 2000; Samu et al., 2003; Conradt & Roper, 2006; Schtickzelle et al., 2007), level of satiation (Wallin & Ekbom, 1988; Wallin, 1991; Wallin & Ekbom, 1994), and forage requirements (Root & Kareiva, 1984). Furthermore, for individual species, differences in movement strategies have been recorded across temporal (Johnson et al., 1992; Morales & Ellner, 2002) and spatial scales (Johnson et al., 1992; Samu et al., 2003), between life-stages (With, 1994; Doak, 2000), and when moving through different habitat environments (Baars, 1979; Wallin & Ekbom, 1988; Crist et al., 1992; Fownes, 2002; Hein et al., 2003). However, previous studies have mainly been undertaken for species associated with open habitat such as agricultural fields and meadowland, and only very few studies have been undertaken with woodland-associated species (see Chapter 4). Understanding the movement of woodland species is of particular importance in highly fragmented landscapes (Bailey, 2007), for example to determine the impacts of fragmentation on the distribution of individual species, and the functioning of ecological corridors or habitat networks (Bennett, 1999, 2003; Vos et al., 2002; Crooks & Sanjayan, 2006). Information on the movement strategies of invertebrate species associated with woodland is severely lacking.

The research described here focused on the woodland-associated invertebrate wood cricket (*Nemobius sylvestris*). In the UK the species has the national status of a 'Species of Conservation Concern' (NBN Gateway, 2007). Wood cricket is a small (~ 1 cm) non-flying cricket species that has a semi-voltine (two-year) life-cycle in the UK (Gabbutt, 1959; Brown, 1978). After overwintering, eggs hatch in June/July and the juveniles (i.e. nymphs) develop throughout the summer and autumn by means of moulting (Gabbutt, 1959; Brown, 1978). Moulting ceases completely in September when the nymphs prepare to overwinter (Gabbutt, 1959; Brown, 1978). In the second year, nymphs continue to develop from April onwards until they reach sexual maturity (i.e. become adults) in July/August and are reproductively active through to September/October until they die (Gabbutt, 1959; Brown, 1978). The species is strongly associated with deciduous woodland and is typically found in relatively open woodland areas such as clearings and in edge habitat along woodland tracks, footpaths, railway lines and woodland peripheries (Richards, 1952; Morvan & Campan, 1976; Beugnon, 1980). They live on the ground and prefer a well-developed leaf litter layer, which serves as shelter, food and breeding ground (Richards, 1952; Brown, 1978; Proess & Baden, 2000). The main habitat requirements identified for this species at the local scale were presence of a thick leaf litter layer, an open canopy and low levels of ground vegetation (Chapter 3).

To date no detailed study has been undertaken of the movement strategy of wood cricket through different habitat environments. Therefore, this study addressed the following aims: (1) to explore the movement strategy of wood cricket nymphs and adults under different ground cover conditions; (2) to determine the rate of movement for both nymphs and adults in these different habitat environments; and (3) to determine the preferred ground cover/habitat of both adults and nymphs when presented with a choice. Based on earlier findings for wood cricket and studies of other invertebrate species it was hypothesised that: (a) differences in movement strategy would be found between life-stages and under different ground cover conditions; (b) nymphs would move more slowly than adults; and (c) leaf litter habitat would be the preferred substrate to move through, for both nymphs and adults.

5.2 Methods

5.2.1 Study site

Between the 5th and 29th of June and the 30th of July and 7th of September 2007 a series of experiments were conducted using wood cricket (*Nemobius sylvestris*) nymphs (6-7th instar) and adult males and females respectively. The experiments were carried out in the Briddlesford area (50° 42' 41.00" N, 1° 13' 30.50" W) situated on the Isle of Wight which is owned by 'The People's Trust for Endangered Species' (PTES), a non-governmental conservation organisation (Figure 13). The majority of woodlands in this area are classified as 'ancient woodland' (Spencer & Kirby, 1992) and are dominated by native deciduous tree species, particularly oak (*Quercus spp.*). Since 2005 extensive new plantings of native tree species have taken place in this area funded by the 'JIGSAW' scheme (Forestry Commission, 2005) in order to increase connectivity between the individual woodland fragments.

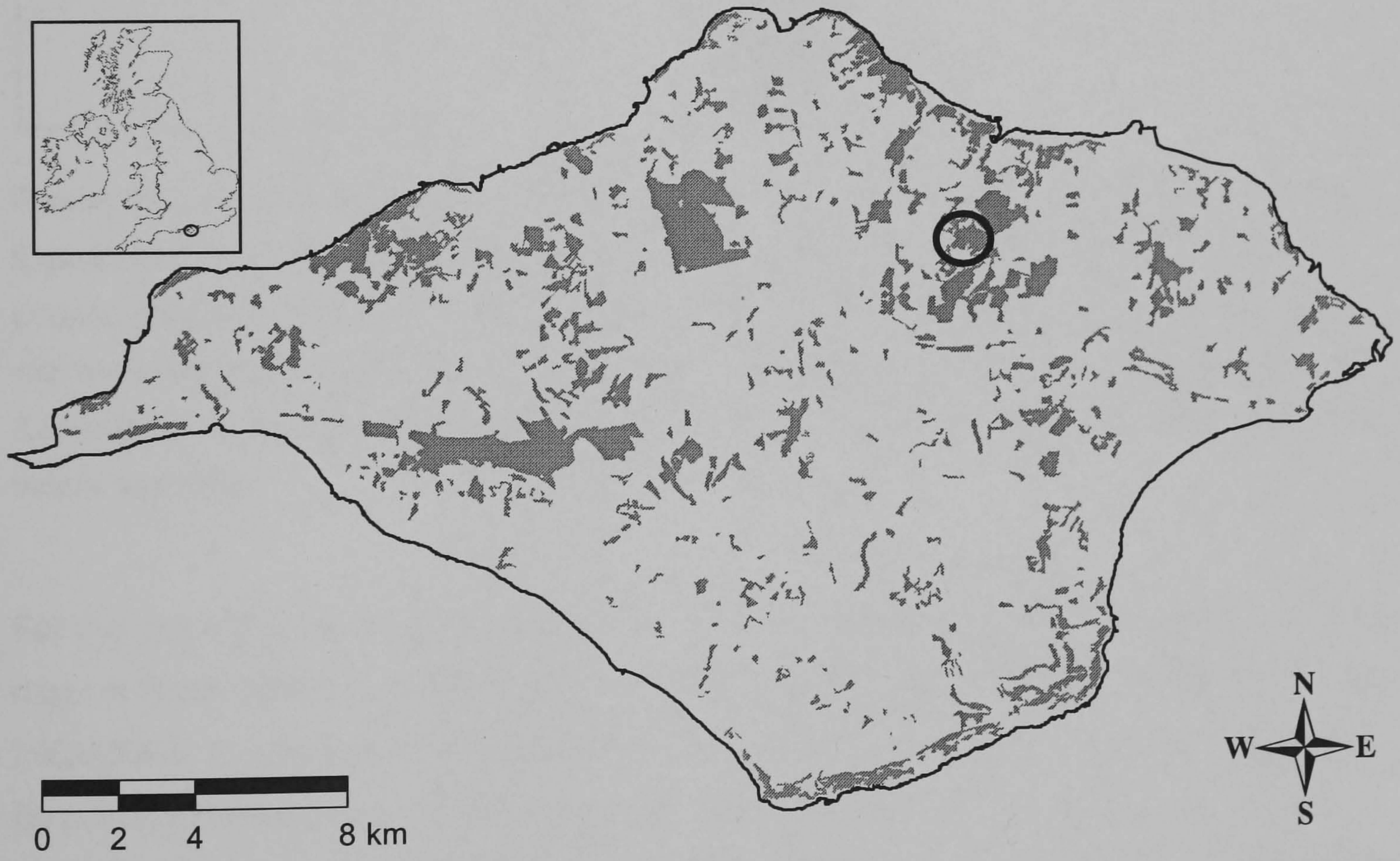


Figure 13: All the woodland fragments on the Isle of Wight (grey). Briddlesford area is highlighted. Derived from digital maps based on the National Inventory of Woodland and Trees (NIWT) (Smith & Gilbert, 2003).

5.2.2 Individual movement experiments

Three separate experiments were undertaken (Experiment 1 – 3). These focused on recording individual movement paths for the two life-stages in order to analyse movement strategies under different ground cover conditions, and to test for preference among different ground cover conditions upon release.

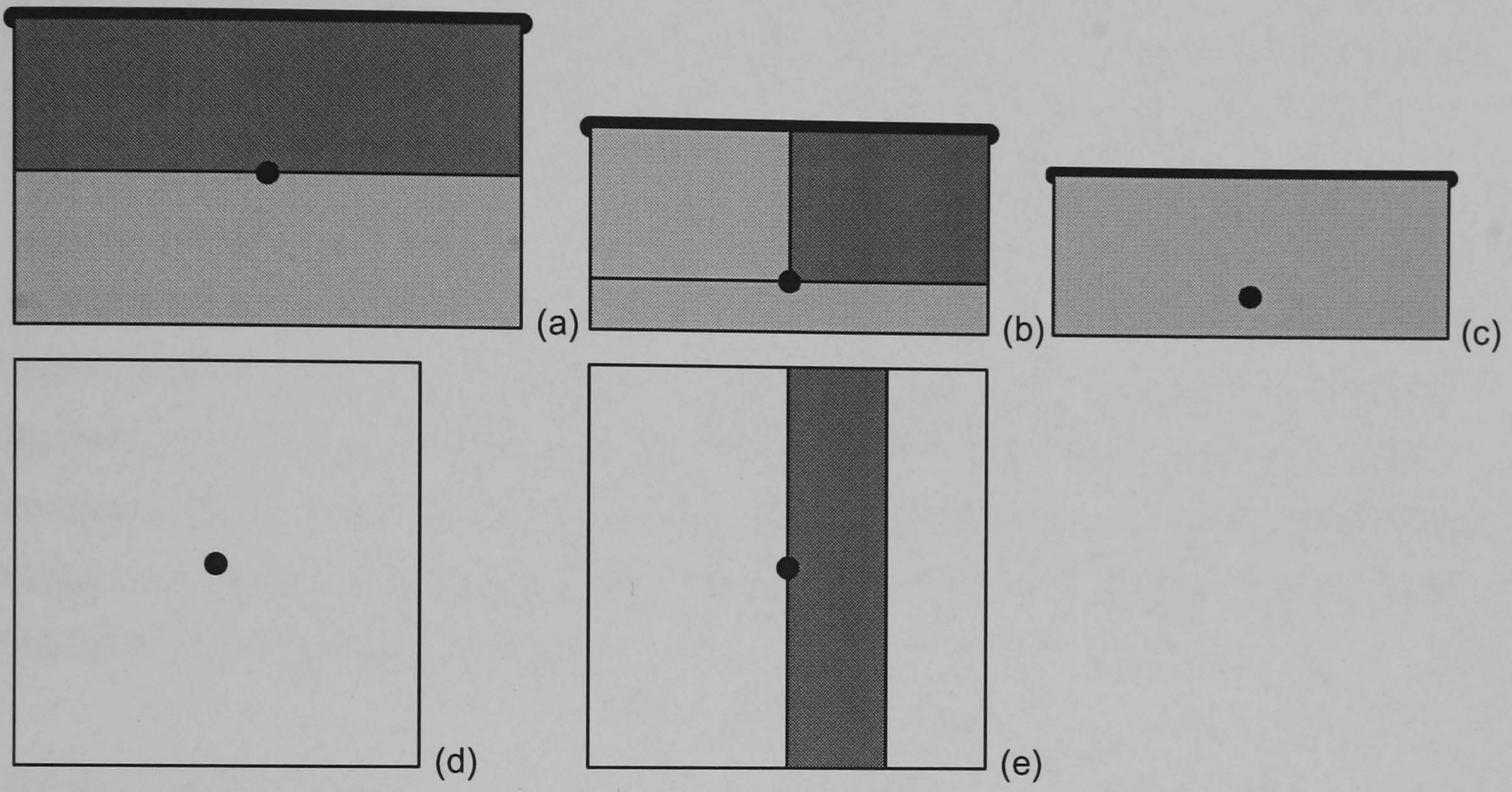


Figure 14: Experimental designs for grid releases. Experiment 1 (a & b), Experiment 2 (d & e), Experiment 3 (c). Black points indicate the point of release. Thick black lines indicate the woodland edge (a & b) and tall grass edge (c). White areas indicate bare soil, light grey areas indicate short grass vegetation and the dark grey areas indicate leaf litter cover (see also Appendix II). All figures have the same scale. As a reference, figure (e) is 4x4 meters (for more details see text).

For the experiments, both the nymphs and adults were caught over the course of three days at three different locations within a large wooded area that was thinned in the year 2003/2004. To catch the wood crickets, a 55 x 55 x 30 cm square wooden enclosure (to confine them) and a custom designed pooter were used. For the duration of the experiments, the nymphs and adults were kept in a square plastic container (35 x 25 x 19 cm) with ample supplies of food (bread, various fungi and oak leaf litter) available. To increase the detection probability, before the experiments the wood crickets were marked by dusting them with non-toxic fluorescent pigment (UV Gear, Mark SG Enterprises, Surrey, United Kingdom, www.uvgear.co.uk) (following Cronin, 2003). Marking was achieved by placing the wood cricket nymphs and adults in a circular plastic container (21 cm wide and 10.5 cm deep) with a small amount of pigment, and shaking the container gently until all specimens were marked sufficiently. Fitness trials conducted in 2006 did not reveal any significant increase in mortality and/or change in behaviour when adopting this marking method.

All experiments were conducted on sites where wood cricket was initially not present (i.e. released wood cricket were strangers to the site). At all experimental site locations, vegetation measurements were carried out using a 50 x 50 cm quadrat. First, ground vegetation cover up to 1 m in height was estimated visually (in %) and mean dominant ground vegetation height was measured using a meter rule (cm). Second, total leaf litter cover was estimated visually and litter depth (cm) measured by taking four separate measurements with a leaf litter probe in the middle of each of four 25 square centimetre sections within the quadrat. Finally, from the centre of the quadrat, canopy closure was measured using a convex spherical densiometer (Forest Densiometers, Bartlesville, US). This involved taking separate readings for the four main compass directions (N, E, S, W), which were averaged for each location. During all experiments mean average daytime temperature at the ground surface did not go below 15 °C, as indicated by meteorological records.

5.2.2.1 Experiment 1

For wood cricket nymphs, habitat choice and individual movement paths were recorded within a 5 x 3 m grid developed within a grassland/hay field adjacent to a mature East facing woodland edge dominated by oak (*Quercus spp.*) (Figure 14a). The grid was constructed using bamboo pegs and garden twine with each grid cell measuring 20 x 20 cm. The surface area within the grid was modified to provide a distinct contrast in ground cover. This was achieved by dividing the grid into two 5 x 1.5 m wide strips running parallel to the woodland edge. The first strip directly bordering the woodland edge was prepared by removing all grass and herbaceous vegetation. Then, to leave a surface entirely covered by leaf litter, a 2 cm thick leaf litter layer was added to this strip. The second strip was covered by grasses and forbs and was located 1.5 m from the woodland edge (Figure 14a). The herbaceous grass strip was prepared by cutting it to an even height using a scythe, producing a mean ground vegetation cover of 97%, a mean sward height of 10 cm and an average litter cover of 3%, 0.5 cm deep. The canopy closure decreased considerably from the woodland edge (65%) toward the field (35% at 3 m from the woodland edge).

On the 13th, 14th and 15th of June single wood cricket nymphs marked with orange dust were released at the centre of the grid just inside the grass strip (Figure 14a). The releases were established by gently evicting an individual by inverting a circular transparent plastic container (9 cm wide, 10 cm deep) at the release site. The released specimens were observed from a position outside the grid (1.5 meters away from the point of release) avoiding the creation of a silhouette against the horizon, as wood cricket are known to orientate towards contrasting dark objects (Campan & Gautier, 1975). To avoid further directional bias, specimens were released in alternating directions. For each individual, habitat choice was recorded and the individual movement paths drawn on gridded paper by recording their exact (step) positions within the grid at two-minute intervals. Individual wood cricket nymphs (and adults) were released until a clear pattern of habitat choice could be revealed with a chi-square 'goodness of fit' test. However, no less than fifteen and no more than thirty-five different individuals were used for each experiment. Observations were terminated either after individuals were observed exiting the grid or remained stationary for more than 5 minutes. This time limit was based on the difficulty of analysing and interpreting the data when individuals demonstrate prolonged stationary periods during their walks (see 5.2.3.1). All individual releases either took place under overcast weather conditions or whilst the release location was in the shade with mean daytime temperatures of 18 °C at ground level.

For the adult releases, several adaptations to this approach were made. In this case, a 4 x 2 m grid was created at the same location (Figure 14b). The interior ground cover was modified by creating two contrasting blocks within a 4 x 1.5 m wide strip both directly bordering the woodland edge. One block (2 x 1.5m) represented herbaceous grass cover, and the other provided leaf litter cover. The remaining 4 x 0.5 m wide strip running parallel (1.5 meters from the woodland edge), represented also herbaceous grass cover (Figure 14b). For this set-up, the same vegetation modifications were applied as for the nymphs. On the 1st and 2nd of August, single wood cricket adult males and females were released (1 : 1) at the junction of the contrasting habitats (1.5 m from the woodland edge). Marked individuals were released by using a transparent plastic circular container (3.5 cm wide, 7 cm deep). The individual wood crickets were released by inverting the container and removing it after 5 s. This was done to avoid a directional bias after release. For each individual, habitat choice was recorded and the individual movement paths drawn on gridded paper by recording their exact (step) positions within the grid at one-minute intervals. Observations were terminated either after individuals were observed exiting the grid or remained stationary for more than six minutes. All individual releases took place either under overcast weather conditions or whilst the release location was in the shade with a mean daytime ground temperature of 19 °C.

5.2.2.2 Experiment 2

For nymphs (19th and 20th of June) and adults (4th and 5th of August), a similar experiment was performed within an oak dominated woodland stand. In this case a 4 x 4 m grid was created on an open woodland track with a mean overhead canopy closure of 92%. Initially, all leaf litter and ground vegetation was removed, resulting in a bare soil cover (Figure 14d). Individual wood crickets were released at the centre of the grid following the methods described above (see 5.2.2.1). However, in this case exact locations within the grid were recorded at 1 min intervals for both nymphs and adults. Furthermore, to avoid directional bias of the released specimens, the position of the observer outside the grid was changed regularly and releases were equally distributed among four alternating directions. Secondly, to create a contrast in ground cover, a 1 x 4 m strip of leaf litter was developed within the grid (Figure 14e). The leaf litter cover for this strip was 100% with a mean depth of 1 cm. Wood crickets were released at the centre of the grid at the edge of the two contrasting habitats (bare vs. leaf litter) following the same method and recording the same data as described above. All releases took place with a mean temperature at ground level of 18 °C.

5.2.2.3 Experiment 3

To test for habitat choice and record movement paths in grass vegetation, a third grid was created on the edge of a recent planting bordering a grazed field (Figure 14c). The vegetation within the new planting was a mixture of dense thistle and grass, 50 – 60 cm in height. The grazed field consisted of a short grass sward 10 cm in height. The height of the short grass habitat was further homogenised by clipping to develop a sharp contrast between the two habitats. In the short grass habitat, a 1.5 x 4 m grid was created bordering the tall grass habitat. On the 4th of August at 8 pm after sunset and on the 24th of August at noon, single adult wood cricket were released on a circular wooden platform (12 cm in diameter), which was placed in the short grass habitat and situated 1 m away from the tall grass edge. Single wood crickets were released in the middle of the platform using a circular 3.5 x 7 cm transparent plastic container. The individual wood crickets were released by inverting the container on the centre of the platform. After 5 seconds the container was removed and the movements of the wood cricket were recorded from a position 2 m away, maintaining a low profile. Male and female wood cricket were released one at a time. For each released cricket, individual movement paths were drawn on gridded paper by recording the location within the grid at intervals of 1 minute. Releases on the 4th August were made under relative cool conditions with a mean temperature at ground level of 13 °C. On the 24th the weather was overcast with a mean temperature of 18 °C.

5.2.3 Analyses

All individual paths were digitised using PowerPoint (Microsoft Office XP, Microsoft Corporation 1983-2001, USA). Coordinates were assigned for each step location within the grid. In this case steps represented the straight-line distances between each location as recorded over a one (or two) minute interval. These coordinates combined with standard rules for right-angled triangles and trigonometry (cosine rule) were then used to calculate step distances, the mean speed (cm min^{-1}) and turning angles between moves with functions available in Excel (Microsoft Office XP).

Initially, the individual paths were tested for the existence of a release effect. This was done by comparing the speed displayed in the first step of each individual path with the speed of subsequent steps. After initial exploration of the speed data and testing for normality (Kolmogorov-Smirnov test), Mann-Whitney and t – tests (for independent samples) were used for the analyses. Furthermore, chi-square ‘goodness of fit’ tests were performed to test for habitat preferences for each life-stage and Fisher’s exact probability tests (appropriate when using small samples) were used to test for difference in habitat preference between the sexes. Finally, Mann-Whitney tests were used to test for speed and path time differences between different habitats, sexes and life-stages. All of the statistical analyses were performed using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA).

5.2.3.1 Walk analyses

The individual paths were further used to analyse the movement strategy of wood cricket under different habitat conditions following Turchin (1998). Before these analyses, all paths were individually evaluated and omitted from further analyses when the displayed movements were influenced by non-experimental external factors (e.g. position of the observer). Furthermore, for these analyses data for adults was pooled, regardless of sex. It was not possible to collect enough data on movement paths through grass habitat to perform this analysis, because the majority of individuals did not show any movement after release. The movement paths over bare soil and through leaf litter were analysed for deviances with a simple uncorrelated random walk (URW) (Turchin, 1998) and a correlated random walk (CWR) model (Kareiva & Shigesada, 1983). Uncorrelated random walk (URW) models assume that organisms move through the environment without any correlation between moves (i.e. no directional persistence or any other kind of correlation between successive displacements) and therefore do not include a parameter that accounts for a directional persistence within the equation. CRW models assume that there is a certain level of directional persistence in the movement of organisms and therefore include parameters that account for this persistence based on absolute turning angles between moves. Therefore, under the CRW formulation individuals are predicted to spread quicker compared to URW models.

Both models assume that move duration, speed and turning angles within each path are not serially correlated. Furthermore, indications for the applicability of a CRW model is when turning angles show an overall positive correlation (i.e. a symmetric distribution around 0° (range -180°/180°)). These criteria were tested as follows. To check the primary assumption to apply the CRW model, first the distribution of the absolute turning angle (range -180°/180°) was explored. From here onwards, for nymphs, paths recorded in 'Experiment 1' were excluded in order to standardise the temporal scale between each recorded step to one minute.

Second, serial correlations for the individual paths were examined. For nymphs the paths used ranged from 6 – 12 consecutive steps and for adults from 6 – 8 steps. For nymphs and adults, paths longer than twelve respectively eight steps were split to create an even distribution for all path lengths based on the number of steps taken. Move duration for these paths was standardised to one minute (being the recorded steps) and therefore were not tested for serial correlations. Speed (cm min^{-1}) and turn angles were tested for presence of serial correlations between subsequent steps by using autocorrelation analyses. Autocorrelation is a method specifically designed to examine correlations within time series data. It correlates each value within a continuous series with the value lagged by one (first order) or more (higher order) previous cases (here each steps within the individual movement paths). Individual paths were analysed for presence of first order and second order autocorrelations in step speed using the autocorrelation function available in SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA). For these analyses, individual paths with a minimum of five subsequent (1-minute) steps were used. Autocorrelation analyses for the turn angles were performed for all paths with three or more recorded steps. In this case, turn angles were analysed by defining them as right (R) or left (L) turns relative to the previous step direction. To test for a first order autocorrelation, subsequent turns for each individual path were paired relative to each previous turn and defined as RR, RL, LR and LL. Deviations from a random sequence were tested by applying a Chi-square test of association for these turn pairs. Furthermore, Chi-square 'goodness of fit' tests were performed to test for turn direction preference (even (LL, RR) vs. alternating (LR, RL)). Finally, Spearman's correlations between step speed and absolute (positive) turn angles (0 – 180 degrees) between steps were performed for all registered paths.

To further test the applicability of the URW or CRW formulation for the species moving through different habitats, net squared displacements (R^2_n) were calculated (Equation 3). Under the URW formulation net squared displacements (R^2_n) typically increases linearly with time. Therefore, R^2_n (Equation 3a) was plotted against time (n) and linear regression analyses was used to assess the overall fit. For testing the CRW model, comparisons were made between (theoretical) predicted and (actual) observed displacements. For these analyses all paths with more than two recorded consecutive steps were examined. Predicted and observed displacements were calculated as net squared displacements (R^2_{n}) using the formula provided by Kareiva and Shigesada (1983) (Equation 3b), employing mean observed values for step length and turn angle. These values were plotted against the number of consecutive steps observed for each recorded path made by the individually released specimens. To asses the appropriateness of this particular CRW formulation for wood cricket movement, the 95% confidence interval for the predicted net squared displacements were included for comparison with the observed values.

Equation 3: Net squared displacement (R^2_n) formulation for (a) URW and (b) CRW under the assumption of symmetric distribution of turning angles as shown in (Kareiva & Shigesada, 1983).

$$R^2_n = nL^2 \qquad \text{(a)}$$

$$R^2_n = nL^2 + (2Lc / 1 - c) * (n - (1 - c^n / 1 - c)) \qquad \text{(b)}$$

L = mean step length (cm)
L^2 = mean squared step length (cm^2)
n = number of consecutive steps

c = mean cosine of the turning angle

Additionally for URW, as a measure of population spread, the diffusion rate (D) ($D = L^2 / 4$; see Turchin (1998)) was calculated in cm^2 min^{-1} as well as the estimated absolute diffusion rate ($\sqrt{D}$) (cm min^{-1}). Furthermore, within the CRW equation (Equation 3b), directional persistence affects the rate of spread through the ratio 'c / 1 – c', with small turning angles (i.e. large c) producing the largest ratio's and therefore the largest displacements. If the predicted net squared displacement (R^2_n) matches the observed than the predicted formulation can be used as a tool to indicate the population spread under the experimental conditions in which it was derived. However, net displacement (R_n) as a measure for distance travelled over time (or as a measure of population spread) is more intuitive than a squared distance (R^2_n) travelled over time (i.e. cm min^{-1} vs. cm^2 min^{-1}, respectively). Therefore, by using the method developed by Byers (2001), estimations for net displacement (R_n) were calculated using the appropriate correction factor (z) ($R_n = z \sqrt{R^2_n}$; with mean absolute turning angle > 30°, $z = 0.89$; see Byers (2001))

5.3 Results

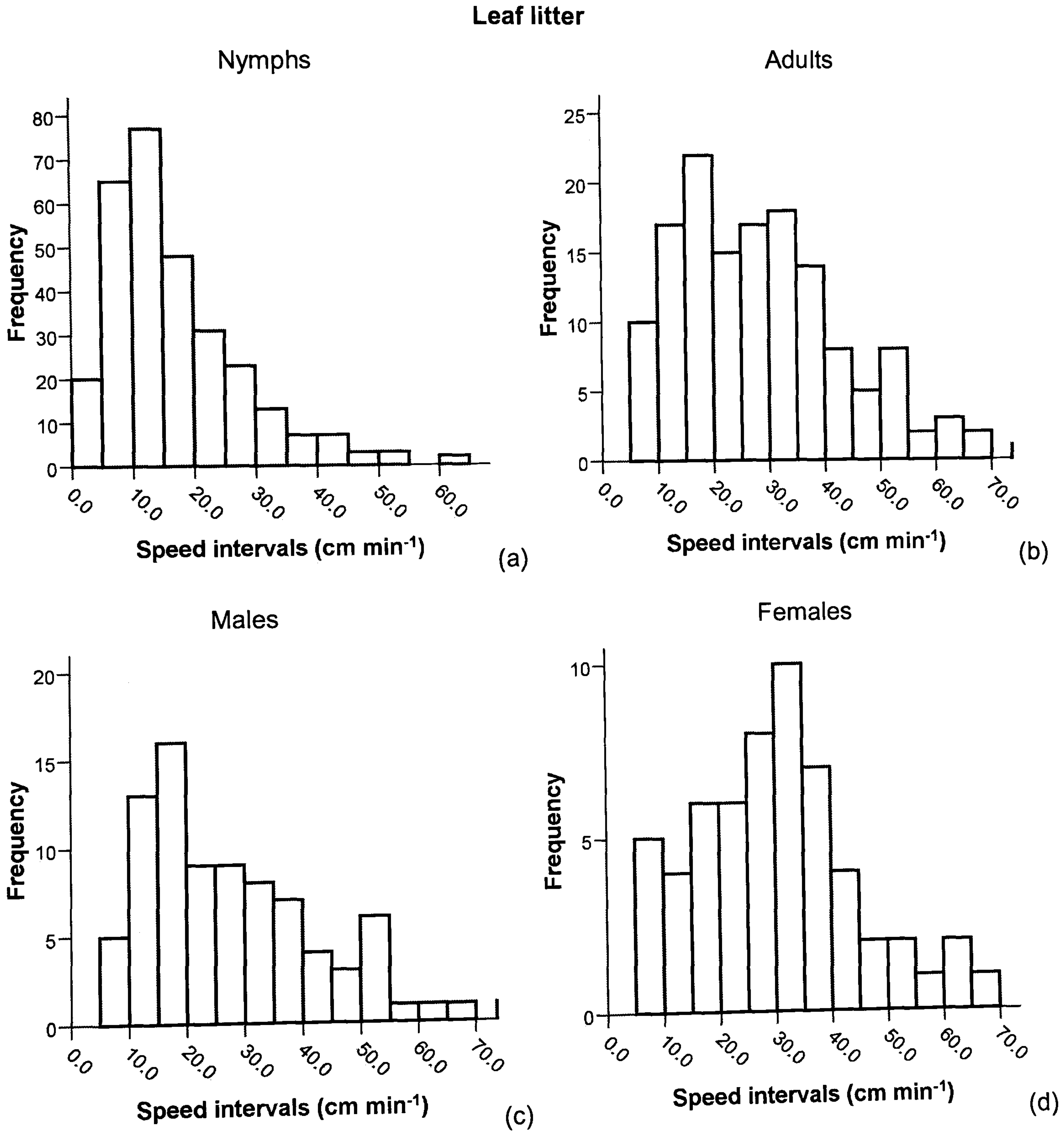
5.3.1 Observations

Both nymphs and adult wood cricket moved primarily by walking. Jumping was only observed when in distress and in order to escape. Over bare soil (Exp. 2), wood cricket performed several fast straight-line movements within the fixed one-minute time step. Stops were used to orientate themselves. Between movements, the insects remained motionless for no more than a few seconds at a time. A few movements of their antennae initiated walking movements. On bare soil, the wood crickets displayed long straight-line movements, seemingly trying to find cover (such as leaf litter) as quickly as possible. The majority of insects moved in a more or less straight line to the edge of the experimental grid (Exp. 2), however some individuals displayed a very haphazard pattern of movement, seemingly being disorientated within the grid. On a surface of leaf litter (Exp. 1 & 2), both wood cricket adults and nymphs exhibited much more 'exploratory' behaviour, displaying haphazard movement through the habitat and often returning to the same location several times. Within leaf litter, they used their antennae to explore the surroundings. After entering the cover of leaf litter, they showed themselves only sporadically in the open, predominantly remaining under dead leaves. Before making another movement, they often remained in one location for several minutes. They repeatedly scanned the surrounding area, their heads emerging from the litter for a few moments often only to withdraw again. If moving, they moved quickly between areas of cover in a straight line. When encountering the edge of contrasting habitat (leaf litter vs. bare soil; see Methods Exp. 2), wood crickets were readily crossing the bare soil habitat, however always after a period of 'scanning' at the edge before making a quick crossing to surrounding leaf litter habitat on the opposite side outside the experimental grid. Through dense herbaceous vegetation or grass habitats (Exp. 3), both nymphs and adults showed only few movements. They appeared 'lost' or disorientated within the dense maze of vegetation predominantly remaining dormant for a prolonged period close to the release site.

5.3.2 Release effect

For nymphs, both in leaf litter habitat and on bare soil, no significant difference was found between the speed displayed in the first step and subsequent steps after release (Mann-Whitney test: $n = 299$, $z = -0.580$, $P = 0.562$; independent samples t-test: $t_{153} = 1.018$, $P = 0.310$, respectively). For adults, speed during the first step on leaf litter did not significantly differ from that during subsequent steps (Mann-Whitney test: n = 142, z = -1.125, P = 0.260). However, over bare soil, the speed displayed during the first step was significantly higher than during the following steps (independent samples t-test: t_{111}= 3.150, P = 0.002), indicating an initial release effect. The first step of each path made on bare soil by adults (both male and female) was therefore omitted from further analyses.

5.3.3 Speed through different habitat



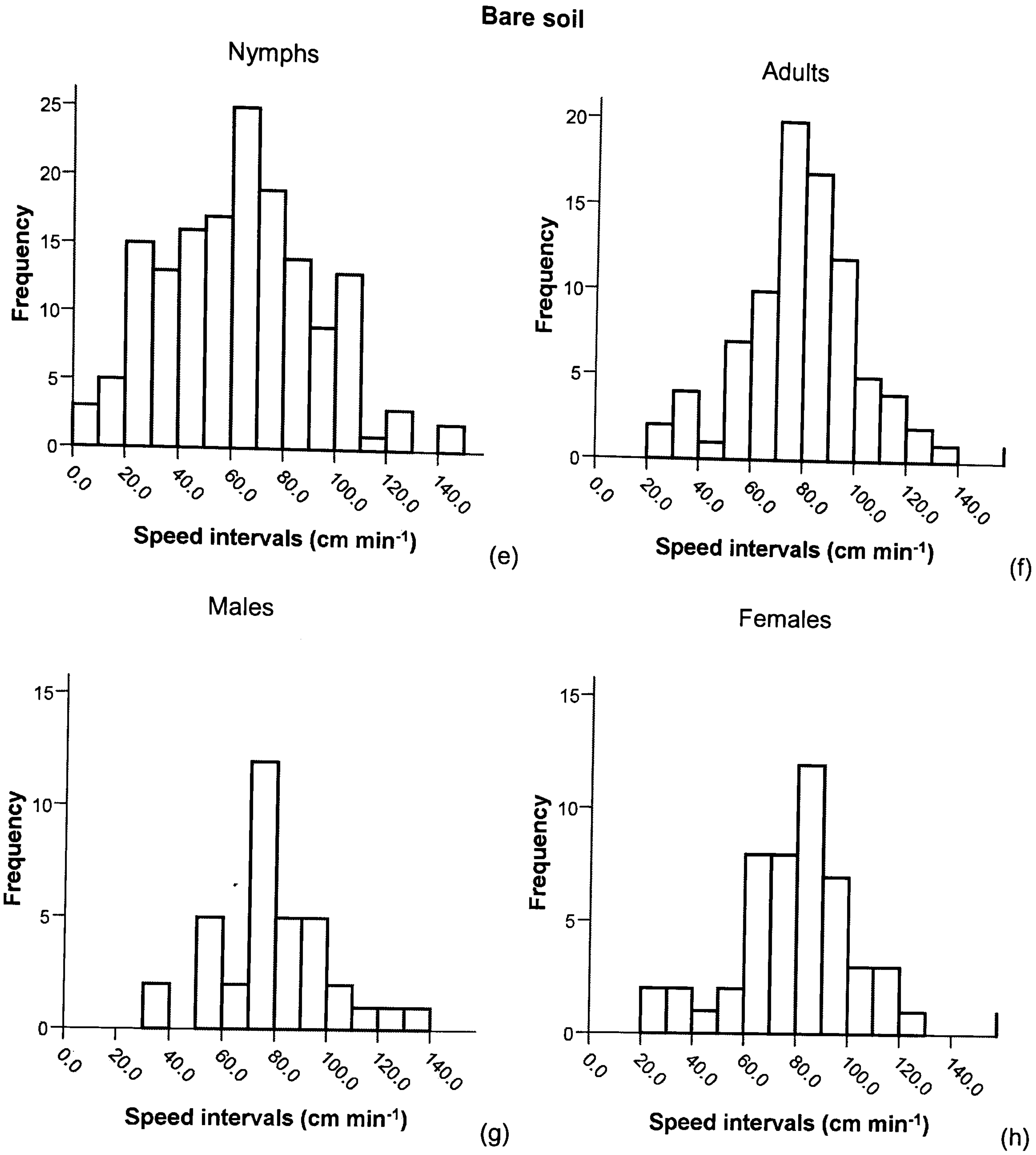


Figure 15: Frequency distribution of speed (cm min $^{-1}$) generated on leaf litter by nymphs (a), all adults together (b), adult males (c) and females (d) and on bare soil habitat for the same groups (e, f, g, h respectively). For figure b & c and f & h one outlier was excluded from the graph for clarity (100.1 cm min $^{-1}$ for fig. b & c and 185.1 cm min $^{-1}$ for fig. f & h). Interval range = 20 (cm min $^{-1}$). $n = n_s$ see Table 11.

For both life-stages, the frequency distribution of speed (cm min $^{-1}$) through leaf litter habitat showed a high amount of variation, but was generally skewed towards relatively low values (Figure 15a – d). Speed over bare soil was similarly highly variable (Figure 15e – h), but was more evenly distributed around the mean value (Table 11), showing a normal distribution. For grass habitat, not enough observations were made to provide a clear frequency distribution.

Table 11: Mean speed (cm min^{-1}) recorded for nymphs and adults generated within different habitat. n_p = number of paths (or individuals). n_s = number of steps taken by all individuals (for all paths) used to calculate the mean speed. Speed = mean step speed (cm min^{-1}). 95% C.I. = 95% confidence interval around the mean speed.

Life-stage	Habitat	n_p	n_s	Speed	95% C.I.	
Nymphs	Bare soil	25	155	62.6	58.0	67.3
	Leaf litter	54	299	16.0	14.7	17.2
	Grass	5	9	4.68	2.81	6.54
Adults	Bare soil	25	86	79.3	73.9	84.7
	Leaf litter	27	142	27.8	25.2	30.4
	Grass	17	41	16.8	12.9	20.6
Males	Bare soil	13	36	78.4	70.9	85.9
	Leaf litter	14	84	27.1	23.5	30.6
	Grass	8	18	15.3	8.89	21.7
Females	Bare soil	12	50	80.0	72.2	87.8
	Leaf litter	13	58	29.0	25.1	32.8
	Grass	9	23	17.9	12.9	23.0

Speed of nymphs on bare soil was higher than their speed through leaf litter (Mann-Whitney test: $n = 454$, $z = -15.31$, $P < 0.001$). No tests were performed for nymphs moving through grass habitat, because of the small number of observations made (n_s = 9; Table 11). Speed of adults was higher on bare soil than in leaf litter and grass habitat (Mann-Whitney test: $n = 228$, $z = -11.57$, $P < 0.001$; $n = 127$, $z = -8.840$, $P < 0.001$, respectively; Table 11). Furthermore, speed within leaf litter was higher than within grass habitat (Mann-Whitney test: $n = 183$, $z = -4.260$, $P < 0.001$; Table 11). No differences were found between adult males and females with respect to speed over bare soil, through leaf litter and through grass habitat (independent samples t-test: $t_{84} = -0.287$, $P = 0.775$; Mann-Whitney test: $n = 142$, $z = -1.163$, $P = 0.245$ and $n = 41$, $z = -0.911$, $P = 0.363$, respectively; Table 11). Between adults and nymphs, adults were significantly faster than nymphs when moving over bare soil and through leaf litter habitat (independent samples t-test: $t_{239} = -4.472$, $P < 0.001$; Mann-Whitney test: $n = 441$, $z = -8.462$, $P < 0.001$, respectively; Table 11).

5.3.4 Time spend in different habitat

Table 12: Paths registered for individuals using only leaf litter habitat or bare soil habitat before exiting the experimental grid (Exp. 2). *n* = number of paths (or individuals) used. Path time = mean time spent (min) within the habitat before exiting the grid. 95% C.I. = 95% confidence interval around the mean path time.

Life-stage		*n*	Path time	95% C.I.	
Nymphs	Leaf litter	7	7.9	4.26	11.5
	Bare soil	7	4.4	3.70	5.16
Adults	Leaf litter	5	8.8	4.12	13.5
	Bare soil	5	2.8	1.18	4.42

For both nymphs and adults released within the 4 x 4 grid (Exp. 2; Figure 14e) observed exiting the grid, the total time spend within leaf litter habitat was significantly higher than time spent on bare soil habitat (Mann-Whitney test: *n* = 14, *z* = -2.030, *P* = 0.042; *n* = 10, *z* = -2.341, *P* = 0.019, respectively; see Table 12). Comparing time spent on bare soil habitat between nymphs and adults, a significantly longer path time was observed for nymphs (Mann-Whitney test: *n* = 12, *z* = -2.040, *P* = 0.041; Table 12), whereas no such difference was recorded in time spend within leaf litter habitat (Mann-Whitney test: *n* = 12, *z* = -0.326, *P* = 0.744; Table 12). No comparison between adult males and females could be made as a result of the small sample size. Finally, the straight-line distance travelled from the release point to the end of each observed path used ranged between 2 and 2.8 m. The results indicated that nymphs and adults covered straight-line distances quicker over bare soil than through leaf litter habitat and over bare soil adults moved faster than nymphs.

5.3.5 Habitat preference

Table 13: Habitat preference (or choice) of wood cricket nymphs and adults (chi-square 'goodness of fit' tests) and Fisher's exact tests for differences in preference between the sexes. Leaf litter/Bare soil or Leaf litter/Grass = number of individuals choosing either habitat.

Life-stage	Leaf litter	Bare soil	χ^2	df	*P*
Nymphs	23	8	7.258	1	0.007
Adults	14	5	4.263	1	0.039
Males	7	3	Fisher's test		1.000
Females	7	2			
	Leaf litter	Grass			
Nymphs	31	2	25.48	1	<0.001
Adults	13	2	8.067	1	0.005
Males	7	2	Fisher's test		0.486
Females	6	0			

Both nymphs and adults preferred moving through leaf litter when offered a choice between leaf litter and bare soil or grass habitat (chi-square test: $P < 0.001 - 0.039$; Table 13) and no difference was observed in habitat preference between adult males and females (Fisher's exact probability test: $P = 0.486 – 1.000$; Table 13).

5.3.6 Walk analyses

5.3.6.1 Turning angle analyses

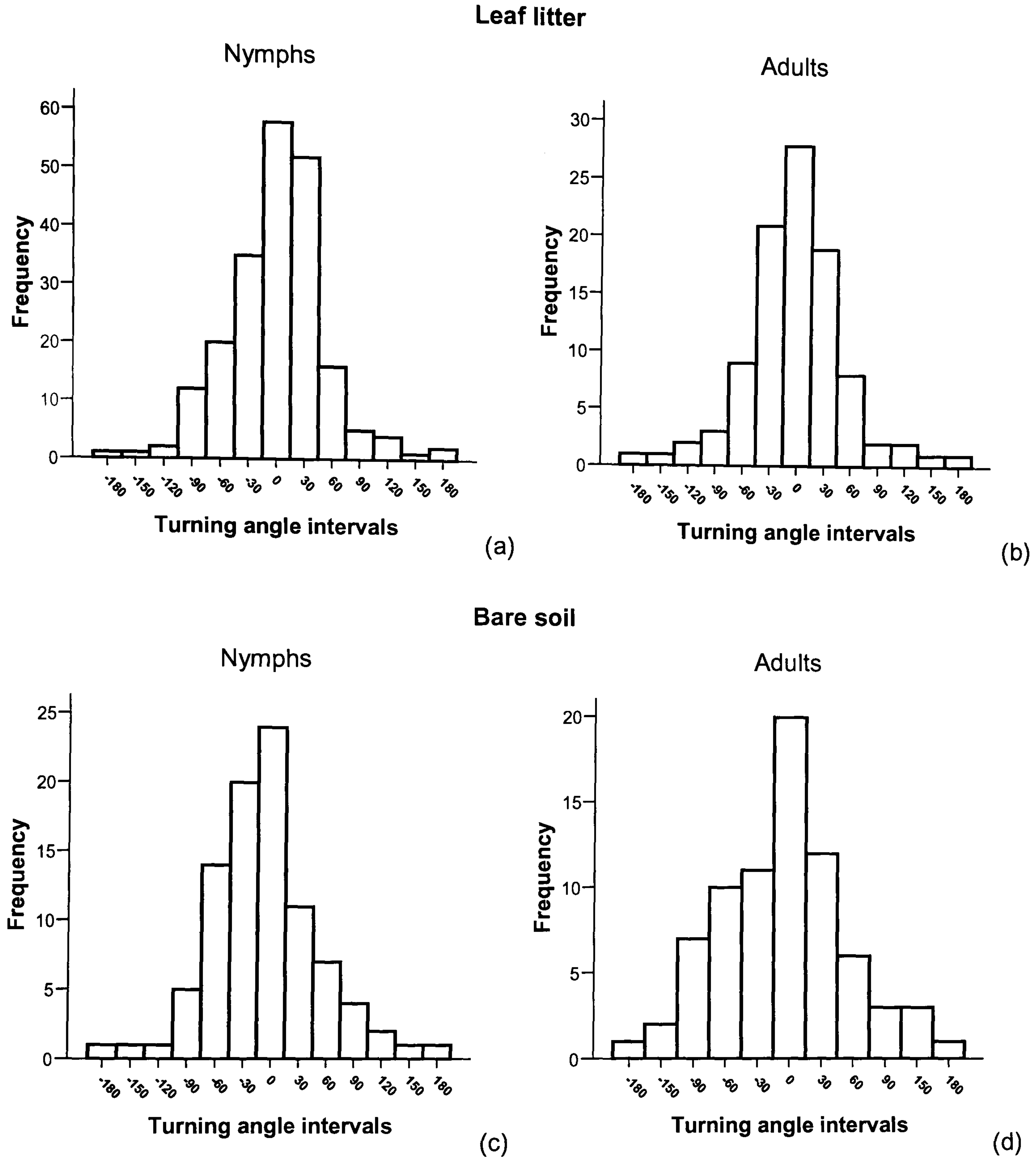


Figure 16: Frequency distribution of turning angles made when moving through leaf litter and over bare soil habitat for nymphs (a, c) and adults (b, d). Values on the x-axis represent the mid-point of the turning angle interval. Interval range = 30°.

The overall frequency distribution for turning angles both for leaf litter habitat and over bare soil show an even distribution around 0° (Figure 16), indicating directional persistence displayed by the species. This violates the primary assumption (i.e. no correlations) made under the URW formulation, however meets the assumption made under the CRW formulation. Therefore, further walk analyses focused on using the CRW formulation.

5.3.6.2 Autocorrelation analyses

Under the URW and CRW formulation, movement duration, speed and turning angles should not be serially correlated, so individual paths and movements should not show an autocorrelation (Turchin, 1998). Where movements were registered within a fixed time interval, movement duration was equal for each registered step, and therefore perfectly autocorrelated. This violates the assumption made under both formulations, however the one-minute time interval was observed to accurately represent individual moves for this species and therefore this violation was considered not to influence further analyses. Out of seven paths, with five or more consecutive steps (see Methods), that were analysed for nymphs, five revealed no significant first or second order autocorrelations for speed (Autocorrelation: $n = 5$, 1st order: df = 1, $P = 0.143 - 0.589$; 2nd order: df = 2, $P = 0.202 - 0.845$). For the two remaining paths, speed was found to be autocorrelated for the first order and partially for the second order (Autocorrelation: $n = 2$, 1st order: df = 1, $P = 0.025 - 0.043$; 2nd order: df = 2, $P = 0.032 - 0.086$). For bare soil, six out of seven paths did not reveal any significant autocorrelations (Autocorrelation: $n = 6$, 1st order: df = 1, $P = 0.195 - 0.946$; 2nd order: df = 2, $P = 0.342 - 0.995$), whereas one did (Autocorrelation:1st order: df = 1, $P = 0.018$; 2nd order: df = 2, $P = 0.037$). For adults, analyses of the individual paths did not reveal any autocorrelations for speed through leaf litter habitat (Autocorrelation: $n = 7$, 1st order: df = 1, $P = 0.093 - 0.982$; 2nd order: df = 2, $P = 0.160 - 0.851$), or over bare soil (Autocorrelation: $n = 7$, 1st order: df = 1, $P = 0.275 - 0.777$; 2nd order: df = 2, $P = 0.099 - 0.553$), indicating no violation of the URW or CRW criteria.

Table 14: Contingency tables for turning angles of subsequent movements (steps) made by nymph and adult wood crickets moving on bare soil and leaf litter with related chi-square tests of association. Turn = turn direction relative to the direction of the previous step. For example: Left – Left (LL) = 7; is number of times an individual took a left turn in succession.

Life-stage	Habitat	Turn	Left	Right	Total
Nymphs	Leaf litter	Left	7	21	28
		Right	22	13	35
		Total	29	34	63
	Bare soil	Left	32	14	46
		Right	9	11	20
		Total	41	25	66
Adults	Leaf litter	Left	12	20	32
		Right	15	17	32
		Total	27	37	64
	Bare soil	Left	20	8	28
		Right	7	19	26
		Total	27	27	54

Life-stage	Habitat	*n*	χ^2	df	*P*
Nymphs	Leaf litter	63	8.974	1	0.003
	Bare soil	66	3.575	1	0.059
Adults	Leaf litter	64	0.577	1	0.448
	Bare soil	54	10.68	1	0.001

Table 15: Results of chi-square 'goodness of fit' tests for displayed movement strategy of nymphs and adults on bare soil and leaf litter based on turning angles grouped in even turns Left/Left + Right/Right (LL + RR) and alternating turns Left/Right + Right/Left (LR + RL) also see Table 14.

Life-stage	Habitat	LL + RR	LR + RL	χ^2	df	*P*
Nymphs	Leaf litter	20	43	8.397	1	0.004
	Bare soil	43	23	6.061	1	0.014
Adults	Leaf litter	29	35	0.563	1	0.453
	Bare soil	39	15	10.67	1	0.001

Table 16: Spearman's rank correlation between speed and turn angle of all individual paths made by nymphs and adults on bare soil and leaf litter.

Life-stage	Habitat	*n*	*r*	*P*
Nymph	Leaf litter	96	0.006	0.955
	Bare soil	91	-0.011	0.920
Adult	Leaf litter	98	0.109	0.287
	Bare soil	76	0.026	0.824

Nymphs moving through leaf litter habitat revealed a first order autocorrelations in their turning angle between consecutive moves (Table 14). Furthermore, alternating direction was favoured over even turns (Table 15, indicating a linear persistence in their movement (i.e. directed movement strategy). Nymphs showed (weak) uncorrelated movement over bare soil habitat (Table 14); however, grouping even and alternating turning pairs together revealed that even turns were favoured over alternating turns (Table 15). Furthermore, even pairs turning left were favoured over even pairs turning right (chi-square test: $\chi^2_1 = 10.26$, $n_{LL} = 32$, $n_{RR} = 11$, $P = 0.001$), indicating a circling movement strategy for nymphs on this substrate. For adults moving through leaf litter, turn pairs were evenly distributed (Table 14 & Table 15), indicating no autocorrelation between consecutive moves. However, over bare soil movements were autocorrelated (Table 14), where (like the nymphs) even turns were favoured over alternating turns (Table 15). Both for nymphs and adults, no significant correlations were recorded between speed and turn angle for movement paths made in leaf litter and over bare soil (Table 16). Together, these results indicated that only adult wood crickets moving on leaf litter met all of the criteria of the CRW formulation.

5.3.6.3 Net squared displacement (R^2_n)

Table 17: Number of paths used for nymphs and adults moving on bare soil and leaf litter, grouped by the number of registered consecutive movement steps (*n* in minutes). Net squared displacement (R^2_n) for both URW and CRW models were calculated using these paths only.

Life-stage	Habitat \ *n*	2	3	4	5	6	7	8	12	Total
Nymphs	Leaf litter	3		4		4		4	3	18
	Bare soil	2	5	6	5	4		3		25
Adults	Leaf litter	1	5	6	7	4		3		26
	Bare soil	8	7	2	5			4		26

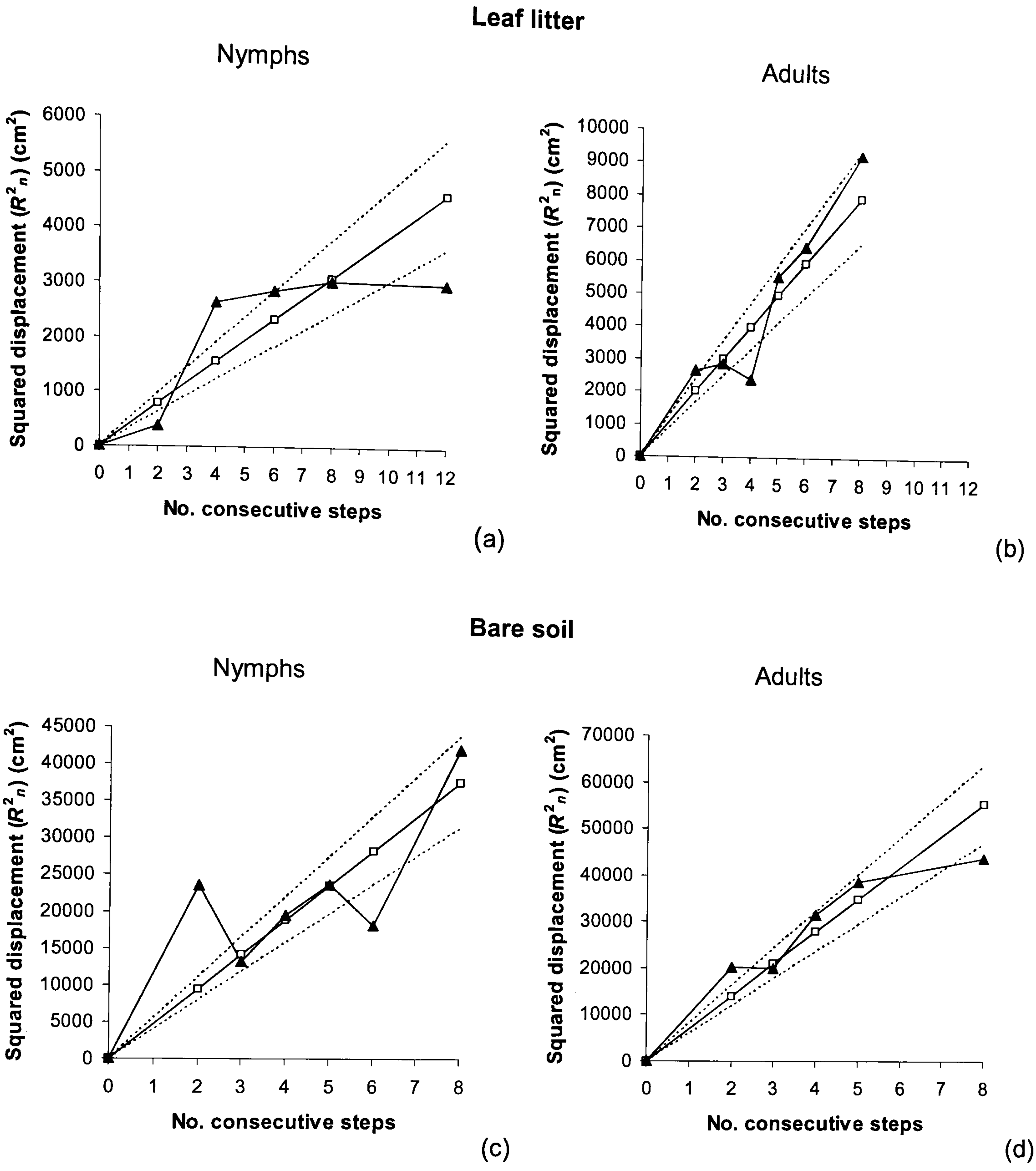


Figure 17: Relationship between the net squared displacement (R^2_n) (cm^2) for CRW, and the number of consecutive movement steps made within leaf litter habitat (a, b) and over bare soil (c, d) for wood cricket nymphs (a, c) and adults (b, d), respectively. —□— = predicted square displacement; —▲— = observed square displacement; ------ indicates 95% confidence interval of the predicted square displacement. In this case net squared displacement (R^2_n) was calculated for each individual path group (see Table 17).

When using the URW model (Equation 3a), linear regression analyses revealed a significantly positive relationship between net squared displacement (R^2_n) and time for adult wood cricket moving through leaf litter and over bare soil (Regression: $R^2 = 0.93$; $F = 40.7$, df = 4, $P = 0.008$; $R^2 = 0.86$; $F = 19.1$, df = 4, $P = 0.022$, respectively), indicating an uncorrelated random walk strategy. The estimated diffusion rate was $D =$

46.9 cm^2 min^{-1} (or 6.85 cm min^{-1}) for adults moving through leaf litter and D = 428 cm^2 min^{-1} (or 20.7 cm min^{-1}) for adults moving over bare soil. For nymphs no linear relationship was found for both leaf litter and bare soil habitat (Regression: $R^2 = 0.52$; $F = 3.25$, df = 4, $P = 0.169$; $R^2 = 0.49$; $F = 3.79$, df = 5, $P = 0.123$, respectively).

Under the CRW model, when observed values exceed the predicted values, more directed movement by the species is suggested, and where the observed values are below the predicted values, more random movement is suggested. Within leaf litter habitat, three out of five observed net squared displacement (R^2_n) values for nymphs did not correspond with the predicted values (Figure 17a; predicted displacement R_n = 5.05 cm min^{-1}). Two values were below the predicted R^2_n and one above. Overall, the observed R^2_n showed a rapid exponential increase, levelling off after four consecutive movement steps (i.e. minutes), reaching an asymptote, indicating that nymphs stayed within a limited area. For adults, however, predicted and observed net squared displacements through leaf litter habitat displayed a good overall fit, with the exception of observed displacements made by individuals making two and four consecutive movement steps, which deviated slightly from the predicted displacement (Figure 17b; predicted R_n = 9.94 cm min^{-1}). Over bare soil predicted and observed R^2_n for nymphs revealed a similar pattern. However, the observed deviations for individuals making two and six consecutive steps were much higher and lower, respectively, than predicted under the CRW model (Figure 17c; predicted R_n = 21.6 cm min^{-1}). Adults moving over bare soil revealed a closer fit between predicted and observed displacements, where only two values deviated slightly from the predicted displacement (Figure 17d; predicted R_n = 26.2 cm min^{-1}). Overall, these results indicate that adult wood cricket moving on/through leaf litter habitat can be modelled using the CRW formulation.

5.4 Discussion

Wood cricket has a two-year life-cycle of which two-thirds is spent as a nymph and one-third as an adult (Gabbutt, 1959; Brown, 1978). To fully understand the dispersal ability of the species it is therefore important to consider both life-stages (Diekotter et al., 2005). This is demonstrated by the results of this study. At the scale of this investigation, the walk strategies found for wood cricket when moving through their preferred natural habitat (i.e. leaf litter) differed considerably between life-stages. When using a fine temporal scale (12 minutes, see Figure 17a), nymphs displayed a movement strategy that changed from a more directed walk to random movements within a fixed area. This indicated that over time nymphs tended to settle down within a certain home range. The behaviour demonstrated by adult wood cricket was strikingly different. For adults moving through leaf litter, the CRW model described the observed movements relatively well, indicating a gradual spread of adults over time. Compared to nymphs, adults therefore showed a higher tendency to disperse. Doak (2000) found similar differences in movement strategy between life-stages for a moth species. Caterpillars of this species were found to move randomly, compared to a more directed movement recorded for the flightless female adult, also indicating a higher tendency of the adult life-stage to disperse (Doak, 2000).

The relationship between net squared displacement (R^2_n) and time that was recorded in this study was found to be close to linear for adult wood cricket moving through leaf litter habitat. In contrast, the relationship was non-linear for nymphs. Furthermore, the estimated diffusion rate (R_n) as calculated from the predicted R^2_n was found to be considerably lower for nymphs than for adults (5.05 and 9.94 cm min^{-1}, for nymphs and adults respectively). This was also reflected in the differences in speed recorded through leaf litter, where nymphs were found to move more slowly than adults. Similar differences were also found between life-stages of a moth (Doak, 2000) and a grasshopper (With, 1994) species, where juveniles showed a lower diffusion rate through their natural habitat than adults. Such differences could be the consequence of the difference in movement strategy, and/or the result of physical constraints (e.g. body size). Together, these results indicate that the largest absolute distance travelled over time is accomplished by the adult stage of wood cricket, and at relatively fine spatio-temporal scales, the adults can be considered more powerful dispersers than nymphs.

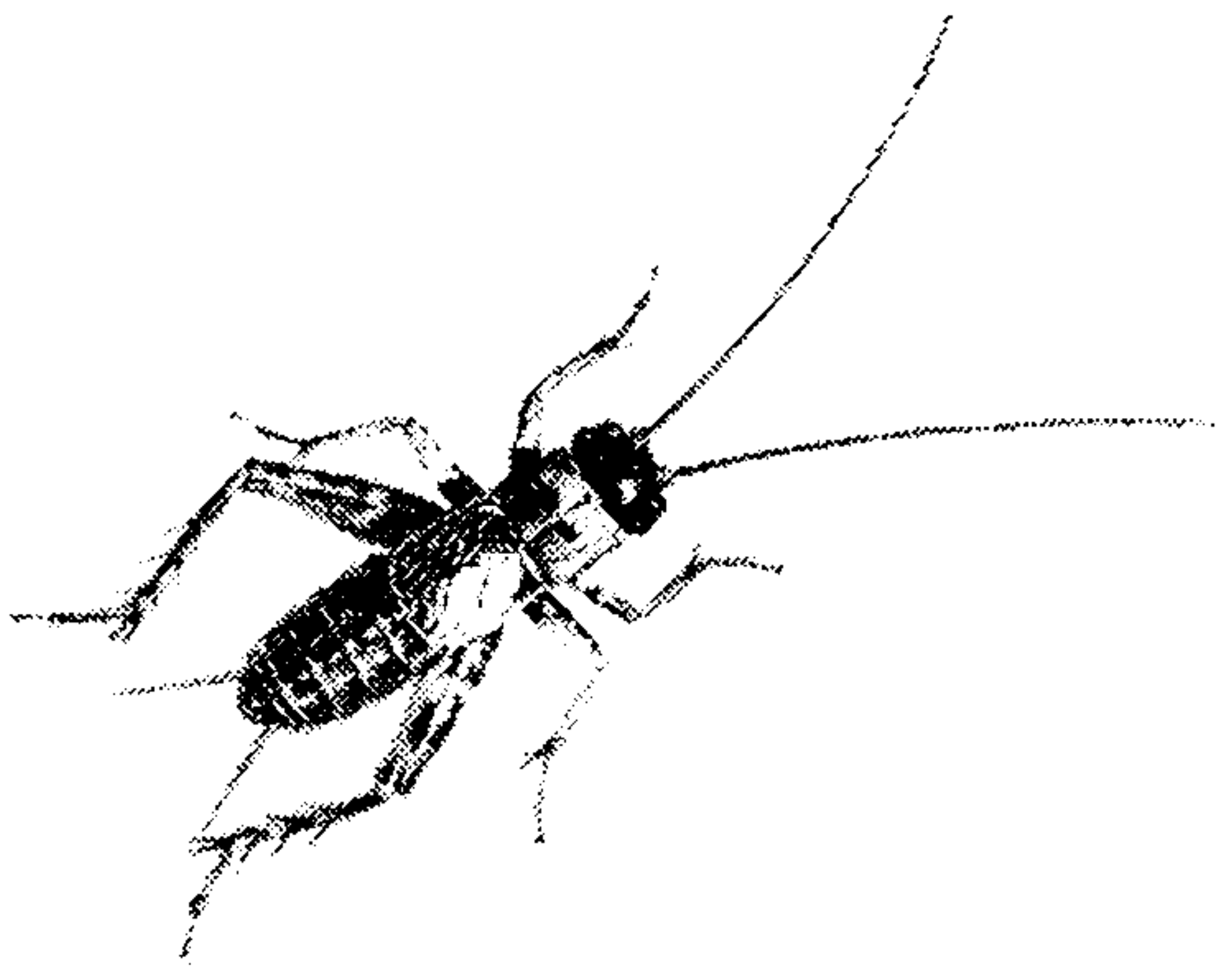
Wood cricket adults and nymphs consistently preferred to move through leaf litter habitat rather than bare soil and grass habitats. This is consistent with the previously documented association of the species with a well-developed leaf litter layer (Richards, 1952; Brown, 1978; Chapter 3). Furthermore, the higher speed recorded and the shorter time spent on bare ground compared to leaf litter habitat (see Table 11 & Table 12) indicated a tendency to locate cover within leaf litter as quickly as possible when moving over bare soil. These differences were also reflected in the movement strategy and estimated diffusion rate for both environments (i.e. leaf litter vs. bare soil). When considering adult movements only, the movement strategy through leaf litter was accurately described as a CRW (i.e. no (auto)correlations; see Figure 17b). This result is similar to that recorded for two woodland-associated carabids, *Pterostichus melanarius* and *Carabus nemoralis,* moving through their preferred woodland habitat environment (Wallin & Ekbom, 1988). However, the movement strategy of adult wood cricket moving over bare soil could not accurately be described as a CRW. Similar results were also observed for *Pterostichus melanarius* and another woodland beetle, *Pterostichus niger*, moving through less favourable habitat (i.e. a cereal field) (Wallin & Ekbom, 1988). Furthermore, these and other carabid species were found to move considerably more rapidly through 'unfavourable' environment than their preferred habitat (Baars, 1979; Wallin & Ekbom, 1988). This difference in the rate of movement was also observed for wood cricket, where the estimated value over bare soil was 2.6 – 4.3 times greater than that recorded through leaf litter habitat. These similar results suggest that woodland invertebrate species tend to use a different movement strategy and move with less velocity within their preferred habitat than when moving through unfavourable environments.

Bare soil can be considered as a ground surface habitat that does not contain the resources that wood cricket need to maintain their fitness (Richards, 1952; Brown, 1978). The pattern of movement revealed by the autocorrelation analyses showed that wood cricket tends to circle when moving over this particular substrate. This pattern was found to be more persistent for nymphs than for adults, possibly related to the greater ability of adults to orientate themselves towards external cues like tree trunks or the preferred leaf litter habitat that surrounded the experimental grid (Campan & Gautier, 1975). A similar circling pattern of movement was observed for Mexican bean beetle when released in a field without its preferred resource/host plant (Turchin, 1998; p 147-150). This pattern was related to their search strategy to find their host plant. This explanation could also be valid for wood cricket when moving over bare soil habitat, where it also displays a similar searching strategy for its primary resource habitat (i.e. leaf litter).

In order to test whether a model describes the movement strategy of a certain species accurately, it is important to analyse the observed movement paths in several different ways with a variety of tests (Turchin, 1998). The individual tests that can be used can be complementary, but do not necessarily confirm each other (Cain, 1990; Turchin, 1998). The analyses of the movement paths that were recorded in the current study clearly showed the validity of this statement. For example, the visual representation of the CRW model showed that the observed net squared displacement (R^2_n) roughly matched the predicted displacement for nymph and adult wood cricket moving over bare soil (see Figure 17c & d), indicating a CRW movement strategy. However, the positive autocorrelation between turning angle indicated that both nymphs and adults moved in random circling patterns. This violated the assumptions made under both the URW and CRW formulations that were tested (see Turchin, 1998), indicating that in these cases neither model describes the movement strategy of wood cricket accurately. Furthermore, for all situations the first assumption under the URW formulation was violated because of an overall bell shaped distribution in turning angle around 0°, indicating the possible CRW strategy. However, overall, the only movement data passing all individual tests for applying the CRW model were that obtained for adult wood cricket moving through leaf litter habitat.

Although relatively few individuals of both nymphs and adults were used for the analyses, this study provides an important insight in how a specialised woodland species moves through its preferred habitat. This is particularly important given the limited knowledge of the dispersal ability of many woodland taxa (Dolman & Fuller, 2003; Bailey, 2007), and the particular lack of information for dispersal of species in different developmental stages and for those that move by walking (Diekotter et al., 2005). Although wood cricket is primarily associated with woodland habitat, analysis of their movement strategy through this type of environment is a first step towards the understanding of the dispersal ability of this species in the wider landscape. For example, connectivity between woodlands for this species is potentially only 'functional' or effective (Crooks & Sanjayan, 2006; Baguette & Van Dyck, 2007) when corridors and/or other landscape features provide suitable habitat (Vos et al., 2002; Crooks & Sanjayan, 2006). If these habitat requirements are met, models describing the movement strategy (e.g. the CRW formulation used in this study) of wood cricket can then provide a means of estimating how rapidly this species can potentially spread though the landscape.

The results of this study indicated the difference in movement strategy through relatively homogeneous habitat environments; however, natural environments are typically highly heterogeneous and may include barriers inhibiting movement and dispersal (e.g. Doak, 2000). Such factors have been found to have a significant impact on the movement strategy and consequently the dispersal ability of a number of invertebrates studied in their natural environment (Johnson et al., 1992; Firle et al., 1998; Doak, 2000; Samu et al., 2003). This highlights the need for further investigations on the dispersal ability of wood cricket and similar woodland species, which should focus on how they move through natural heterogeneous environments at a range of spatio-temporal scales.



6 Factors influencing dispersal of a woodland invertebrate: a case study of wood cricket (*Nemobius sylvestris*)

6.1 Introduction

Dispersal is widely considered to be a key process influencing the survival of species within fragmented landscapes (Hanski & Gilpin, 1997; Kindvall, 1999; Turner et al., 2001; Fahrig, 2003; Diekotter et al., 2005; Ranius, 2006). However, the dispersal ability of many groups of species is poorly known (Dolman & Fuller, 2003; Ranius, 2006). Deriving reliable estimates of dispersal ability in natural environments represents an ongoing challenge, but is highly important in terms of analysing population persistence and spread (Turchin, 1998; Trakhtenbrot et al., 2005). Investigations of specific movement strategies using experiments undertaken at fine spatio-temporal scales can provide valuable initial insights into the dispersal ability of species (Turchin, 1991; Turchin, 1998; Samu et al., 2003). However, dispersal typically takes place over larger scales (Levin, 1992), and therefore the dispersal capability of a species through natural environments needs to be examined at a range of spatio-temporal scales.

A common approach to quantify dispersal or population spread is to fit a dispersal function (i.e. kernel) to observational data obtained in the field (Turchin, 1998). This method has been applied to a large range of animal species (e.g. Turchin & Thoeny, 1993; Rudd & McEvoy, 1996; Smith et al., 2002; Byrom, 2002; Telfer et al., 2003; Truve & Lemel, 2003; Burrows & Tarling, 2004; Smith & Green, 2006). Curves commonly used to describe the spread of species, such as the fraction of a population moving a certain distance, are often based on equations such as the negative-exponential and inverse-power functions (Turchin, 1998). The most characteristic difference between these two curves is the behaviour of the tail, where the exponential function typically predicts a lower frequency of long-distance dispersal events than the power function, which is characterised by a fatter tail (Turchin, 1998). Studies on the dispersal ability of invertebrates have mainly focused on relatively mobile (i.e. flying) species in the context of metapopulation functioning (see Hanski, 1998) within fragmented landscapes. For some species, observations made in the field were best described by a negative-exponential function (Conrad et al., 1999; Baguette et al., 2000; Kuras et al., 2003; Baguette, 2003; Ranius, 2006) whereas for others the inverse-power function was found to provide a better fit to the data obtained (Hill et al., 1996; Roslin, 2000; Baguette et al., 2000; St Pierre & Hendrix, 2003). Identification of species-specific dispersal kernels is a useful indicator of the dispersal ability of a species.

Few studies have examined relatively immobile invertebrate species that predominately move by walking (Diekotter et al., 2005). Compared to flying invertebrates, such species move over finer scales, and can therefore be considered more vulnerable to habitat fragmentation (Tscharntke et al., 2002; Diekotter et al., 2005). Some studies have investigated dispersal of such species by fitting dispersal curves to field data. For example, Chapman et al. (2007) fitted several different dispersal kernels to observational data and tested their performance within a broader model describing interpatch dispersal for a walking leaf beetle. They found support for using the inverse-power function to describe dispersal for this species, where the negative-exponential curve did not adequately fit the data (Chapman et al., 2007). However, the majority of studies that examined walking species did not fit dispersal curves to data collected in the field. These studies predominantly used movement data in other ways, for instance to describe population structure (Clark, 1962; Aikman & Hewitt, 1972; Ritz & Kohler, 2007), or to evaluate the persistence of the species within the wider landscape (Kindvall, 1999; Baur et al., 2005; Diekotter et al., 2005), often using some form of modelling approach. Most of the invertebrate species for which dispersal curves have been obtained were associated with open semi-natural grassland habitats. Studies of woodland-associated species that move by walking are generally lacking in the literature (Chapter 4).

In order to halt and reverse the effects of habitat fragmentation, conservation policy and practice is increasingly focusing on the creation of habitat networks (Hobbs, 2002). Networks are typically created through the development of links or corridors to increase connectivity between individual habitat fragments (Bennett, 1999, 2003; Crooks & Sanjayan, 2006). However, the degree of habitat connectivity within a given landscape is highly dependent on the characteristics of the species being considered (Crooks & Sanjayan, 2006; Baguette & Van Dyck, 2007). Particular features in the landscape can function either as conduits or barriers to different species (Bennett, 1999, 2003; Hobbs, 2002). The role of developing corridors as conduits in terms of facilitating species dispersal is still considered to be controversial (Bennett, 1999, 2003; Crooks & Sanjayan, 2006; Bailey, 2007). For example, a recent review of the functioning of hedgerows as possible corridors between woodlands found insufficient empirical evidence to establish their role in facilitating species dispersal (Davies & Pullin, 2007). Nonetheless, the development of habitat networks utilising corridors has been widely applied in practice (Hobbs, 2002; Bennett, 2004a). In the UK, for example, a large number of initiatives have recently been implemented aiming to reconnect woodland habitat (Peterken, 2000; Peterken, 2002; Humphrey et al., 2003; Humphrey et al., 2005), despite the lack of a firm evidence base regarding the effectiveness of this approach (Bailey, 2007).

To address these issues, research was undertaken on a woodland invertebrate, the wood cricket (*Nemobius sylvestris*) on the Isle of Wight, UK. This island was selected because it was one of eight key areas in the UK that have been the focus of special conservation efforts regarding woodland creation targeted under the 'JIGSAW' scheme (Forestry Commission, 2005), and has since been the focus of ongoing conservation management involving woodland habitat restoration and expansion (Forestry Commission, 2006a; 2007). A number of woodland areas scattered over the island, lying within a predominantly agricultural matrix, were specifically targeted for reforestation activities in order to increase connectivity between woodland fragments (Quine & Watts, 2007). This provided an opportunity to examine the potential impacts of developing a woodland habitat network on the distribution of an individual species. Wood cricket was selected for study as it is a species of national conservation concern (NBN Gateway, 2007) that might be expected to benefit from the development of a woodland habitat network, given its association with woodland and relatively limited dispersal ability (Bailey, 2007).

Wood cricket is a small (~ 1 cm) non-flying cricket species that has a semi-voltine (two-year) life-cycle in the UK (Gabbutt, 1959; Brown, 1978). After overwintering, eggs hatch in June/July and the juveniles (i.e. nymphs) develop throughout the summer and autumn by means of moulting (Gabbutt, 1959; Brown, 1978). Moulting ceases completely in September and nymphs will then overwinter (Gabbutt, 1959; Brown, 1978). The second year, nymphs continue to develop from April onwards until they reach sexual maturity (i.e. become adults) in July/August and are reproductively active through to September/October until they die (Gabbutt, 1959; Brown, 1978). The species is strongly associated with deciduous woodland and is typically found in relatively open areas such as clearings and in edge habitat along woodland tracks, footpaths, railway lines and woodland peripheries (Richards, 1952; Morvan & Campan, 1976; Beugnon, 1980). The insects live on the ground and prefer a well-developed leaf litter layer, which serves as shelter, food and breeding ground (Richards, 1952; Gabbutt, 1959; Brown, 1978; Proess & Baden, 2000). At the landscape scale, the species was found to be associated primarily with relatively large woodland patches that were situated in close proximity to each other (Chapter 2). The main habitat requirements identified for this species at the local scale were presence of a thick leaf litter layer, an open canopy and low cover of ground vegetation (Chapter 3). The species was further found to prefer leaf litter over other substrates for performing their daily activities and adult wood crickets were found to perform more directed movement through this substrate than nymphs (Chapter 5).

No detailed study has been undertaken previously of the dispersal ability of wood cricket in natural environments. Therefore the aims of this study were: (1) to model empirically the dispersal of wood cricket nymphs and adults (males and females); and to determine (2) to what extent wood cricket nymphs and adults (males and females) move along corridors and through sub-optimal habitat; (3) what factors influence their choice of habitat; (4) whether wood cricket nymphs and adults (males and females) can cross a water barrier; and (5) to what extent adult wood cricket are able to orientate themselves in the landscape. From earlier studies on wood cricket and preliminary field observations it was further hypothesised that: (a) wood cricket males show higher dispersal ability than females; (b) more open habitat would be preferred over more closed vegetation; (c) neither nymphs nor adults would be able to cross a water barrier; and (d) adult wood cricket would show a positive orientation towards distinct terrestrial features.

6.2 Methods

Between the 5th and 29th of June and the 30th of July and 7th of September 2007 a series of experiments were conducted using wood cricket (*Nemobius sylvestris*) nymphs (6-7th instar) and adult males and females respectively. The experiments were carried out in the Briddlesford area (50° 42' 41.00" N, 1° 13' 30.50" W) situated on the Isle of Wight, which is owned by 'The People's Trust for Endangered Species' (PTES), a non-governmental conservation organisation (Figure 18). The majority of woodlands in this area are classified as 'ancient woodland' (Spencer & Kirby, 1992) and are dominated by native deciduous tree species, particularly oak (*Quercus spp.*). Since 2005 extensive new plantings of native tree species have taken place in this area funded by the 'JIGSAW' scheme (Forestry Commission, 2005) in order to increase connectivity between the individual woodland fragments.

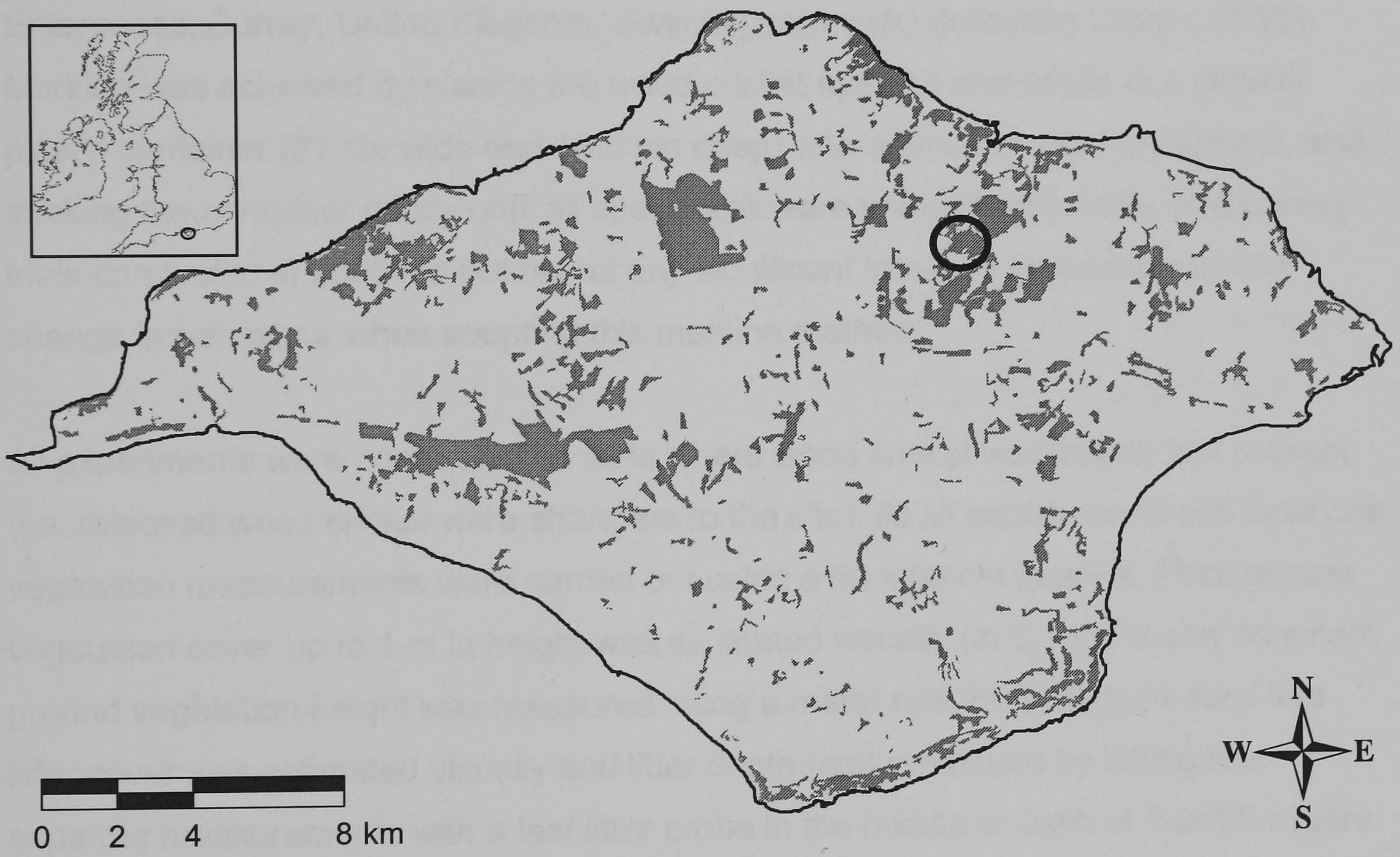


Figure 18: All the woodland fragments on the Isle of Wight (grey). Briddlesford area is highlighted. Derived from digital maps based on the National Inventory of Woodland and Trees (NIWT) (Smith & Gilbert, 2003).

A series of experiments are presented here examining wood cricket dispersal strategy and capacity. Experiment 1 focused on examining dispersal strategy of released wood crickets under semi-natural conditions in a semi-controlled environment within woodland habitat. Experiment 2 & 3 focused on dispersal capacity of released wood crickets along linear features under natural uncontrolled conditions outside woodland, and several surveys were carried out to monitor their natural spread. Experiment 4 focused on the ability of wood cricket to cross a watercourse barrier between two habitat locations, and Experiment 5 – 8 examined the ability of wood cricket to orientate themselves towards different features within the landscape.

For the experiments, both the nymphs and adults were caught over the course of three days at three different locations within a large wooded area that was thinned in the year 2003/2004. To catch the wood crickets, a 55 x 55 x 30 cm square wooden enclosure (to confine them) and a custom designed pooter were used. For the duration of the experiments, the nymphs and adults were kept in a square plastic box (35 x 25 x 19 cm) with ample supplies of food (bread, various fungi and oak leaf litter) available. To increase the detection probability, before most experiments the wood crickets were marked by dusting them with non-toxic fluorescent pigment (UV Gear, Mark SG Enterprises, Surrey, United Kingdom, www.uvgear.co.uk) (following Cronin, 2003). Marking was achieved by placing the wood cricket nymphs and adults in a circular plastic container (21 cm wide and 10.5 cm deep) with a small amount of pigment, and shaking the container gently until all specimens were marked sufficiently. Preliminary trials conducted in 2006 did not reveal any significant increase in mortality and/or change in behaviour when adopting this marking method.

All experiments were conducted on sites where wood cricket was initially not present (i.e. released wood cricket were strangers to the site). At all experimental site locations, vegetation measurements were carried out using a 50 x 50 cm quadrat. First, ground vegetation cover up to 1 m in height was estimated visually (in %) and mean dominant ground vegetation height was measured using a meter rule (cm). Second, total leaf litter cover was estimated visually and litter depth (cm) measured by taking four separate measurements with a leaf litter probe in the middle of each of four 25 square centimetre sections within the quadrat. Finally, from the centre of the quadrat, canopy closure was measured using a convex spherical densiometer (Forest Densiometers, Bartlesville, US). This involved taking separate readings for the four main compass directions (N, E, S, W), which were averaged for each location. During all experiments mean average daytime temperature at the ground surface did not decline below 15 °C, as indicated by meteorological records.

6.2.1 Dispersal experiments

6.2.2 Experiment 1

Five circular enclosures were created on a forest track within an oak-dominated stand. The enclosures ranged in size from 1 to 5 m radius (see Appendix II). The enclosures were constructed from 50 cm high translucent sheet plastic (thickness 0.25 mm). This was inserted into the ground to a depth of 5 cm and supported by a framework of bamboo canes. The interior habitat of the individual enclosures was homogenised by clearing the ground surface of most of its herbaceous vegetation, resulting in a mean ground vegetation cover of 10% and a mean vegetation height of 10 cm. Furthermore, to create a homogenous leaf litter layer, litter was added resulting in a mean litter cover of 99%, 2.5 cm deep. This particular ground habitat was found to be the preferred substrate where wood cricket develops and most frequently occurs (Chapter 3 & 5). The mean overhead canopy closure for all sites was 90%.

At the centre of each enclosure, 50 wood cricket nymphs were released simultaneously at noon on the 11th of June (see Appendix II). Inside the enclosures, circular pitfall traps (constructed from translucent plastic drinking cups, 7 cm wide and 7.5 cm deep) were placed directly against the periphery of the plastic enclosure boundary, spaced 63 cm apart (see Appendix II). The pitfall traps were filled with an odourless water-detergent solution (50 : 1) to prevent wood cricket nymphs from escaping after capture. To increase the detection probability, wood crickets were marked by dusting them with orange non-toxic fluorescent pigment. After marking, a small amount of leaf litter was added to the marking container. The marked specimens were then released 2 h after marking by gently tipping the entire contents of the container at the centre of the individual enclosures. After the initial release, continuous observations of the released population within the smallest enclosure (1 m radius) took place for the duration of 1 h. Following this period, all the enclosures were surveyed five times for five successive hours by examining all of the pitfall traps along the enclosure perimeter, together with the surrounding (leaf litter) habitat, for presence of marked wood cricket nymphs. During the following four days, all enclosures were surveyed at 24 h intervals. For each survey, the number and location of wood cricket nymphs were recorded, either in the pitfall traps or against the plastic periphery. During the first 48 h the weather was dry with sunny spells with a mean temperature at ground level of 18 °C during the surveys. During the second 48 h the weather varied between heavy showers and sunny spells, with a mean temperature of 15 °C.

A second release experiment was conducted for adult wood cricket at the same location. For this experiment, the 2 – 5 m enclosures and an additional enclosure with a radius of 7 m were used without operating the pitfall traps, because these were observed not to work in the first release experiment (see previous paragraph). On the 31st of July, 20 marked adult males (M) and 20 females (F) were released at noon at the centre of each enclosure. After the initial release, wood cricket within the smallest enclosure (2 m radius) were continuously observed for 1 h. Subsequently all enclosures were surveyed at a 1 h interval for five successive hours. The following five days each enclosure was surveyed daily at regular intervals of 24 h. Within each enclosure the number, sex, location and distance from the enclosure periphery was recorded for each wood cricket observed. The survey performed after 48 h took place on a day (2nd of August) that was predominantly overcast with short periods of rain. On this day the mean temperature at ground level was 14 °C during the survey. For all the other days the weather was bright and sunny, with a mean temperature of 19 °C during the surveys.

6.2.3 Analyses

For the nymphs, to test for habitat preference within the enclosures, chi-square 'goodness of fit' tests were performed. The first test was used to test for preference in canopy closure (CC) between the south-west facing side of the track (CC 91%) and the north-east facing side (CC 94%). The sample included data collected within the 2 – 5 m enclosures, dividing the total number of observed wood cricket nymphs into observations made on the south-west facing side of the track vs. observations made on the north-east facing side. The 1 m enclosure was excluded, because there was no contrast in habitat within this enclosure. The second test was based on differences in litter and soil compaction, where less compacted soils were present outside the boundaries of the forest track compared to within. Here the test sample included the 3 – 5 m enclosures, dividing the total number of nymphs observed into observations made within the forest track habitat vs. the forest floor habitat. The 1 and 2 m enclosures were excluded, because there was no contrast in habitat within the enclosures in this respect. To test the hypothesis that wood cricket nymphs would be caught in the pitfall traps after reaching the enclosure periphery, a chi-square 'goodness of fit' test was used. For this test, the number of wood cricket nymphs caught in the pitfall traps was compared with the numbers observed against the enclosure periphery. Finally, for each enclosure the average proportion of the population (50 individuals for each enclosure) found at the periphery (corrected for the number caught in the pitfall traps) was calculated and plotted against distance from the point of release (i.e. the enclosure radius). For this data, the inverse-power function and the negative-exponential function were fitted as regression curves. The 1 m enclosure data were excluded from this analysis because the sampling strategy caused too much disturbance, leading to an underestimation of the number of observations at the circumference.

For the adult population, to test for habitat preference within the enclosures, chi-square 'goodness of fit' tests were performed (as for nymphs; see above). The first test sample included data collected within the 2 – 7 m enclosures, dividing the total number of adult wood cricket observed into observations made on the south-west facing side of the track (CC 91%) vs. observations made on the north-east facing side (CC 94%). The second test sample included the 3 – 7 m enclosures, dividing the total number observed into observations made within the forest track habitat vs. the forest floor habitat. To test for differences in the number of males vs. females arriving at the enclosure periphery over time (i.e. to test what sex is the primary disperser), chi-square 'goodness of fit' tests were performed. For this test the number of males and females observed in the 3 – 7 m enclosures were included. Data collected in the 2 m enclosure were excluded, because both males and females were observed reaching the periphery at the same time in similar numbers during the first 5 h of continuous observations, indicating no difference in dispersal strategy within this habitat home range (12.6 m^2). To test for differences between female/male couples vs. individual females observed at the enclosure periphery over time, chi-square 'goodness of fit' tests were performed. This test was performed to test the hypothesis whether males attract females. For this test, data collected within the 2 – 7 m enclosures was used.

To test for differences between nymphs and adults that were observed at the enclosure peripheries, chi-square 'goodness of fit' tests were performed. For these analyses only data collected in the enclosures that were used during both experiments were included, being the 2 – 5 m enclosures. Differences were tested (1) between the total number of nymphs and adults found dispersing over time, and (2) if there were differences between the life-stages with respect to the absolute distances they were able cross within 96 hours. The sum of all observations per day for all enclosures together and the sum of all days together for each individual enclosure was used for these analyses. The observational data were corrected for the differences in sample size by first calculating the individual proportion for nymphs and adults separately and multiplying these by 100 to obtain standardised comparable values for both groups. For example, the total number of nymphs and adults released in the four enclosures used in these analyses was 200 and 160 respectively. If 30 observations were made for nymphs and 25 for the adults, the corrected numbers that were used were 30/200 x 100 and 25/160 x 100 for nymphs and adults respectively.

Furthermore, for each enclosure the mean proportion found at the periphery of the male ($n_M = 20$), female ($n_F = 20$) and total ($n = 40$) wood cricket population was calculated and plotted against distance (i.e. the enclosure radius). These proportions were calculated for the first 96 hours, the total 120 hours and for the last 96 hours (i.e. excluding data collected in the first 24 hours). For these data, the inverse-power function and the negative-exponential function were fitted as regression curves. Furthermore, for both nymphs and adults, straight-line movement rates (m day $^{-1}$) were calculated for the number of wood cricket that arrived at each of the enclosure peripheries over the first and second 24 h after the initial release. For these individuals, the straight-line distance travelled over time was equal to the radius of the enclosure it was observed in. For calculating these rates, for nymphs the data collected within the 2 – 5 m enclosures and for adults data from the 3 – 7 m enclosures were used. Rates were calculated with the pooled data from all enclosures together. Finally, differences between the regression curves (i.e. inverse-power) for nymphs vs. adults and males vs. females were tested with a paired-samples t-test. All statistical analyses were performed using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA).

6.2.4 Experiment 2

On the 26th of June, four groups of 50 wood cricket nymphs (marked with pigment) were released (for release method see Experiment 1) at four locations (Site 1 – 4) (see Figure 19) and surveyed for three consecutive days. This three day release experiment was performed at four locations, representing a junction of linear (wooded) landscape features connected to a main body of woodland. For each individual location, the survey time was standardised for all survey days (30 – 40 min). The survey procedure involved walking slowly through the different habitat features in a zigzag manner. Where a marked specimen was observed, the location was marked using a bamboo cane. After the three-day survey period, straight-line distances from the point of release to the individual canes were measured with a tape measure. All surveys were undertaken under dry weather conditions; however, the weather during this period was a mix of heavy rain, which principally occurred in the evenings and mornings, and dry weather with frequent sunny spells during the day. For the adults a similar release experiment was performed on the 3rd of August on 'Site 1 & 2' and an additional 5th site (Figure 19) using 50 adult wood crickets (25 males and 25 females, marked with pigment). These sites were surveyed for three consecutive days around noon and in the evening, 24/30, 48/54 and 72/78 hours after the initial release.

6.2.5 Experiment 3

For the adults a second mass release was initiated at four new sites (6 – 9) (Figure 19) representing locations where different linear (wooded) habitat features were running out of the main woodland area. On the 5th of August, a preliminary survey was carried out in order to establish that no stridulating males were present along the selected features. Following the initial survey, 40 adult male and 20 female (non-marked) wood crickets were released on the 6th of August at these selected locations (following the release method as described in Experiment 1). Between the 25th and 26th of August, twenty days after the initial release, these locations were re-surveyed four times. The survey was performed by walking a distance of 60 m along the edge of each linear feature. Wood crickets presence was established by sound recognition of stridulating males, following the survey method of Proess and Baden (2000). Male wood cricket produce a very distinctive sound by stridulation, which is not readily confused with any other species (Proess & Baden, 2000). After every 5 m interval, a 5 min pause was taken in order to determine presence or absence by listening for stridulation. Locations where wood cricket was heard were marked with bamboo canes. For all marked locations, straight-line distances from the release point were recorded. Standard habitat measurements were made along the linear features and at all marked presence locations. The prevailing weather during all survey days was bright and sunny with a mean daytime temperature of 23 °C.

6.2.6 Analyses

For the nymph releases (Experiment 2) the following analyses were performed. For each site, after testing for normality in the data (Shapiro-Wilk test), differences in distances recorded between days were analysed using Mann-Whitney tests. For 'Site 1 & 2', chi-square 'goodness of fit' tests were used to test for habitat preference based on the choice of edge and for 'Site 3 & 4' chi-square 'goodness of fit' tests were used to test for habitat preference based on the individual habitat measurements made at each location (Figure 19). To examine the effect of overhead canopy cover, Mann-Whitney tests were used to test for differences in canopy closure of sites where wood cricket was present between survey days. Finally, for 'Site 1 & 2', Mann-Whitney tests were used to test for differences in canopy closure for the locations where wood cricket was present and where they were not found. For this analysis, habitat measurements for presence locations at each edge were compared with habitat measurements at the opposing edge at the same distance from the release site. For adults, no statistical analyses could be performed owing to low numbers of relocated insects. All statistical analyses were performed using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA).

6.2.7 Surveys

A survey was conducted to examine the advance of wood cricket over several years focussing on an east-facing mature woodland edge located at 'Site 1' (Figure 19). This site was first surveyed on the 21st of July 2005 (mean daytime temperature of 25 °C), by slowly walking along the woodland edge, and by stopping at regular intervals to listen for stridulating males. Locations where wood cricket was present along the woodland edge were recorded with a hand-held GPS device (Garmin III GPS V, Garmin Europe) Ltd, Romsey, UK). In 2006, this site was re-surveyed on the 28th of July (24 °C) after re-fencing had taken place along the woodland edge in early June of that year. Finally, this location was surveyed twice on the 5th (24 °C) and 25th (23 °C) in August 2007. For each year, wood cricket presence, abundance and advance along the edge were recorded. Straight-line distances from the main woodland body to the furthest recorded presence site along the woodland edge were measured within ArcGIS (version 9.1, ESRI, Redlands, California, USA).

On the 5th and 25-26th of August 2007, fields adjacent to the new plantings (Site 10) and 'Site 2 & 4' were surveyed for the presence of stridulating wood cricket males (Figure 19). Positions where wood cricket was present were marked using bamboo canes. For all locations straight-line distances to the nearest woodland edge and to the edge of the nearest new planting were measured with a measuring tape. Furthermore, compass readings were performed to establish the exact locations on an OS map (scale 1 : 17). Additionally for 'Site 10', straight-line distances to the nearest permanent wood cricket location within the main woodland body (identified during a previous field survey in 2005) were measured using the locations recorded on the OS map.

6.2.8 Release sites

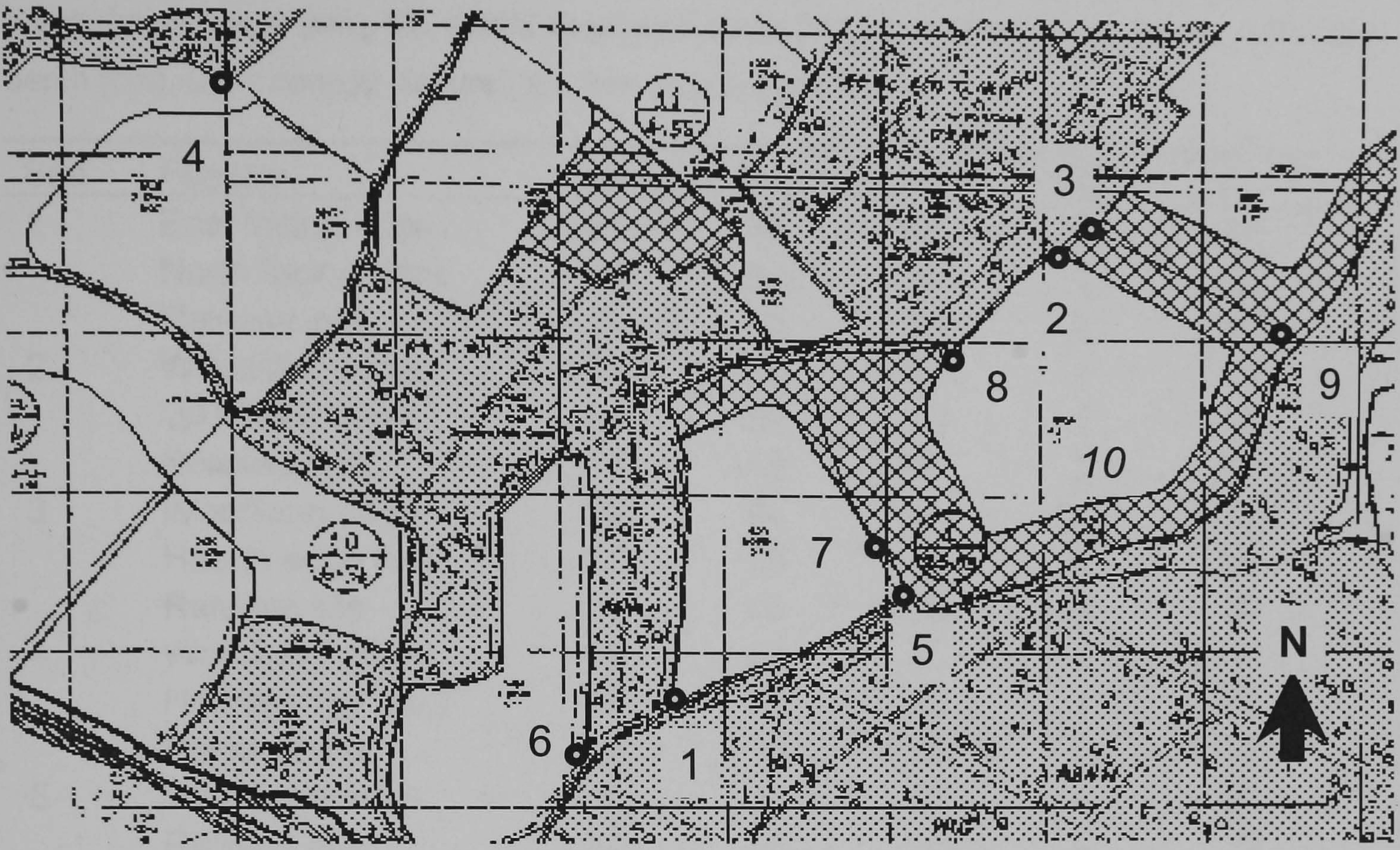


Figure 19: Release locations (**o**) for Site 1 – 9. Site *10* represents a survey site only. White areas are grassland, light grey (dotted) areas are broadleaved woodland and checkered areas are new 'JIGSAW' plantings dominated by tall semi-natural herbaceous vegetation (see also Appendix II). Square blocks represent 100 x 100 m. Map courtesy of PTES.

Table 18: Vegetation characteristics for the habitat edges (mean values) and release sites. VH = vegetation height (cm), VC = total vegetation cover (%), LC = total litter cover (%), LD = litter depth (cm), CC = canopy closure (%). See also Appendix II.

Site	Feature	VH	VC	LC	LD	CC
1	East facing edge	47	36	64	2	82
	North facing edge	44	23	58	1	88
	Release site	5	10	30	3	89
2	Woodland edge	22	26	80	2	99
	'JIGSAW' edge	24	65	15	1	23
	Release site	15	18	85	2	99
3	Woodland edge	29	94	1	0.5	19
	Hedge edge (cut)	13	93	9	1	39
	Release site	10	45	75	3	30
4	Woodland edge	45	64	4	1	40
	Hedge edge (cut)	12	34	38	1	72
	Release site	15	15	75	2	92
5	Woodland edge	45	35	60	2	86
	Release site	10	15	80	2	93
6	Woodland edge	22	97	16	1	78
	Release site	10	80	50	1	94
7	Hedge edge	24	100	24	1	63
	Release site	15	100	10	1	83
8	Woodland edge	11	60	10	0.5	65
	'JIGSAW' edge	60	100	0	0	0
	Release site	10	100	0	0	38
9	Hedge edge	53	100	0	0	9
	Release site	20	95	5	0.5	47
10	Grassland	20	100	0	0	0

Site 1 had a north-eastern orientation representing a mature woodland strip (edge facing East) located adjacent to a main woodland area with its edge facing North. The adjacent field was used as a hay field (with autumn grazing) dominated by nettle (*Urtica dioica*) at the periphery (50-80 cm high). Both stand edges had a mixture of mature broadleaved trees dominated by oak.

Site 2 had a southern orientation with one mature woodland edge running in a south-western direction and one edge running along a recent new planting in a south-eastern direction. The adjacent field was used for grazing cattle and was dominated by short grass (10-15 cm high). The woodland edge had a mixture of mature broadleaved trees dominated by oak, where the 'JIGSAW' edge was dominated by low shrub and tall grass (25-50 cm high).

Site 3 had a southern orientation with a mature woodland edge running in a south-western direction and another edge running uphill along a hedge in a south-eastern direction. The woodland edge had a mixture of mature broadleaved trees dominated by oak with bramble (*Rubus spp.*) spreading from the woodland edge. The hedge was composed of a mixture of native shrub species such as hawthorn (*Crataegus monogyna*), blackthorn (*Prunus spinosa*), hazel (*Corylus avellana*) and bramble. This site was located within the boundaries of a new planting, dominated by tall grass/herbs and low shrubs (25-50 cm high). To provide contrast in edge vegetation, a 1.5 m x 20 m long strip of vegetation was cut along the hedge edge. Furthermore, at the release site situated within the cut strip, leaf litter was added to a 1 m x 0.5 m wide patch bordering the hedge.

Site 4 displayed a southern orientation with a mature woodland edge running in a western direction and an edge running along a hedge with oak standards in an eastern direction. The woodland edge was composed of a mixture of mature broadleaved trees dominated by oak with bramble spreading from the woodland edge. The hedge was composed of a mixture of native shrub species with oak standards and bramble spreading from the edge. This site was located within the boundaries of a new planting, dominated by tall grass and herbs (25-50 cm high). To provide a contrast in edge vegetation, a 1.5 m x 20 m long strip of vegetation was cut along the hedge edge, which included the location of the release site.

Site 5 was situated along a north-facing mature woodland edge similar to *Site 1*.

Site 6 had a western orientation with a mature woodland edge running in a northern direction and a mature hedge edge running in a southern direction. The adjacent field was used as a hay field (with autumn grazing) dominated by a grass and herb vegetation at the periphery. The woodland edge was composed of a mixture of mature broadleaved trees dominated by oak and the hedge was composed of a mixture of native hedge species. In the preliminary survey of this site, wood cricket was found to be present along the hedge edge, but not along the woodland edge.

Site 7 had a western orientation with an edge comprised of a hedge with standards (oak dominated) running in a northern direction. The hedge was composed of a mixture of native shrub species with occasional mature deciduous trees. The adjacent field was used as a hay field (with autumn grazing) dominated by a grass and herb vegetation at the periphery.

Site 8 had a southern orientation with a mature woodland edge running in a north-eastern direction and another edge running along a recent new planting in a southern direction. The adjacent field was used for grazing cattle and was dominated by short grass. The woodland edge was composed of a mixture of mature broadleaved trees dominated by oak, whereas low shrubs and tall grass species dominated the edge of the new planting. In the preliminary survey of this site, wood cricket was found to be present at several locations within the grazed field (10-15 cm sward height).

Site 9 had a south-western orientation with a mature hedge running in a north-western direction. The hedge was composed of a mixture of native shrub species and was also situated within a new planting, dominated by tall grass/herbs and low shrubs (50 – 70 cm height).

Site 10 was characterised by sites where wood cricket was found to be present naturally, prior to the experiments. These sites were located either on the edge of a new planting dominated by tall grass/herbs (35-70 cm height) or within a grazed field dominated by grass (10-20 cm height) bordering a north-facing mature woodland edge dominated by oak. For locations of the sites and further details on the vegetation characteristics, see Figure 19, Table 18 and Appendix II.

6.2.9 Experiment 4

To test whether wood cricket nymphs were able to cross a watercourse, an island was created in an artificially created pool on a woodland track within an oak dominated stand (canopy closure 90%). The island was 75 cm long and 30 cm wide. Around the island, a 25 cm wide and 2 cm deep watercourse was created. On the island, a 1 cm thick mixture of coarse litter mulch was added. On the 21st of June at noon, 15 wood cricket nymphs marked with orange dust were released two hours after the initial marking. The release was achieved by gently inverting a circular transparent plastic container (9 cm wide, 10 cm deep) at the centre of the island and releasing the specimens after 15 seconds from within the container. Activities of the nymphs were then continuously observed for an hour. Subsequent observations were made three and four hours after the initial release on the same day. The number of nymphs escaping the island was recorded including observations on direction of the escape attempts. During the experiment, the weather was dry with sunny spells with a mean daytime temperature of 17 °C at ground level.

For adult wood crickets, a similar experiment was performed at the same location. In this case, the island was 85 cm long and 55 cm wide with a 35 cm wide and 2 cm deep watercourse surrounding it (see Appendix II). On the 2nd of August, 10 marked adult males and 10 females were released at the centre of the island as described above. Activities of the adults were continuously observed for the first two hours after release. Time of escape attempt, direction and sex were recorded. Two more surveys were performed, 24 and 48 hours after release. For these surveys, the number and sex of wood cricket remaining on the island were recorded. During this experiment, the weather was predominantly dry and sunny with a mean daytime temperature of 18 °C at ground level. For both life-stages, chi-square 'goodness of fit' tests were performed to test for crossing capability and a Fisher's exact probability test was performed to test for differences in crossing capability between the sexes, both using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA).

6.2.10 Orientation experiments

To test what factors influence the orientation capability of wood cricket, an experiment was conducted following the method of Beugnon (1979) and Mieulet (1980). For this experiment, a cardboard platform (50 cm in diameter) was used. For all releases, the release platform was orientated horizontally by using a convex spirit level. Single wood cricket were released using a circular 3.5 x 7 cm transparent plastic container. The individual wood crickets were released by inverting the container at the centre of the platform (see Appendix II). After 15 seconds, the container was removed and the movements of the wood cricket were recorded from a position 1.5 m away, maintaining a low profile. At each location a minimum of 12 wood crickets (Male : Female, 1 : 1) were released, singly. For each released individual: sex, movement paths, exit location relative to an edge (i.e. woodland or grassland edge), and the direction of the sun relative to the exit location were recorded. Furthermore, the height and the angle from each release location towards the nearest edge being either woodland or grass was calculated and/or measured using a clinometer (ClinoMaster, Silva Sweden AB). To test for directional preferences, chi-square 'goodness of fit' tests were performed using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA).

6.2.11 Experiment 5

To test whether wood cricket orientates towards and prefers tall grass vegetation to short grass, an environment was created on the edge of a new planting bordering a grazed field. The vegetation within the new planting was a mix of dense thistle and grass, 50 – 60 cm in height. The grazed field consisted of a short grass sward 10 cm in height. The short grass habitat was further homogenised in terms of vertical structure by clipping. Releases were made on two locations at this site. On the 24th of August around noon, ten male and ten female wood crickets were released on the circular platform that was placed on the ground surface, half-lying within the tall grass vegetation and half within the short vegetation. The weather was overcast with a mean daytime temperature of 18 °C at ground level. On the 26th of August, a second release was undertaken with the release platform placed 1.25 m away from the tall grass edge (see Appendix II). Ten male and ten female wood crickets were released around noon under bright and sunny conditions with a mean temperature of 22 °C recorded at ground level.

6.2.12 Experiment 6 – 8

To test which factors influenced the ability of wood cricket to orientate themselves towards a woodland edge, three release experiments were performed. For these experiments releases were made from a raised platform 60 cm above ground level, using a tripod (following Beugnon, 1979; Mieulet, 1980) (see Appendix II). This method was used to avoid orientation bias towards the surrounding herbaceous vegetation.
Experiment 6: On the 24th of August, five releases were initiated along a 45 m transect between two mature (oak dominated) woodland edges. The mean height of the trees forming these edges was 13 m, measured with a clinometer. The first release was conducted in the middle of the transect 22.5 m away from both edges. A further two releases were performed on each side of this point at 20 and 15 meters from either edge. All of the releases occurred between noon and 18.00 h under overcast weather conditions.
Experiment 7: On the 26th of August between 10.00 h and noon, another four releases were initiated along a 50 m long transect running uphill away from a mature (oak dominated) woodland edge (17.5 m in height) into a grazed field with the sun predominantly shining towards the woodland edge. Releases were performed at distances 30, 35, 40 and 50 m away from the woodland edge.
Experiment 8: On the 26th of August at noon a single release was initiated at a site 50 m from a mature (oak dominated) woodland edge (19.5 m in height) within the grazed field opposite the second transect with the sun shining away from the woodland edge.

6.3 Results

6.3.1 Dispersal strategy (Experiment 1)

Continuous observations within the first hour after release revealed that wood cricket nymphs moving away from the release site within the enclosures showed random explorative behaviour, by moving (i.e. walking) back and forth through the habitat. Jumping was only observed when disturbed. The majority of the released nymphs remained within the immediate vicinity of the release site. This situation was still evident 96 hours after the initial release and was observed in all five enclosures. Furthermore, nymphs that reached the periphery tended to remain close to this artificial boundary. When observed moving along the boundary towards one of the pitfall traps, they were not inclined to fall in when reaching them. When reaching the outer rim of the trap the nymphs briefly stopped moving to examine the surroundings with their antennae, and then returned into the leaf litter. The first nymphs reached the periphery of the 1 m radius enclosure within 10 minutes. Further observations showed that for all enclosure sizes the first nymphs that reached the periphery averaged a straight-line movement rate of ≥1 m hour $^{-1}$.

Adults that were released displayed explorative movement, mainly undertaken by walking. Jumping was only observed when disturbed. They moved randomly back and forth through the leaf litter. When reaching the enclosure boundary, they tended to return to the habitat to continue their exploration. After the first 24 hours following release, males were heard stridulating within the enclosures and over time males and females were increasingly observed in pairs. Contrary to the nymphs, after 96 hours the adults were evenly distributed within the enclosures and were generally observed some distance away from the boundary instead of directly adjacent to it. The first adult arriving at the periphery of the 2 m radius enclosure took 55 minutes to do so. In the 2-4 m enclosures, the first adult reaching the periphery demonstrated a straight-line movement rate of ≥1 m hour $^{-1}$. This rate was not observed within the 5 and 7 m enclosures (i.e. rates were < 1 m hour $^{-1}$).

Table 19: Summary of the total number of observations made for the nymph populations (n = 50) released in the individual circular enclosures for four consecutive days. The numbers indicate both the number of nymphs caught in the traps and observed at the periphery. Radius: the radius of the enclosures in meters.

Radius	24 h	48 h	72 h	96 h	Total
1	12	15	11	10	48
2	14	17	12	10	53
3	6	15	9	12	42
4	6	12	9	7	34
5	6	8	5	8	27
Total	44	67	46	47	204

In general, the number of nymphs observed at the periphery decreased with an increase in enclosure size (Table 19). The percentage of the total nymph population (n = 250) observed at the periphery of all enclosures together ranged from 17.6 – 26.8% with a mean of 20.4% per day (Table 19). Comparing the total number of observations made between the first day and subsequent days showed a significantly higher number observed on the second day (chi-square test: $\chi^2_1 = 4.766$, $n_{24h} = 44$, $n_{48h} = 67$, P = 0.029; Table 19), but no difference was observed for the following days.

Table 20: Summary of the total number of observations made for the adult populations released (20 M : 20 F) in the individual circular enclosures for five consecutive days. Radius = radius of the enclosures in meters. M = Male, F = Female, G Total = Grand Total.

	24 h		48 h		72 h		96 h		120 h		Total	
Radius	M	F	M	F	M	F	M	F	M	F	M	F
2	12	7	9	6	10	7	18	9	11	8	60	37
3	5	3	12	6	8	9	10	7	11	9	46	34
4	7	1	9	5	8	4	8	3	10	5	42	18
5	2		2	1	3		3	2	2	4	12	7
7	1		4	1	4		2		5	2	16	3
Total	27	11	36	19	33	20	41	21	39	28	176	99
G Total	38		55		53		62		67		275	

For the adults, the number of observations at the periphery decreased with an increase in enclosure size (Table 20). All first arrivals at each individual enclosure periphery were males and on every survey day, the total number of males that was observed was higher than the number of females (Table 20). The percentage of the total adult population (n = 200) observed at the periphery of all enclosures together ranged from 19.0 – 33.5% with a mean of 27.5% per day. Comparison of the total number of observations made between the first and subsequent days did not show any difference for the first three days. Only for the final day of survey was the number of observations higher compared to the first day; for all adults together (chi-square test: $\chi^2_1 = 8.010$, $n_{24h} = 38$, $n_{120h} = 67$, $P = 0.005$; Table 20) as well as for females (chi-square test: $\chi^2_1 = 7.410$, $n_{24h} = 11$, $n_{120h} = 28$, $P = 0.006$; Table 20), but not for males (chi-square test: $\chi^2_1 = 2.182$, $n_{24h} = 27$, $n_{120h} = 39$, $P = 0.140$; Table 20).

6.3.1.1 Males vs. Females

Table 21: Chi–square tests (goodness of fit) for differences between the number of males and females arriving at the enclosure periphery over time (for 3 – 7 m enclosures; see Methods).

Time	Male	Female	χ^2	df	P
24h	15	4	6.368	1	0.012
48h	27	13	4.900	1	0.027
72h	23	13	2.778	1	0.096
96h	23	12	3.457	1	0.063
120h	28	20	1.333	1	0.248
Total	116	62	16.38	1	<0.001

Overall, male wood crickets were almost twice as often observed at the periphery of the enclosures than females (Table 21), indicating a higher dispersal tendency for males and confirming the initial observations. However, the number of females increased more over time compared to the number of males. After 72 h from the initial release the number of females observed did not significantly differ anymore from the number of males observed (Table 21). Furthermore, the number of females attracted to males by appearing as a pair within the enclosures increased over time. After 72 h the number of pairs was significantly higher than the number of single females observed (Table 22) and overall significantly more pairs were observed than single females (Table 22), indicating that females are attracted to males and confirming the initial observations.

Table 22: Chi–square tests (goodness of fit) between the number of female/male (F + M) pairs and single females (F) observed at the enclosure periphery over time.

Time	F + M	F	χ^2	df	*P*
24h	6	5	0.091	1	0.763
48h	11	8	0.474	1	0.491
72h	15	5	5.000	1	0.025
96h	16	5	5.762	1	0.016
120h	25	3	17.29	1	<0.001
Total	73	26	22.31	1	<0.001

6.3.1.2 Nymphs vs. Adults

Table 23: Chi–square tests (goodness of fit) for differences between the number of nymphs and adults arriving at the enclosure periphery over time. Numbers are corrected for differences in total sample size (see Methods). Only data from enclosure 2 – 5 m were used.

Time	Nymph	Adult	χ^2	df	*P*
24h	16	23	1.256	1	0.262
48h	26	31	0.439	1	0.508
72h	18	31	3.449	1	0.063
96h	19	38	6.333	1	0.012
Total	79	123	9.584	1	0.002

Between nymphs and adults, several different patterns were observed in the number of individuals that reached the enclosure peripheries. Overall, the number of adults reaching the enclosure periphery exceeded the number of nymphs, indicating a higher tendency of wood cricket adults to disperse (Table 23). The total number of adult wood crickets being able to cover straight-line distances of 2 – 3 m was significantly higher than for nymphs (Table 24). However, for the larger distances of 4 and 5 m, no differences were found, indicating a similar ability in both life-stages to disperse longer distances (Table 24). Together this indicates that although fewer nymphs disperse than adults, similar numbers are able to disperse long distances.

Table 24: Chi–square tests (goodness of fit) for differences between nymphs and adults that were able to cover the straight-line distance indicated, over a period of 96h. Numbers are corrected for differences in total sample size (see Methods).

Distance	Nymph	Adult	χ^2	df	P
2 m	27	49	6.368	1	0.012
3 m	21	38	4.898	1	0.027
4 m	17	28	2.689	1	0.101
5 m	14	8	1.636	1	0.201

6.3.1.3 Movement rate of dispersers

Table 25: Straight-line movement rate (m day $^{-1}$) for wood cricket nymphs and adults that reached the enclosure periphery within the first and second 24h after the initial release, and the mean rate for both days together (0 – 48 h). 24-48h include only the additional number of individuals observed at the periphery of each individual enclosure compared to the number observed in the first 24h. Proportion of released population = n / n_{total}. For nymphs, n_{total} = 200 (data enclosure 1 excluded); adults, n_{total} = 160 (data enclosure 2 excluded); males, n_{total} = 80; and females, n_{total} = 80.

Life-stage	Interval	n	Proportion	Rate
Nymphs	0-24h	32	0.16	3.13
	24-48h	20	0.10	1.67
	0-48h	52	0.26	2.56
Adults	0-24h	19	0.12	3.84
	24-48h	21	0.13	2.07
	0-48h	40	0.25	2.91
Males	0-24h	15	0.19	4.00
	24-48h	12	0.15	2.08
	0-48h	27	0.34	3.15
Females	0-24h	4	0.05	3.25
	24-48h	9	0.11	2.06
	0-48h	13	0.16	2.42

In the case of nymphs and adults (males and females), a general increase in the number of observations was recorded over the first 48 h after release (Table 19 & Table 20). After this period, the number of observations stabilised over time (Table 19 & Table 20). Overall, the proportion of wood crickets that were observed moving increased with a decrease in mean movement rate when using a 24 h or a 48 h time interval. The proportions of the nymph and adult population moving were similar after

48 h (0.26 – 0.25; Table 25), however the adults displayed higher movement rates over all time intervals compared to the nymphs (Table 25). During the first 24 h, only 5% of the total female population reached the enclosure periphery, whereas over the next 24 h double this value was recorded (11%) (Table 25). The proportion of males and females reaching the enclosure periphery over the second 24 h was similar (0.15 – 0.11), with similar movement rates recorded (2.08 – 2.06). However, overall males showed a higher proportion of the population moving and displayed higher mean movement rates (Table 25). The results indicated that a quarter of the population of wood cricket nymphs and adults dispersed (i.e. diffuse) with a straight-line movement rate of 2.56 / 2.91 m day $^{-1}$, respectively. This further indicated that there was a difference in dispersal 'tendency' between individuals within the population, where the majority of the population (75%) diffused with lower rates or not at all.

6.3.1.4 Trapping success

The observation of wood cricket nymphs not falling into the pitfall traps was confirmed statistically, as over the course of the experiment wood cricket nymphs were more frequently found outside (OUT) traps than within (IN) the pitfall traps (chi-square test: $\chi^2_1 = 93.35$, $n_{\mathrm{IN}} = 33$, $n_{\mathrm{OUT}} = 171$, $P < 0.001$).

6.3.1.5 Habitat choice

Table 26: Chi–square tests (goodness of fit) for habitat choice of wood cricket within the enclosures. SW facing/NE facing = number of individuals found at the south-west (SW) facing side of the forest track vs. the north-east (NE) facing side. Track/Forest = number of individuals found in habitat present on the track vs. habitat of the forest floor.

	Habitat choice				
Life-stage	SW facing	NE facing	χ^2	df	P
Nymphs	97	57	10.39	1	0.001
Adults	193	121	16.51	1	<0.001
Males	130	70	18.00	1	<0.001
Females	63	51	1.263	1	0.261
	Track	Forest			
Nymphs	48	54	0.353	1	0.552
Adults	127	70	16.49	1	<0.001
Males	87	43	14.89	1	<0.001
Females	40	27	2.522	1	0.112

The total number of nymphs observed at the enclosure periphery of the south-west facing side of the track was significantly higher (with a canopy closure (CC) of 91%, all other habitat variables being equal) than the total number observed at the north-east facing side of the track (CC 94%) (Table 26). A similar pattern was revealed for all adults together and for males only, indicating an overall preference for locations with low canopy cover for both life-stages. However, for females, no significant difference was found (Table 26). The total number of nymphs and adult females observed within the habitat represented on the forest track was not found to be significantly different from the observed number present within the forest floor habitat (Table 26). However, for males and all adults together, significantly more individuals were observed within the track habitat (Table 26).

6.3.1.6 Modelling dispersal

The cumulative data of the observations made within each enclosure were pooled and transformed to provide the mean proportion of the total population dispersing over the straight-line distance from the release point to the enclosure periphery. Both for nymphs and adults, data for the first four survey days (96 h) were plotted against dispersal distance (Figure 20). Furthermore, two additional maximum straight-line dispersal distances were also plotted that were obtained from separate group release experiments (see Methods, Experiment 2). The maximum straight-line dispersal distance that was included for nymphs was 29.5 m and was recorded in a group release experiment at 'Site 1' (Table 28). Of the initially released population (50), one individual was observed at this distance 72 h after release (proportion: 0.020 (1/50); Table 27). The maximum dispersal distance for adults (males and females) was derived from observations made at 'Site 2' (Table 28). Three individual males were found at 26 – 27 m from the initial release site after 60 days. Therefore, the maximum distance for dispersing adults was set to 26.0 m. One-hundred crickets were released at this location (50 nymphs, 25 males, 25 females; see Methods, Experiment 2). Therefore, the total proportion of the adult population that was observed moving this distance was estimated to be 0.030 (3/100) (Table 27). For adults males the proportion was calculated to be 0.060 (3/50) (Table 27), assuming an equal representation of both sexes in the released nymphs. No direct long-distance dispersal events were recorded for females. However, because males were found to disperse twice as often as females within the enclosures (see total numbers observed, Table 20), the proportion of the female population dispersing the maximum observed distance was estimated to be 0.030 (i.e. half the proportion of males) (Table 27).

Table 27: Proportions of the total population moving in a straight-line distance (m) from the release point to the enclosure periphery for nymphs ($n = 50$ per release site) and adults (Male (M) & Female (F)) ($n = 40$, $n_M = 20$, $n_F = 20$), averaged over the first 96 hours after release. Maximum observed distances and related proportions were derived from additional release experiments (see text).

Distance	Nymphs	Adults	Males	Females
2	0.293	0.488	0.613	0.363
3	0.222	0.375	0.438	0.313
4	0.177	0.281	0.400	0.163
5	0.139	0.081	0.125	0.038
7		0.075	0.138	0.013
26.0		0.030	0.060	0.030
29.5	0.020			

Equation 4: Inverse-power function

$$P = a D^{-b} \text{ or } \mathrm{LN}(P) = \mathrm{LN}(a) - b\mathrm{LN}(D)$$

Equation 5: Negative-exponential function

$$P = e^{-bD} \text{ or } \mathrm{LN}(P) = -bD$$

P = proportion of the population moving

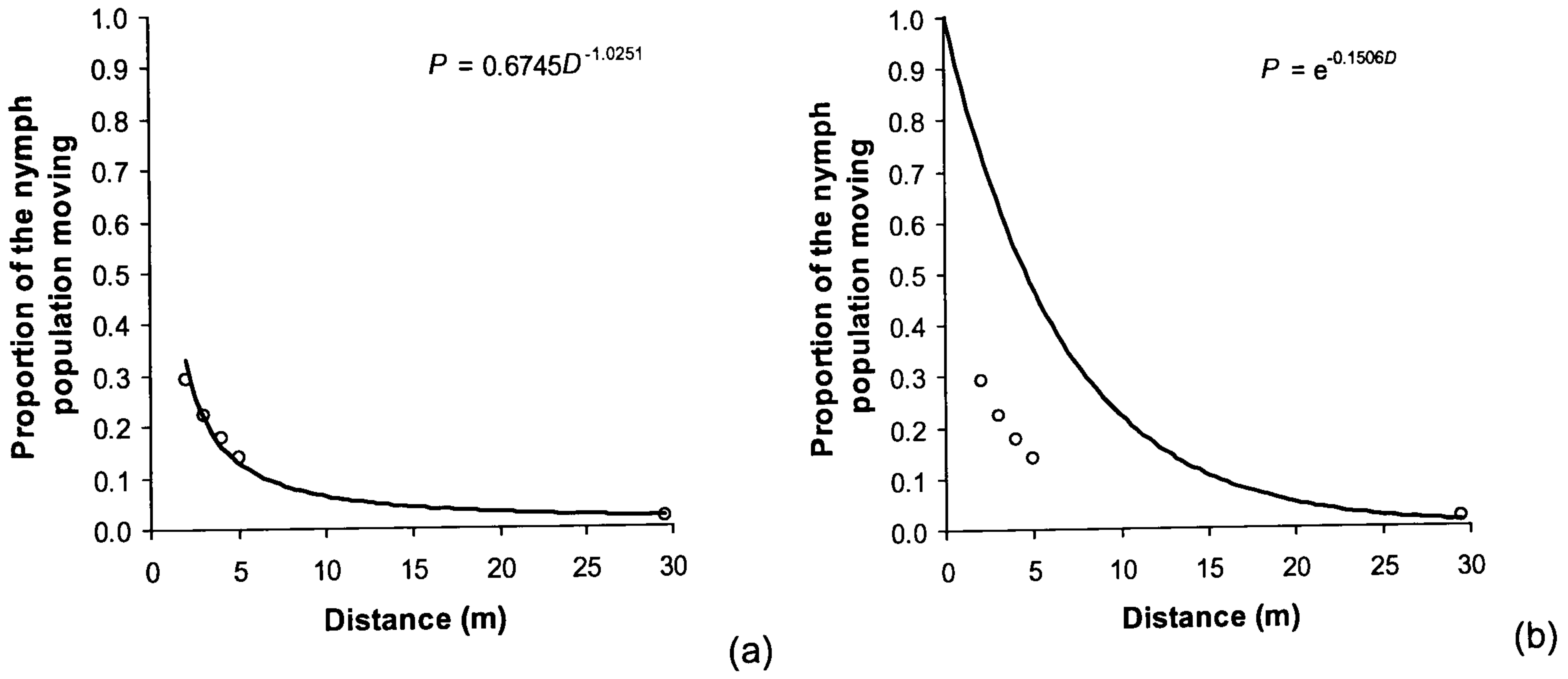
D = distance (m)

a = constant

b = slope of the regression curve

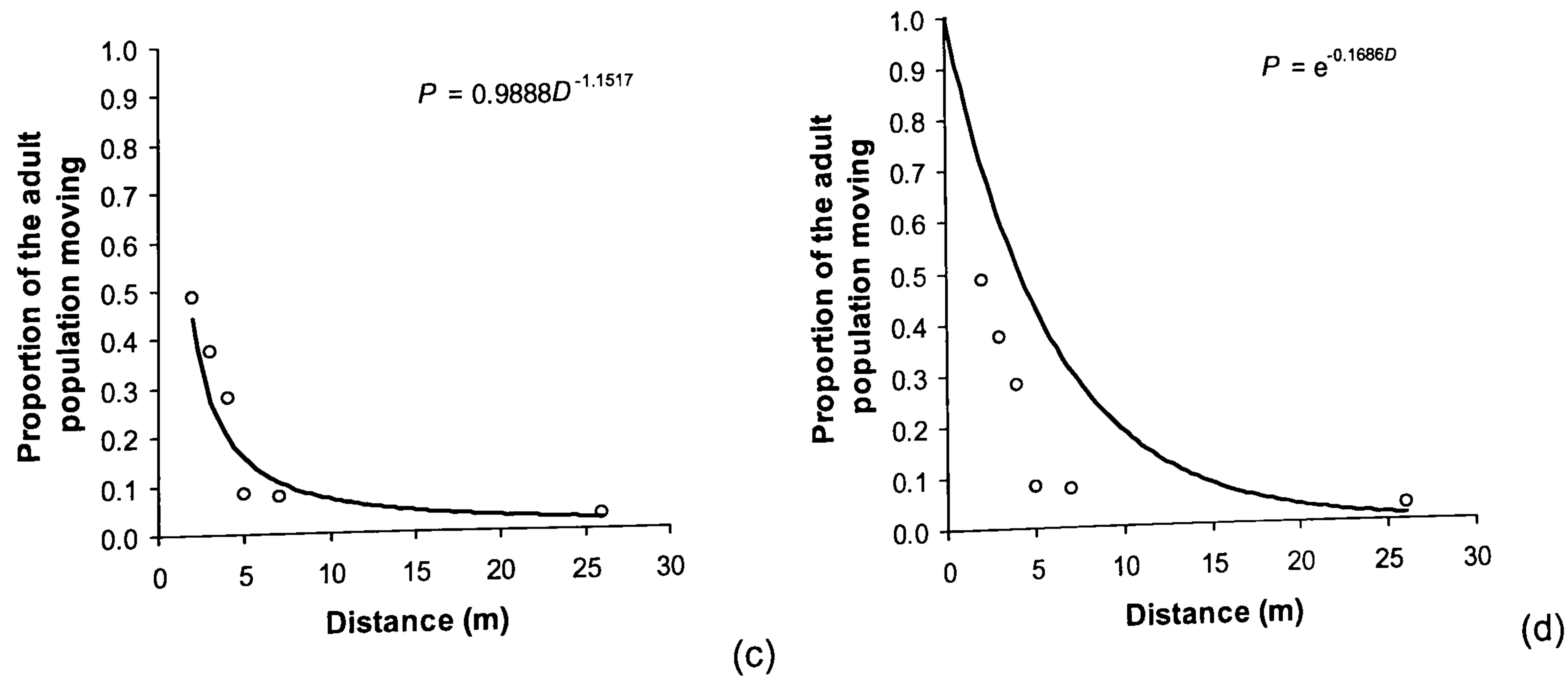
The negative-exponential curve and the inverse-power curve were fitted to the data presented in Table 27 (Figure 20). To test the fit of the inverse-power function, LN(P) was regressed upon LN(D), and LN(P) on D for the negative-exponential function (see Equation 4 & Equation 5). For the nymphs the inverse-power curve provided the best fit (Power: $R^2 = 0.993$, $F_{1,4} = 446.0$, $P < 0.001$ vs. Exponential: $R^2 = 0.807$, $F_{1,5} = 16.74$, $P = 0.015$) (Figure 20a & b). This was also the case for all adults considered together as well as for males only (Adults: Power: $R^2 = 0.867$, $F_{1,5} = 26.04$, $P = 0.007$ vs. Exponential: $R^2 = 0.779$, $F_{1,6} = 17.68$, $P = 0.008$; Males: Power: $R^2 = 0.851$, $F_{1,5} = 22.84$, $P = 0.009$ vs. Exponential: $R^2 = 0.782$, $F_{1,6} = 17.97$, $P = 0.008$; Figure 20c – e). The better fit of the inverse-power curve was further confirmed by examining the distribution of the residuals and plotting the individual curves against the field data (see Figure 20: e.g. compare fit power curve (a) with fit exponential curve (b)). For adult females the negative-exponential curve explained a slightly higher amount of the variation compared to the inverse-power curve after 96h of observations (Females: Power: $R^2 = 0.526$, $F_{1,5} = 4.441$, $P = 0.103$ vs. Exponential: $R^2 = 0.611$, $F_{1,6} = 7.842$, $P = 0.038$). However, when examining the distribution of the residuals and the fit of the individual curves, the inverse-power equation was found to describe the data more closely (also see Figure 20f). Furthermore, for the female population, when including the observations made on the fifth day, the fit of the inverse-power curve improved significantly (96h: Power: $R^2 = 0.526$, $F_{1,5} = 4.441$, $P = 0.103$ vs. 120h: Power: $R^2 = 0.733$, $F_{1,5} = 10.98$, $P = 0.030$). For the male and total adult population, no improvements were observed in the degree of fit when including the observations for the fifth day.

Nymphs



(a) (b)

Adults



(c) (d)

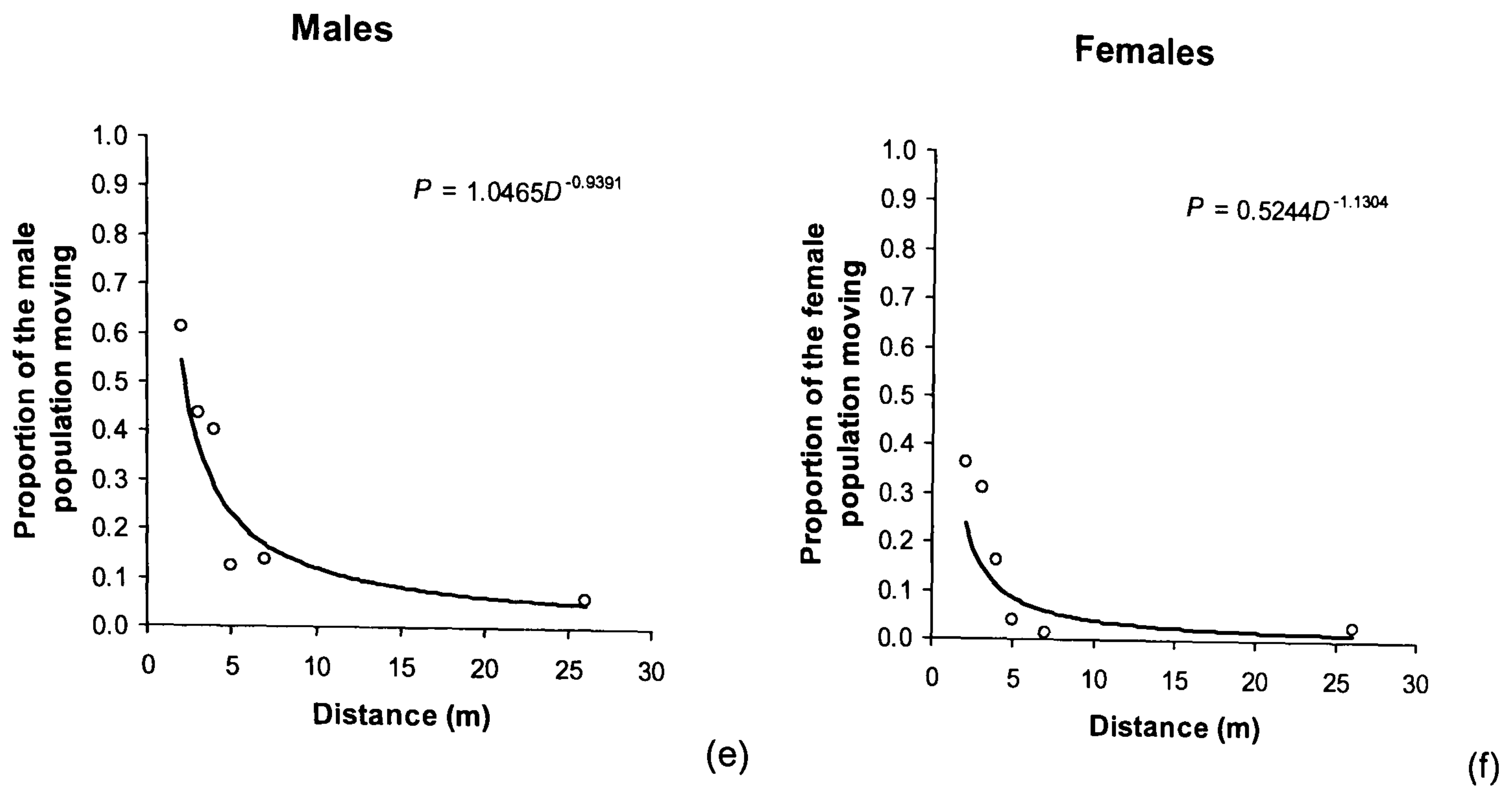


Figure 20: The proportion of the wood cricket population moving in the first 96h after release fitted against distance. (a) inverse-power function (ipf), and (b) negative-exponential function (nef) fitted for nymphs, (c) ipf for all adults, (d) nef for all adults, (e) ipf for males (nef: $b = 0.1342$)), (f) ipf for females (nef: $b = 0.1939$)).

The mean distance (D') moved by individuals within the population is given by $1/b$ (Harrison et al., 1988; Hill et al., 1996; Baguette et al., 2000). For the nymph population, the inverse-power function predicted a mean dispersal distance of 0.98 m (1/1.0251). The mean value predicted by the inverse-power function for all adults was 0.87 m (1/1.1517), and 1.07 m (1/0.9391) for males and 0.88 m (1/1.1304) for females. The graphs displaying the inverse-power curve for both nymphs and adults all show a rapid decline in the number of wood crickets moving with distance. Less than 10% of the released populations was shown to move further than 15 m from the release point (see Figure 20a, c, e & f). Furthermore, when comparing the individual relationships, the inverse-power curves derived for nymphs vs. adults (Paired-samples t-test: $t = -4.777$, df = 44, $P < 0.001$) and males vs. females (Paired-samples t-test: $t = 6.293$, df = 44, $P < 0.001$) were both significantly different from each other. Between life-stages, the predicted proportion of the nymphs dispersing was found to be lower than adults up to 20 m in distance. From this point onwards, the proportions were more or less equal indicating that similar proportions in these life-stages reach their maximum dispersal distance. The predicted proportion of males dispersing was overall higher than predicted for females, indicating higher dispersal ability for males compared to females.

6.3.2 Dispersal capacity (Experiment 2, 3 & Surveys)

The following observations were made during the three-day group release experiment (Experiment 2). For wood cricket nymphs, all release sites (apart from 'Site 3') were at locations with high canopy closure (92 – 99%). Nymph movements were observed to be directed towards the nearest open (i.e. sunnier) habitat locations. Dispersing nymphs were also readily observed in short and tall grass habitat with relatively low leaf litter availability. Ground vegetation composition seemed to be of lesser importance than canopy closure in this respect. Nymphs were quite clearly visible when surveying the area around the release sites. Re-sighting success using this survey method for the nymphs ranged from 28 – 73% after 48 h from the moment of release. However, when using this method for adults only very low re-sighting percentages (2 - 12%) were achieved, making it impossible to perform any statistical analyses on these data. The second mass release (Experiment 3) for adult wood cricket initiated on 'Site 6 – 9' also displayed low relocation success. Of the 40 adult males released at each site, 5 – 10% was relocated for 'Site 6 – 8', with no observations recorded for 'Site 9'.

Table 28: Maximum absolute dispersal distances (m) recorded per survey site over time. LS (location) = Life-stage and location of re-sighting. WE = woodland edge, JE = edge of new planting, GL = grassland, HE = hedge edge. Time: 3 - 60 d (days) is time elapsed between first release and recorded maximum distance (Max dist.). 60 days covered a period including 2 releases; initially 50 nymphs and 40 days later 50 adults (25 M, 25 F). 2 y (years) is the period between establishment of the new plantings and the moment of survey. 3 y is the number of annual surveys. The maximum distance (m) measured over 3, 20 and 60 days represents straight-line distances from the point of release. The 2 y distances represent straight-line distances to the nearest woodland edge. The 3 y distance represents progression from the point where wood cricket was found in 2005. Vegetation measurements for the individual re-sighting locations: VH = mean vegetation height (cm), VC = total vegetation cover (%), LC = total litter cover (%), LD = litter depth (cm), CC = canopy closure (%).

Site	LS (location)	Time	Max dist.	VH	VC	LC	LD	CC
1	Nymphs (WE)	3 d	29.5	30	45	90	1.5	72
	Nymphs (GL)	3 d	23.0	10	85	10	0.5	54
	Adults (WE)	3 d	5.5	10	20	45	1.5	89
	Adults (WE)	3 y	0.0	47	36	64	2.0	82
2	Nymphs (JE)	3 d	8.5	5	95	10	1.5	6
	Nymphs (WE)	3 d	6.0	10	30	85	2.0	98
	Adults (GL)	60 d	26.0	20	100	-	-	0
	Adults (WE)	60 d	27.0	20	20	80	4.0	79
3	Nymphs (HE)	3 d	1.5	10	35	80	2.0	33
4	Nymphs (HE)	3 d	9.5	15	35	30	1.5	60
5	Adults (WE)	3 d	2.5	10	5	75	3.0	90
6	Adults (WE)	20 d	5.0	20	100	10	1.0	88
7	Adults (HE)	20 d	12.0	30	100	30	1.0	40
8	Adults (WE)	20 d	2.0	15	100	30	1.0	46
	Adults (GL)	2 y	23.0	20	100	-	-	0
9	Adults (JE)	20 d	-	-	-	-	-	-
10	Adults (GL)	2 y	55.0	30	100	-	-	0

6.3.2.1 Site 1

Distance from the release point where nymphs were found was significantly greater on the second day of survey compared to the first day (Mann-Whitney test: n = 28, z = -2.459, P = 0.014). Nymphs significantly chose to move along the east-facing woodland edge rather than the north-facing edge (chi-square test: χ^2_1= 14.73, P < 0.001) and no nymphs or adults were recorded on the north-facing woodland edge further than 1 m away from the release site. To test that nymphs choose locations with lower canopy closure over time, differences between locations where wood cricket nymphs were present were tested between the first and the second day. Canopy closure was found to be significantly lower for locations where nymphs were found on the second day compared to the first day of survey (Mann-Whitney test: $n = 28$, $z = -2.044$, $P = 0.041$). Also, locations where wood cricket nymphs were present on the east-facing woodland edge displayed significantly lower percentages of canopy closure compared to locations at the same distance from the release site at the opposite north-facing woodland edge (Mann-Whitney test: $n = 24$, $z = -2.377$, $P = 0.017$), indicating both their choice and preference for lower levels of canopy closure.

The three year survey carried out at this location (see Surveys in Methods) did not show any signs of wood cricket advance along the east-facing woodland edge (Table 28). In 2005, wood cricket was found at high densities up to 80.0 m along the edge from the main woodland area. In 2006, wood cricket was found up to the same maximum distance; however the population density was considerably reduced. In 2007, wood cricket was still observed no further than 80.0 m along the woodland edge; however, population numbers had slightly recovered compared to the previous year.

6.3.2.2 Site 2

Nymphs released in the three-day release experiment (Experiment 2) dispersed both along the edge of the new planting as well as along the woodland edge (Table 28). However, three individuals were found to have dispersed info the adjacent grazed field (Max dist. = 6.5 m; VH = 10, VC = 100, CC = 20). The maximum dispersal distance recorded for the nymphs (8.5 m) was recorded for an individual dispersing along the edge of the new planting (Table 28). Furthermore, dispersing nymphs significantly chose to move along the 'JIGSAW' edge through the tall grass/shrub vegetation compared to the woodland edge (chi-square test: $\chi^2_1 = 29.43$, $P < 0.001$). There was no significant difference found for distance from the release point where nymphs were found between the first and second day of survey (Mann-Whitney test: $n = 44$, $z = -1.097$, $P = 0.273$). There was also no significant difference found for canopy closure for locations where nymphs were found between the first and second day of survey (Mann-Whitney test: $n = 44$, $z = -0.779$, $P = 0.436$). However, locations where wood cricket was present on the grass/shrub edge did display significantly lower percentages of canopy closure compared to locations at the same distance from the release site at the opposite woodland edge (Mann-Whitney test: $n = 28$, $z = -4.558$, $P < 0.001$), indicating the preference (over ground cover habitat) for habitat locations with low levels of canopy closure.

The maximum straight-line dispersal distance recorded for adults was 4.0 m after three days from the moment of release (Experiment 2). The location of this individual was recorded along the edge of the new planting within herbaceous/grass habitat (10 – 40 cm high) with an overhead tree canopy closure of 35%. After releasing both nymphs and adults (n_{total} = 100) over a period of 60 days, adult stridulating males were relocated within the near vicinity of the release site, along the woodland edge and within the grazed field. The highest maximum straight-line dispersal distance was recorded for an individual that had dispersed along the woodland edge (27.0 m) (Table 28). However, two individuals were also recorded within the grazed field at a similar distance of 26 m from the release site. Furthermore, compared to the woodland edge, slightly more individuals were relocated within the grazed field (5 vs. 3, after 60 days from the initial release), indicating similar ability to move through both grass and woodland/leaf litter habitat. No adult males were recorded along the tall herbaceous vegetation edge between the grazed field and the new planting during these surveys, indicating an overall preference for the woodland edge.

6.3.2.3 Site 3

During 'Experiment 2', nymphs significantly chose to stay within the improved release patch of short grass with added leaf litter rather than moving into the surrounding short/tall grass habitat (chi-square test: χ^2_1= 48.56, $P < 0.001$), only showing a maximum dispersal distance (of 1.5 m), 72 h after the moment of release (Table 28). Furthermore, no single nymph was observed moving along the hedge edge. Together, this indicated that they preferred to stay in the suitable habitat conditions provided by the small release patch with added leaf litter and low canopy cover.

6.3.2.4 Site 4

During 'Experiment 2' conducted for wood cricket nymphs, the maximum straight-line dispersal distance of 9.5 m was recorded along the hedge edge (Table 28). Distance from the release point where nymphs were found was significantly greater on the second day of survey compared to the first day (Mann-Whitney test: n = 38, z = -3.059, P = 0.002) and canopy closure was significantly lower for locations where nymphs were found on the second day compared to the first (Mann-Whitney test: n = 38, z = -3.233, P = 0.001), confirming the preference for low levels of canopy closure. Furthermore, dispersing nymphs significantly chose short grass over moving into tall grass habitat (chi-square test: $\chi^2_1 = 11.31$, $P = 0.001$). However, from the second day onwards equal numbers of nymphs were found within the uncut herbaceous 'JIGSAW' habitat and the (hand cut) short grass habitat. During the survey for adults carried out 60 days after the nymphal release, no stridulating males were recorded at this site, indicating no colonisation success.

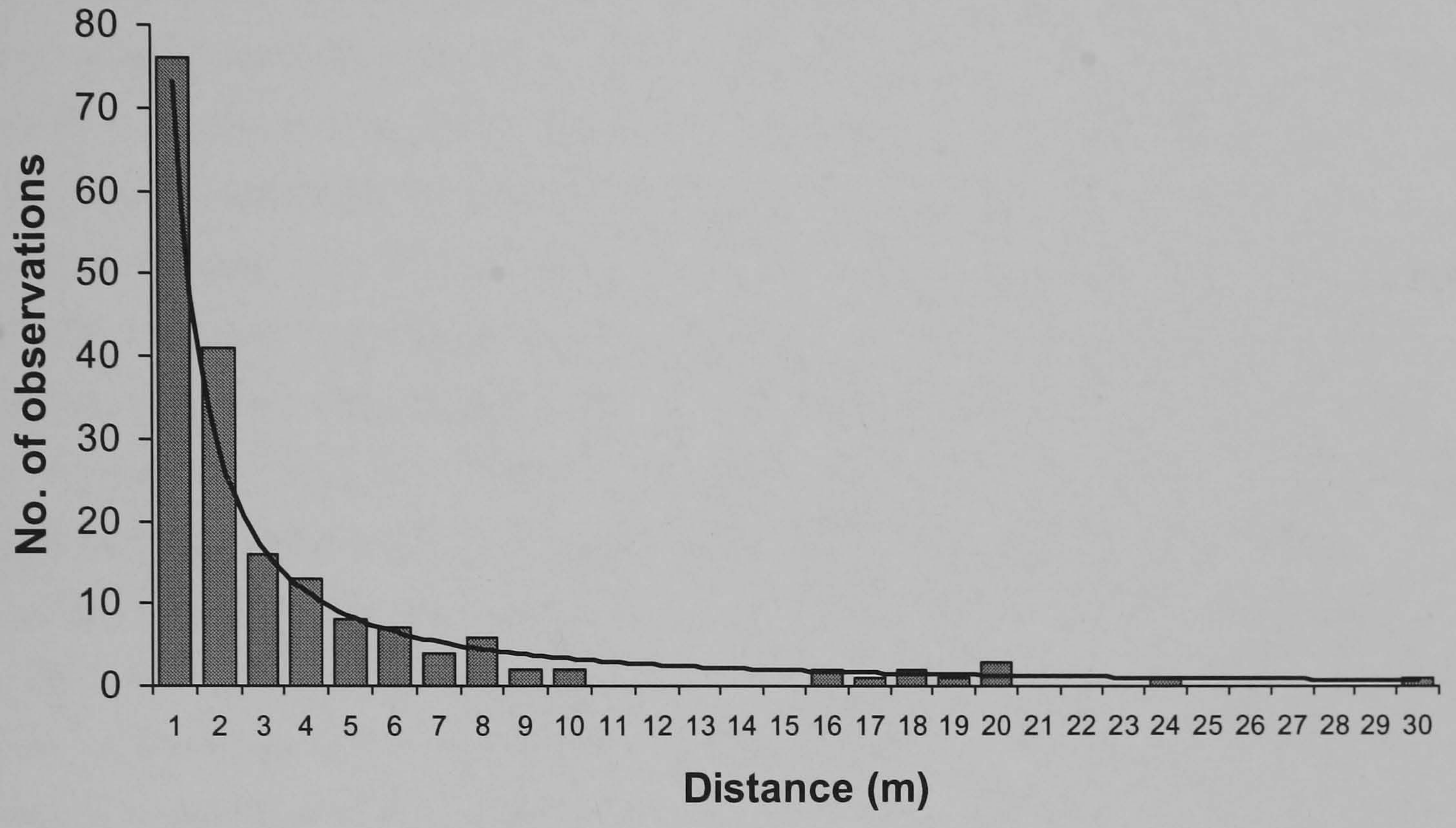


Figure 21: Frequency distribution of the number of wood cricket nymphs observed in 'Experiment 2', for all sites (1-4) together during 72h of observation. Inverse-power curve fitted to the data ($R^2 = 0.921$), confirming the relationships presented earlier (see Figure 20a). Distance (m): straight-line distances from the point of release to the location of observation. n = 186. Mean absolute distance travelled for all nymphs observed = 1.62 m day^{-1}.

6.3.2.5 Site 5

Three days after the initial release (Experiment 2), adult wood crickets were only observed close to the release site on a west-facing bank covered in sparse bramble with a well-developed leaf litter layer underneath. The maximum dispersal distance (2.5 m) was also recorded at this location (Table 28).

6.3.2.6 Site 6 - 10

Twenty days after the initial release (Experiment 3), one male wood cricket was relocated along the mature woodland edge (5.0 m) at 'Site 6' (Table 28), with another male and female observed at the release site. At 'Site 7', one male was relocated along the hedge edge at 12.0 m from the release point (Table 28) and another at 3.0 m within the hay field underneath a sward of cut grass. At 'Site 8', several wood crickets were relocated within the mature woodland edge close to the release site not more than 2.0 m away (Table 28) and another two were relocated within the grazed field at 3.5 and 4.0 m distance under low canopy closure conditions (6 and 0%, respectively). No individuals were relocated along the edge of the new planting. Additionally, at the preliminary survey (5th August) two individuals were heard stridulating within the grazed field at a maximum distance of 23.0 m from the woodland edge (Table 28). This indicated that wood cricket was already present near release 'Site 8' before the 'artificial' release. For 'Site 9', no individuals were relocated. For 'Site 10', the maximum distance that was recorded for an individual that had moved away from a woodland edge was 55.0 m. This individual was located within the grazed field 18.0 m from the two-year-old new planting (Table 28). Furthermore, the maximum distance recorded for an individual male wood cricket from the nearest (permanent) source population situated within the boundaries of the main woodland body across a small woodland stream was 98.0 m. Several more recordings were made within the grazed field as well as along the edge of the new planting. Distances from the woodland edge to these points ranged from 23.0 – 45.0 m and distance from the woodland source ranged from 64.5 – 90.0 m.

6.3.3 Island releases (Experiment 4)

6.3.3.1 Observations

After release, both nymphs and adults aggregated around and moved along the island shore, actively looking for a way to cross. When making an attempt to cross the watercourse, the majority leaped approximately half way across the width of the watercourse (10-15 cm for the nymphs and 15-20 cm for the adults), after which they swam the remaining distance, often in a straight-line to the shore. They reached the shore by one or several powerful swimming bursts, propelling themselves by rapidly kicking their hind legs. Both nymphs and adults stayed afloat because of water tension; however contrary to adult wood cricket, nymphs were observed to sink less deep into the water mainly floating on their legs rather than their bodies. The longer time spent in the water, the shorter and less frequent the movements became. The majority of the observed escape attempts (8 out of 9 for the nymphs and 14 out of 15 for the adults) were directed to the nearest forest edge, 2.5 meters away from the island shore.

6.3.3.2 Crossing capacity

Overall nymphs crossed the watercourse more readily than did adult wood crickets. Within the first hour after release 9 out of the initial 15 released nymphs actively crossed the watercourse from the island to the opposite shore, with two more attempting to do so, but returning to the island. For the adults only one (female) out of the initial 20 wood cricket that were released succeeded in crossing the watercourse within the first hour. This was a significant lower number compared to the nymphs (chi-square test: χ^2_1= 9.308, P = 0.002). Furthermore, within five hours, 13 out of 15 nymphs (87%) had crossed the 25 cm wide watercourse. However, for the adults, over the first two hours, 15 (7 males, 8 females) attempts were made of which only 6 (3 males, 3 females; 30% of the total) succeeded. All other adult wood cricket returned/or remained on the island. After 24 hours, 35% of the released adult population was still present on the island, and 7 males and 5 females (65%) successfully made the crossing. Only after 48 hours did the adults match the nymphs with 9 males and 8 females (85%) having crossed the 35 cm wide watercourse. However, altogether both nymphs and adults were clearly capable of and preferred leaving the island by crossing the watercourse with no differences observed between the number of males and females succeeding in making this crossing (Table 29).

Table 29: Displayed 'escape' success from the island by crossings the watercourse for wood cricket nymphs (after 5 h) and adults (after 48 h) (chi-square 'goodness of fit' tests) and between sexes (Fisher's exact tests). Crossed/Remained = number of individuals that crossed the watercourse or remained on the island.

Life-stage	Crossed	Remained	χ^2	df	P
Nymphs	12	3	5.400	1	0.020
Adults	17	3	9.800	1	0.002
Males	9	1	Fisher's test		1.000
Females	8	2			

6.3.4 Orientation experiments (Experiment 5 – 8)

6.3.4.1 Orientation towards tall grass edge

When given a choice between tall grass (50-60 cm) and short grass (10 cm) habitat (Experiment 5), all released wood crickets moved towards the tall grass vegetation (n = 20), indicating a significant positive orientation towards the higher vegetation. However, when released at 1.25 meters away from the tall grass edge, wood cricket showed no preference for moving towards the higher vegetation (chi-square test: $n_{tall} = 13$, $n_{short} = 9$; $\chi^2_1 = 0.250$, $P = 0.617$), indicating a random orientation at this distance. The edge perception toward the tall grass habitat calculated as the angle from the release point was 39 ° and 18 ° for these 2 release locations, respectively.

6.3.4.2 Orientation towards woodland edge

Table 30: Chi-square (goodness of fit) tests for the orientation of wood cricket at different distances from a woodland edge (Experiment 6 – 8). Distance: distance from the woodland edge in meters. Distance = 50 (2) indicates the release location of 'Experiment 8' with a different sun direction compared to the other locations. Angle = angle measured from the release location to the top of the woodland edge (in degrees). Edge/Field = number of wood cricket exiting the release platform towards the woodland edge or towards the field.

Distance	Angle	Edge	Field	χ^2	df	P
15	34	16	3	8.895	1	0.003
20	30	14	1	11.27	1	0.001
30	24	16	0			<0.001
35	21	12	3	5.400	1	0.020
40	19	15	3	8.000	1	0.005
50	15	8	5	0.692	1	0.405
50 (2)	15	5	8	0.692	1	0.405

Up to 40 m from a woodland edge under an orientation angle of > 19° wood cricket showed a positive preference for moving towards the woodland edge (Table 30). However, for distances with a visual angle towards the woodland edge of 15°, wood cricket showed no significant orientation effect, both when the sun was shining away and toward the woodland edge (Table 30). For all release locations, wood cricket demonstrated a significant preference for moving away from the direction of the sun (chi-square test: $P < 0.001 – 0.029$) with the exception of release 50 (2) (chi-square test: $n_{away} = 9$, $n_{to} = 5$, $\chi^2_1 = 1.143$, $P = 0.285$), confirming earlier findings (see Beugnon, 1979; Mieulet, 1980).

6.4 Discussion

In a previous study, the higher speed generated by wood cricket adults and the more directed movement strategy found in experiments at a small spatio-temporal scale suggested a higher dispersal ability for adults compared to nymphs (Chapter 5). Furthermore, in the same investigation, no differences were observed in dispersal ability between the sexes based on their speed (Chapter 5). However, as shown here, when including larger spatial and temporal scales for observation, similar numbers of nymphs and adults were shown to be able to cover the maximum straight-line distance (Table 24), and fewer females were found to disperse compared to males (Table 21). This indicates that the scale of investigation influences the observed patterns and the relative importance of related processes. Moreover, when surveying the spread of wood cricket over increasing time intervals, the maximum observed distance from the release sight was found to similarly increase (Morvan et al., 1978; and this study), indicating the importance of observing dispersal over long temporal scales. Together, these results indicate the importance of recording movements over a range of spatio-temporal scales in order to fully assess the dispersal ability of this species.

To fully understand the dispersal ability of a species it is important to consider both juvenile and adult life-stages (Diekotter et al., 2005). In this study, overall and in the smaller enclosures more adults than nymphs were found to show a tendency to disperse, supporting previous results (Chapter 5). However, equal proportions of the total released population of wood cricket nymphs and adult were found to perform long-distance dispersal. As wood cricket has a two-year life-cycle of which two-thirds is spent as a nymph and one-third as an adult (Gabbutt, 1959; Brown, 1978), this result is highly important in terms of inferring their life-time dispersal ability. Similar observations were made for the bush cricket (*Pholidoptera griseoaptera*) in a study conducted in Switzerland by Diekotter et al. (2005). This non-flying species also has a preference for deciduous wooded edges, where it can be found at low densities preferably within tall grass; along woodland edges, in woodland clearings and along hedges (Diekotter et al., 2005). Diekotter et al. (2005) also found no differences in dispersal ability between juveniles and adults of this species. Together these results highlight the importance of considering all individual life-stages when assessing the dispersal ability of non-flying cricket species.

In adult crickets, differences in dispersal ability between the sexes are usually not observed (e.g. Kindvall, 1999; Diekotter et al., 2005). However, for wood cricket, significant differences were found between the dispersal ability of males and females. During the enclosure experiment conducted in this study, all the initial dispersers were found to be adult males. Furthermore, males were observed to disperse twice as often as females. This indicates that males were more inclined to disperse than females, which only significantly matched numbers of males at the enclosure periphery after 48 hours of movement activity. This was most likely the result of male stridulation attracting the females, as has been found in several other cricket species (Marshall & Haes, 1988; Simmons & Ritchie, 1996; Scheuber et al., 2003). In this study, the number of wood cricket pairs that were observed to increase at the enclosures peripheries over time indicated the positive influence of this factor. This indicates that for wood cricket, adult males are initially more likely to disperse further and may be followed by females attracted by their stridulation. This also indicates that for this species during the adult phase, males can be considered as the primary dispersers.

In this study, dispersal of both adults and nymphs was most accurately described by the inverse-power function. Given the possible limitations of the current study, in terms of the experimental designs and sample sizes adopted, this result should clearly be interpreted with caution. However, previous research has found that the inverse-power function is more accurate and robust than the negative-exponential function when using relatively few individuals over a short period of time (Fric & Konvicka, 2007), as in the current study. Furthermore, the combined data from the release experiments (Site 1 – 4) conducted with the nymphs recorded an accurate description of the data using the inverse-power equation (Figure 21). Similarly, after conducting further analyses on mark – resight data of wood cricket adults collected in France (Morvan et al., 1978), again a more accurate description of the data was obtained using the inverse-power equation than when using the negative-exponential relationship. This data set was gathered under similar habitat conditions as included within the enclosures used here, but over a period of 30 days (Morvan et al., 1977; 1978). These combined results suggest that the inverse-power function does seem appropriate to describe dispersal for both wood cricket nymphs and adults. Compared to the exponential equivalent, this means that although only a small portion of the wood cricket population shows a tendency to disperse, a relative large amount is predicted to disperse to their maximum ability. Furthermore, use of the inverse-power equation for describing the dispersal of species that move by walking is also supported by results from other studies. The frequency distribution of the number of bush cricket (*Metrioptera bicolour*) dispersing through their preferred dry grassland habitat environment, within a matrix of pine forests and arable land, closely matched the relationship found here for wood cricket

(Kindvall, 1999). For the walking leaf beetle investigated by Chapman et al. (2007), the inverse-power curve was also found to approximate dispersal observed in the field better than the negative-exponential function. This indicates that although the relationship obtained might have been influenced by the experimental design adopted here, the inverse-power equation does seem more appropriate compared to the negative-exponential equation to describe the dispersal of non-flying species in this type of investigation.

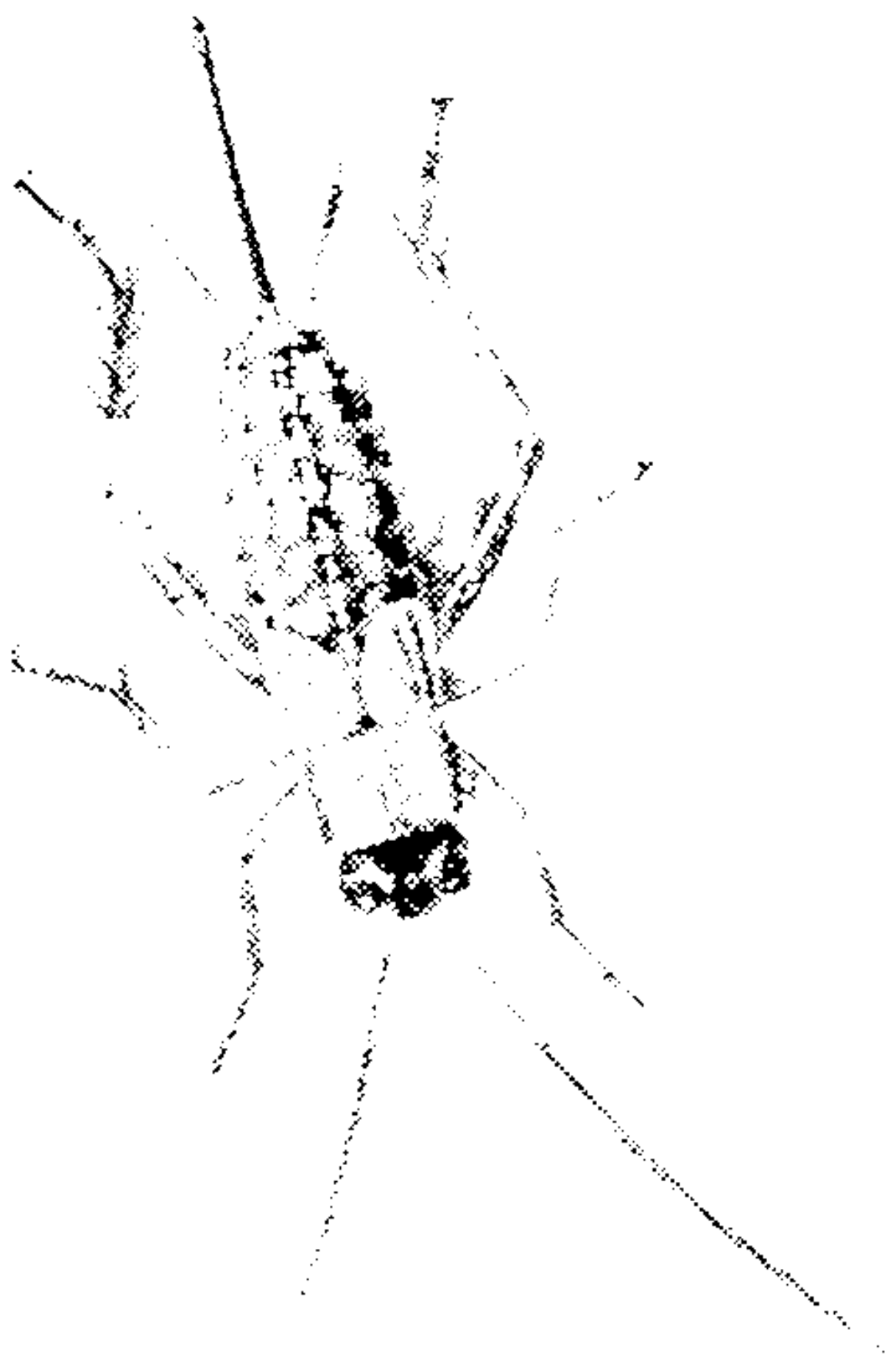
The majority of individuals in both life-stages were found to equally settle down into the limited area of the enclosures, preferring the areas characterised by low degrees of canopy closure, and engaging in their normal daily activities of feeding and in case of the adults courting and mating. This tendency of wood cricket nymphs and adults to settle down and remain within a limited area during their entire life-cycle was also found in earlier studies conducted in France (Morvan & Campan, 1976; Morvan et al., 1977; 1978). A preference to remain within a specific area of suitable habitat has also been found for grasshoppers (Clark, 1962; Aikman & Hewitt, 1972). This indicates that similar to other Orthoptera, for both life-stages of wood cricket the home range requirements can be met at small spatial scales under suitable habitat conditions. Overall, wood cricket was found to be more sedentary than other cricket species. Within the enclosures, wood cricket nymphs and adults displayed a mean movement rate of 3.13 and 3.84 m day^{-1} over the first 24 h after release, respectively. However, these rates were calculated only for the individuals observed at the periphery of the enclosure, which amounted to 12% of the adult and 16% of the nymph population, thus indicating that the majority of individuals moved shorter distances. For the bush cricket (*Pholidoptera griseoaptera*), Diekotter et al. (2005) found that nymphs and adults of this species were equally sedentary, but showed higher movement activity than wood cricket. In this case the daily movement rate was calculated over the first 24 h using all distances that were observed for the released population, recording mean movement rates of 1.7 – 3.8 m day^{-1} for juveniles and 3.0 – 6.3 m day^{-1} for adults (Diekotter et al., 2005). For another cricket species living in herb-rich meadows, similar rates were obtained for males, which moved a mean distance of 2.8 m day^{-1} (Ritz & Kohler, 2007). By using the inverse-power function for both nymph and adult wood crickets, it was further estimated that the mean distance that each wood cricket individual dispersed during their life-cycle averaged less than 2 m. This suggests that compared to other cricket species for which data are available, movement of wood cricket is relatively limited.

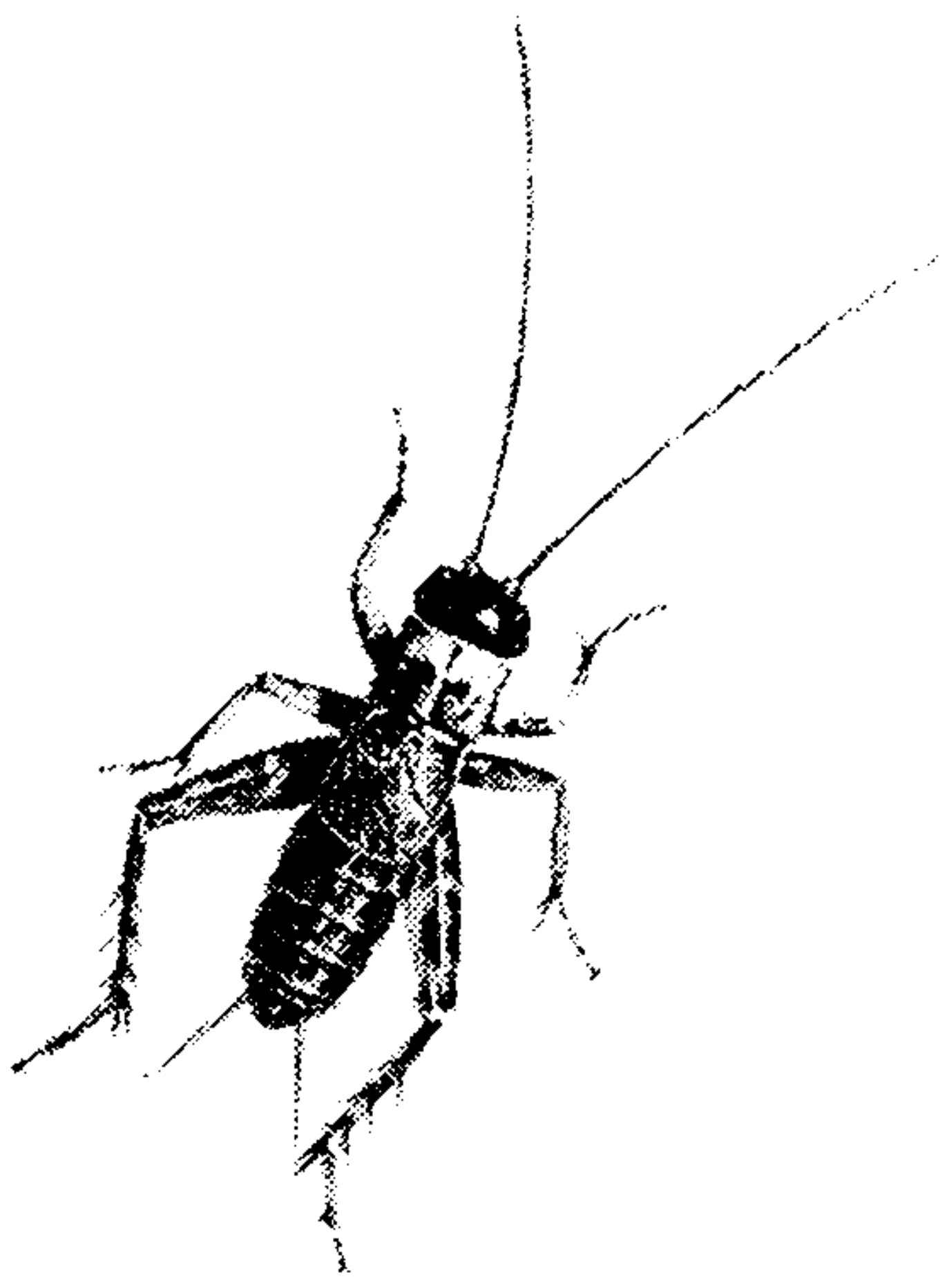
Ninety-six hours after release, only small proportions of wood cricket nymph (13.5%) and adult (7.5%) populations showed the ability to cover the longest straight-line distance of 5 and 7 m, respectively, through their preferred leaf litter habitat. These limited dispersal distances achieved by the species are supported by earlier observations of wood cricket nymphs and adults moving through this type of habitat (Gabbutt, 1959; Morvan & Campan, 1976; Morvan et al., 1977; 1978). Similar observations indicating that only few individuals move long distances through their preferred habitat by walking have been made for a leaf beetle (Chapman et al., 2007) and a bush cricket species (Kindvall, 1999). However, the current study also showed that some nymphs were capable of moving up to 30 m in 72 hours through preferred habitat. Owing to low re-sighting success, no such observations were made over this timescale for adult wood cricket. However, dispersal distances of 27 m over a period of 60 days and 55 m during one life-cycle were observed for adult males (Site 2 & 10, Table 28). Furthermore, in a previous mark-recapture experiment within continuous open woodland habitat, adult wood cricket were shown to be able to disperse up to 60 m over a period of 30 days (Morvan et al., 1978), and Richards (1952) noted that single adult male wood cricket were sometimes heard stridulating up to a mile (1.6 km) from a main colony. These observations together suggest that at least some nymphs and adults (males) are able to disperse relatively long distances. If adult females are able to disperse similar distances as the adult males, these observations are important in terms of the ability of this species to spread and establish new populations at locations where suitable habitat is available.

Together, the release experiments and field surveys provided a deeper insight into the ability of wood cricket to move through the heterogeneous habitat environment associated with the agricultural matrix and recently established tree plantations surrounding the woodland fragments where it occurs. Both nymphs and adults were shown to be able and willing to move through less favourable grassland habitat and able to cross obstacles such as watercourses. Richards (1952) found several individual wood cricket males stridulating relative long distances away from larger populations, indicating their possible role as dispersers. In this study, similar observations were made with single wood cricket males found stridulating up to 90 m away from a source population that was located within woodland separated by a small forest stream, suggesting dispersal across the stream. Furthermore, some individual males were observed within grassland habitat up to 55 m away from their closest preferred woodland habitat environments. A similar distance (50-60 m) was also recorded over a period of 30 days for individuals moving through preferred woodland habitat (Morvan et al., 1978), which might indicate that this absolute distance represents the upper limit of the life-time dispersal capability of wood cricket. It is likely, though, that individuals choosing to disperse away from woodland habitat through the relatively unfavourable matrix are unlikely to establish new populations, unless they encounter suitable woodland habitat enabling them to reproduce.

Previous studies of the development of the perceptual ability of wood cricket within natural environments have revealed that adults show a tendency to orientate themselves towards contrasting terrestrial features (Campan & Gautier, 1975; Beugnon, 1979; Mieulet, 1980). This ability is not universal among invertebrates; for example, the ability to orientate towards terrestrial cues was found to be minimal in a wolf spider species (Bonte et al., 2004). However, in the current study it was revealed that the perceptual range of wood cricket adults had an upper limit between 40 and 50 m when released from a mature woodland edge. This value is larger than that obtained (30 m) for a habitat-specialist butterfly species that was released at different distance from its preferred habitat of wet meadow/peat bog environments (Schtickzelle et al., 2007). This relative high ability of orientation might help explain why some adult wood crickets actively disperse away from suitable habitat, being able to navigate towards distant terrestrial cues. More importantly, this observation also gives an indication for when woodland fragments can be considered functionally disconnected for wood cricket (Crooks & Sanjayan, 2006). Together with the maximum distance (55 m) that was observed for males penetrating unfavourable matrix habitat, it is suggested that woodland fragments separated by more than 50-60 m of non-woodland matrix habitat, might therefore be considered as effectively isolated for this species (also see Chapter 2).

Establishing a woodland habitat network under these circumstances might prove beneficial for wood cricket. The development of habitat corridors and 'stepping stones' between woodland fragments that are further apart than 60 m could be a useful conservation strategy. The positive effect of maintaining linear features within an agricultural matrix in terms of colonisation success has been shown in detailed studies on Roesel's bush-cricket (*Metrioptera roeseli*) (Berggren et al., 2001; Berggren et al., 2002). Results suggested that these features helped in facilitating dispersal and the persistence of this cricket species within the wider landscape (Berggren et al., 2001; Berggren et al., 2002). For wood cricket, corridor functioning would be highly dependent on factors such as tree and ground vegetation cover, leaf litter presence and the geographical orientation of the corridor edges (see Chapter 3). Edges represented by short vegetation in the transition zone between grazed grassland directly bordering mature woodland habitat, were found to be more readily used than edges characterised by tall herbaceous vegetation and young tree regeneration (e.g. Site 2 & 8). Maximum movements of wood cricket were recorded along mature woodland edges up to 27 m (Site 2) and 29.5 m (Site 1) and only up to 8.5 m along the taller vegetation edges represented by the newly developed corridors (e.g. Site 2) (see Table 28). Particularly over time, no wood cricket were observed or heard in the latter edge habitats. Together these observations indicated that newly created corridors possibly need to 'mature' to such an extent that the habitat matches the requirements of wood cricket before the species will be inclined and able to use it, as suggested for other species (Gruttke, 1994; Bennett, 1999, 2003; Bailey, 2007). Another key factor determining corridor functioning was the geographical orientation of the edge. Wood cricket populations were not found to progress along an east-facing suitable habitat edge over a period of 2 years (Site 1), but were found to move along a south-facing edge up to 27 m over 60 days (Site 2) (see Table 28). These findings indicate that corridors can potentially function if suitable edge conditions are present. The ongoing investment and effort in creating woodland habitat networks therefore has the potential to facilitate the spread and population viability of wood cricket, given enough time.





7 Thesis discussion

7.1 Introduction

Current woodland restoration programs are increasingly looking at large scale restoration schemes in order to increase woodland cover and connectivity (Humphrey et al., 2003; Humphrey et al., 2005). The development of habitat networks has become a major conservation strategy in recent years, aiming at reversing the negative effects of habitat loss and fragmentation (Bennett, 1999, 2003; Bennett, 2004a; Crooks & Sanjayan, 2006). However, the basic assumptions underpinning such strategies are largely untested for species associated with woodland habitat (Bailey, 2007). Furthermore, the lack of information on dispersal ability of many woodland taxa (Dolman & Fuller, 2003), makes relevant theories describing spatial population dynamics, for instance metapopulation theory (Hanski & Gilpin, 1997), potentially inadequate for explaining species presence and persistence within woodland landscapes. For many woodland invertebrate species, local scale processes are potentially more important in terms of species persistence, especially for those species showing high dependence on woodland habitat conditions and those that have a limited dispersal ability (Tscharntke et al., 2002). The applicability of these large scale concepts and principles for woodland-associated invertebrates therefore needed to be evaluated (Dolman & Fuller, 2003).

The importance of examining a range of spatial and temporal scales to address issues in ecology (Wiens, 1989) was illustrated by the results of this project. First, factors influencing wood cricket (*Nemobius sylvestris*) presence measured at different spatial scales were found to change and differ in importance (Chapter 2 & 3). Both factors measured at a fine scale within woodlands and factors measured at coarser landscape scales were able to explain wood cricket presence, but differed in explanatory power (Logistic regression: Chapter 2 & 3). This indicated that key factors predicting wood cricket presence and their importance changed at different spatial scales, as has been found in other multi-scale studies on single species (e.g. Rukke & Midtgaard, 1998; Rukke, 2000). Second, the systematic review, examining movement rates of woodland-associated invertebrates, revealed a large variety of spatio-temporal measures used (Chapter 4). Some studies examined range expansion of species on a yearly basis at scales ranging from meters (Porter et al., 1988; Holway, 1998) to kilometres (Liebhold et al., 1993), whereas others looked at movement strategies using fine spatio-temporal scales of m min^{-1} (Hagvar, 2001; Ross et al., 2005) or m sec^{-1} (Haddad, 1999). Furthermore, where different techniques were used at different spatio-temporal scales, considerable differences in rates were sometimes obtained (e.g. Kennedy, 1994; Chapter 5 & 6). Translating values into one uniform spatio-temporal rate in most cases would be unrealistic (e.g. Levin, 1992); therefore I had to take this scaling issue into account in order to produce valid comparisons between the habitat specialism groups. Therefore, only rates with the same spatio-temporal scale (m day^{-1}) were and could be used for further analyses (Chapter 4).

Finally, the dispersal experiments of wood cricket found differences in dispersal ability and related processes when assessing different spatio-temporal scales (Chapter 5 & 6). For instance, at small spatial scales the straight-line distances that were achieved by nymphs and adults through leaf litter were found to be significantly different and averaged 16.0 and 27.8 cm min^{-1}, respectively (Chapter 5). This would translate to distances of up to 9.60 – 16.68 m $hour^{-1}$. However, at larger spatio-temporal scales, no differences were found between the straight-line movement rate for dispersing nymphs and adults. Furthermore, for both life-stages only a quarter of the population was observed to be able to cover straight-line distances of up to 2.91 m on a daily basis with the other 75% moving less (Chapter 6). This indicated that with increasing spatio-temporal scales of investigation, the observed absolute distances moved decreased and differences between life-stages changed. Altogether, these examples highlighted the fact that species responses and relationships changed when using different spatial and temporal scales of investigation (Wiens, 1989; Levin, 1992). From the onset of this study, it was not known at what scales wood cricket would operate and what processes would be important in terms of their colonisation success. Identifying what the appropriate scale should be for wood cricket conservation was therefore one of the key issues that needed to be addressed in this research project.

This project was designed to address these questions and gaps in knowledge with a focus on wood cricket and related woodland-associated invertebrates. This chapter focuses on assessing whether current woodland management initiatives and policy are appropriate for the conservation of wood cricket and similar woodland invertebrate species (Objective 3, see 7.2). The sub-objectives that will be addressed are: (1) to determine the appropriate scale for conservation directed at wood cricket and associated invertebrate species, and (2) to evaluate the potential gain of creating forest habitat networks for wood cricket and associated species. Furthermore, this chapter is aimed to critically evaluate the research project as a whole and to give further direction to future research and conservation management.

7.2 Methods

Project objectives:

1. To review the empirical evidence regarding the dispersal ability of different species and functional groups of organisms, in relation to their ecological traits and the characteristics of wooded landscapes.
2. To analyse the key factors influencing species colonisation of woodlands, with particular reference to processes operating at the landscape scale, through a programme of field-based research.
3. To examine the potential impacts of current approaches to development and management of wooded landscapes on species composition.

Each chapter presented in this thesis addressed one or a specific part of the original project objectives. For each chapter, these objectives were translated into specific aims matching the context of the individual investigations that were carried out. Objective 1 was addressed in Chapter 4; Objective 2 was addressed in Chapters 2, 3, 5 & 6; and Objective 3 is addressed in this chapter (see Chapter outline and aims; Chapter 1).

The key processes that were examined in this project were dispersal and colonisation of species associated with woodland habitat (see Project objectives). For the fieldwork program (Objective 2), these issues were addressed using a multi-scales approach (Chapter 2, 3, 5 & 6; Figure 23). Fieldwork was performed in and around the woodland fragments on the Isle of Wight (Figure 22) and data were gathered and analysed across a range of spatio-temporal scales (Chapter 2, 3, 5 & 6; Figure 23). Furthermore, prior to the detailed investigations on dispersal of wood cricket (Chapter 5 & 6), a systematic review was carried out examining the dispersal ability of different woodland-associated invertebrates (Objective 1; Chapter 4). The review was used to explore the factors affecting dispersal ability of woodland invertebrates and to attempt making generalisations in terms of habitat specialism groups (Chapter 4). The key results and factors influencing wood cricket presence and colonisation found in the fieldwork program (Chapter 2, 3, 5 & 6) are displayed in Figure 23, and together with findings from the systematic review (Chapter 4) will be further discussed in the following sections.

7.3 Discussion of results

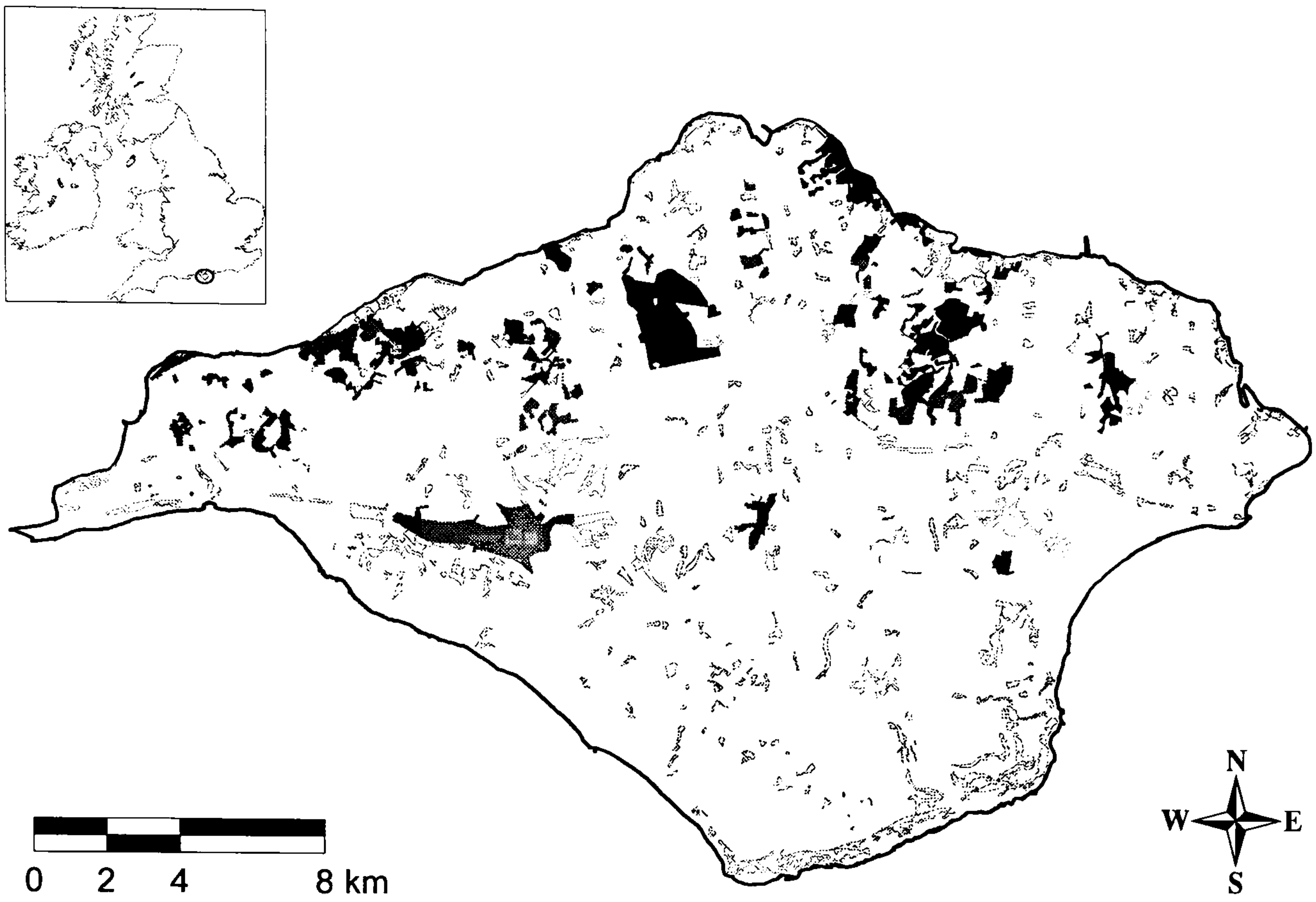


Figure 22: Distribution of wood cricket (*Nemobius sylvestris*) on the Isle of Wight as determined by the landscape scale survey (Chapter 2). The black patches represent woodlands where wood cricket was found. The grey and black patches together represent all the surveyed woodlands (see Chapter 2). The white, grey and black patches together represent all the woodlands on the island. Derived from digital map based on the National Inventory of Woodland and Trees (NIWT) (Smith & Gilbert, 2003).

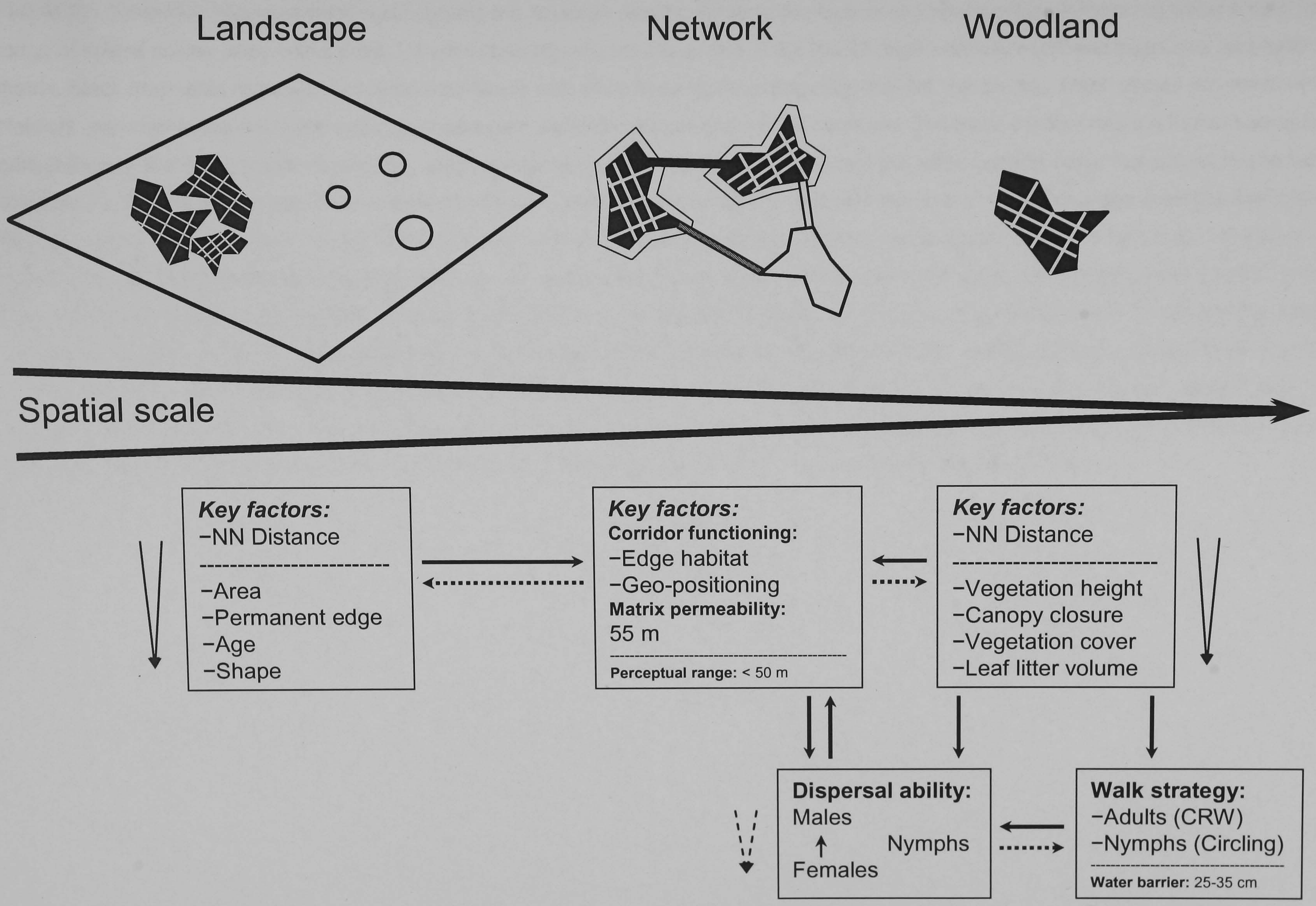

Landscape
Network
Woodland
Spatial scale
Key factors:
-NN Distance
-Area
-Permanent edge
-Age
-Shape
Key factors:
Corridor functioning:
-Edge habitat
-Geo-positioning
Matrix permeability:
55 m
Perceptual range: < 50 m
Key factors:
-NN Distance
-Vegetation height
-Canopy closure
-Vegetation cover
-Leaf litter volume
Dispersal ability:
Males
Females
Nymphs
Walk strategy:
-Adults (CRW)
-Nymphs (Circling)
Water barrier: 25-35 cm

Figure 23: Schematic representation summarising the research results, showing the factors and relationships influencing wood cricket colonisation across the range of spatial scales used in this project. Landscape: represents the outline of the Isle of Wight with six woodland fragments embedded in the agricultural matrix. Black fragments represent occupied woodlands with white lines representing edge habitat (i.e. tracks). Open circles represent unoccupied woodlands. Network: represents two occupied and one unoccupied woodland interconnected by corridors. The black corridor has the highest potential to facilitate wood cricket dispersal and population interaction; grey corridor has an intermediate potential and the white corridor has a low potential (see further text). Thin black lines around the occupied fragments indicate the distance wood cricket is able to penetrate the matrix. Woodland: see previous description of black fragments. Box diagram: indicates the key results of the research project obtained across the range of spatial scales that were included in the investigation. The boxes are placed under the features/scales where the results were obtained (e.g. walk strategy was obtained at a fine spatial scale (≤ 16 m^2) within and outside woodlands). Landscape – *Key factors* (Chapter 2); Woodland – *Key factors* (Chapter 3); Network – *Key factors*: Corridor functioning, Matrix permeability, Perceptual range (Chapter 6); Network/Woodland – Dispersal ability (Chapter 6); Woodland – Walk strategy (Chapter 5) and Water barrier (Chapter 6). Wedge arrows indicate a decrease in: (1) spatial scale (middle wedge arrow pointing to right), (2) importance of the factors determining wood cricket presence (solid wedge arrows pointing downward), (3) dispersal ability (dotted wedge arrow pointing downwards). All other arrows indicate interactions and/or influence of the individual factors upon each other (see further text). Orientation for all schematic drawings is North.

Figure 24: Wood cricket population dynamics within a large woodland fragment (Firestone copse: 99.5 ha) embedded in the agricultural matrix on the Isle of Wight. Thick black outline represents the woodland periphery. Within the woodland boundary: grey areas represent inhabited wood cricket locations; white areas are predominantly closed canopy woodland stands including pure coniferous, broadleaved and mixed stands; dotted highlighted areas represent locations with permanent suitable edge habitat where large 'source' populations of wood cricket are present; straight single thin lines indicate different woodland stand sections; convoluted single thin lines indicate paths; highly convoluted single thin lines indicate small streams; double thin lines represent woodland tracks or roads; solid arrows indicate likely routes taken by wood cricket to disperse through this woodland (mainly along edges or through open canopy stands); dotted arrows indicate routes that were used but are now unsuitable to facilitate dispersal (mainly former clear cuts and thinning/coppice sites); + indicate locations where wood cricket was present; x indicate locations where wood cricket was absent. This map is based on Ordnance Survey MasterMap data acquired under a 'Contractor licence for the use of Ordnance Survey Digital Mapping Products' with the Forestry Commission, UK. Orientation is North.

7.3.1 Landscape scale (Chapter 2)

At the landscape scale, wood cricket populations were found to be evenly distributed over the northern part of the Isle of Wight (Chapter 2; Figure 22). This study further indicated that wood cricket was found in areas containing predominantly large woodland fragments in close proximity to each other, with ancient woodland characteristics and with a high amount of edge habitat (Landscape; Figure 23). This implies that areas where all these criteria are met have the highest potential to support wood cricket populations on the Isle of Wight. For conservation management purposes, the habitat model that was developed in this study might prove useful in making preliminary landscape suitability assessments (Fleishman et al., 2002). Based on fragment size and proximity to the woodland fragments in the wider landscape, this model can be used to make predictions where wood cricket can be or potentially is present in the landscape. Furthermore, in this study, landscape variables influencing wood cricket presence were extracted from readily and often freely available 'remote sensed' digital data. Assessing the landscape to identify priority areas for wood cricket conservation can therefore be relatively straightforward using GIS software (e.g. ArcGIS) and/or aerial photography (e.g. Google Earth) (Chapter 2 & Figure 22). For instance, wood cricket was mainly found in areas with larger woodlands in close proximity to each other, which can easily be identified (Figure 22). These areas can then be analysed in more detail regarding the presence of ancient woodland site characteristics and the amount of edge habitat present. This quick preliminary assessment can save time when directing further efforts to verify the actual status of wood cricket presence in the field.

On the Isle of Wight, targeted and untargeted restoration schemes have been implemented to reverse the effects of fragmentation and increase the amount of woodland area (Forestry Commission, 2003; 2005; 2006a; Quine & Watts, 2007). Untargeted woodland expansion has been funded throughout the UK with limited restrictions on where new woodland should be created (Forestry Commission, 2003). However, initiatives were also undertaken specifically focused on extending and creating woodland on strategic locations in order to increase the level of connectivity between existing semi-natural woodland fragments (Forestry Commission, 2005). In their study on the effectiveness of both schemes, Quine & Watts (2007) found that a more targeted approach showed a higher 'de-fragmentation' effect at the landscape scale than untargeted woodland expansion. A similar result was found in a simulation study by Lee & Thompson (2005) where random addition of woodland within a fragmented landscape resulted in a poorer performance regarding de-fragmentation than more targeted habitat expansion. These examples highlight the effectiveness of a more targeted approach in increasing the level of structural or physical connectivity between habitat patches within the landscape.

On the Isle of Wight, wood cricket was found to be present in the areas that were undergoing these targeted woodland expansions (e.g. Briddlesford, see Chapter 6). Increasing structural connectivity often positively influences the functional connectivity for species (Crooks & Sanjayan, 2006; Baguette & Van Dyck, 2007). Functional connectivity is highly species dependent and involves to what extent a species is able to move through the landscape and/or interact between distinct habitat patches (Crooks & Sanjayan, 2006). In an agricultural landscape, based on the species' dispersal ability, the intervening land-use type (i.e. the 'hostile' matrix) and distance that separates distinct habitat patches are often the main factors determining this level of functional connectivity. The current pattern of distribution of wood cricket suggests that areas where fragments are relatively large (> 9.5 ha) and in close proximity to each other (< 50 m) (see Figure 22 & Figure 23, Landscape – Key factors) represent a higher level of functional connectivity for the species. Therefore, a targeted approach in restoring, connecting and increasing woodland habitat in areas where distances between fragments are relatively small seems highly relevant to effectively increase the structural and functional connectivity for wood cricket and possibly other similar invertebrate species.

7.3.2 Woodland scale (Chapter 3)

One of the key factors found in the landscape scale study that influenced wood cricket presence indicated the importance of edge habitat availability for wood cricket within woodlands (Permanent edge; Chapter 2). This was confirmed by the pattern that was observed of individual wood cricket populations within woodlands. This pattern revealed that most populations were found in edge habitat along tracks, the woodland periphery, in clearings and in gaps (Figure 24). In particular, provision of enough permanent edge habitat within the interior of woodlands was found to be highly important for maintaining a sustainable wood cricket population (Chapter 3). As a direct result of permanent low cover of ground vegetation, low canopy closure and high availability of leaf litter (Woodland – Key factors (below line); Figure 23), large 'source' populations were found to develop at these permanent edge habitat locations (Brouwers, pers. obs.). It was further found that large woodlands provided more permanent edge habitat, hence the strong relationship found between wood cricket presence and woodland area (Area; Chapter 2). Large woodland areas were generally found to be more heavily and frequently managed than smaller woodlands (Brouwers, pers. obs.). These activities seemed closely positively correlated with the amount of available habitat for wood cricket. In these larger managed woodlands, commercial tree harvesting and conservation activities (e.g. re-instatement of coppice rotation) not only creates more open habitat but also involves presence and maintenance of open tracks and roads for tree extraction (e.g. Firestone copse; Figure 24). Furthermore, the Isle of Wight is and has been the focus of extensive woodland restoration efforts including the restoration of planted ancient woodland sites (PAWS) by removing non-native tree species (Defra, 2005; Forestry Commission, 2006a; 2007). These activities were found to increase canopy openness, and with initial low levels of ground vegetation cover, improved habitat conditions for wood cricket on the ground by the increased amount of sunlight availability. Active management of woodlands therefore has a positive effect on wood cricket populations by providing more suitable habitat.

An important factor influencing presence of wood cricket was the level of sunlight availability on the ground. One of the main factors influencing these conditions was the openness of the canopy. The main features characterised by more or less permanent open canopy conditions were found to be woodland tracks and the woodland periphery. Wood cricket occurrence was strongly positively related with the proximity to occupied locations along these permanent features (Woodland – NN Distance; Figure 23). Furthermore, an investigation of the spatial pattern of wood cricket populations within a large woodland fragment revealed that these features also seem to play a key role in the process of wood cricket dispersal and population spread (Figure 24). Wood cricket seemed to spread and disperse from the main source populations within the woodland by using edges of open tracks and forest peripheries (Figure 24). Almost all populations that were found were more or less (inter)connected with the source populations this way (Figure 24). In Figure 24, the most likely routes that wood cricket use(d) are indicated by arrows. These routes were largely based on the openness of the canopy made by direct observations within this woodland. However, where these routes clearly correlated with the (permanent) tracks and roads within the woodland (Figure 24), use of GIS based imagery (e.g. OS MasterMap imagery in ArcGIS) and/or aerial photography (e.g. Google Earth) could be helpful in making a quick assessment of the permeability of occupied woodland areas. It was further observed that wood cricket could rapidly colonise (i.e. within 1-2 summers) new felling/coppice clearings that were created adjacent to occupied woodland tracks (Brouwers, pers. obs.). Where felling and management interventions often take place in rotation, strategic planning of these activities could benefit wood cricket for instance by focussing these activities around the 'corridors' used by the species to spread through the woodlands.

To summarise; ride and track edges, woodland peripheries and open areas within woodlands (e.g. coppice sites) were found to be the main habitat locations where wood cricket could be found. These features were also found to be preferred by a wide range of woodland-associated invertebrates and therefore are highly important for maintaining woodland invertebrate diversity (Bratton & Andrews, 1991; Warren & Key, 1991; Greatorex-Davies et al., 1994). Additionally, for wood cricket, the woodland rides and tracks were not only important as habitat locations but also seemed to function as conduits facilitating their spread within woodlands. Within woodland management focusing on maintaining suitable habitat is therefore equally crucial (as landscape scale initiatives) to ensure the persistence of wood cricket and similar invertebrate species.

7.3.3 Network scale (Chapter 5 & 6)

Colonisation success of wood cricket was found to be dependant and influenced by multiple factors (Figure 23). The factors that influence the dispersal ability of wood cricket will largely determine the potential success of a habitat network. The ability to disperse away from suitable habitat through unfavourable habitat conditions was not affected by potential physical barriers within the landscape such as small watercourses (Water barrier; Figure 23) and was possibly positively influenced by their ability to orientate themselves towards distinct habitat features in the landscape (Perceptual range; Figure 23). Furthermore, both nymphs and adults were found to have similar dispersal power, and females seemed less inclined to disperse than males (Dispersal ability; Figure 23). However, in order for individual woodland fragments to potentially be colonised, it was found that they had to be close together (Landscape; Figure 23, median distance between occupied woodland fragments: 50 m; see Chapter 2). A possible upper bound for the maximum distance between individual fragments was found to be 55 meters in this respect (Matrix permeability; Figure 23). Therefore, for wood cricket, fragments separated more than 50 – 60 m from each other by non-woodland matrix habitat are thought to be effectively isolated.

When distances between fragments exceed this maximum distance, connectivity could be established by developing corridors between individual fragments (Network; Figure 23). However, in order for corridors to function, edge habitat would have to meet the same basic requirements as was determined here within woodland (Woodland – Key factors (below line); Figure 23). The ability of wood cricket to disperse along corridors was mainly driven and influenced by the physical structure of the edge and positioning of these corridor features within the landscape (Corridor functioning; Figure 23). The edges that were found to function best were mature woodland edges directly bordering arable/grassland characterised by low ground vegetation cover (Chapter 6). A further decisive habitat requirement was the exposure of a corridor edge to the sun, which is likely related to the ambient temperature at ground level (Corridor functioning: Geo-positioning; Figure 23; Chapter 6). As an example, in Figure 23 (Network), if all other edge habitat requirements are met, the black corridor between the occupied woodland fragments has the highest potential to act as a conduit between populations. This is so because it runs in an East – West direction, maximising exposure of its South – facing edge to the sun (Figure 23). Along this type of edge, wood cricket was observed to spread (Site 2; Chapter 6). Furthermore, although the white corridor is shorter, the grey corridor has a higher potential to facilitate the colonisation process of the unoccupied woodland, again because of the higher exposure of its edge to the sun (Figure 23).

Providing permanent suitable breeding habitat along corridors also seemed to influence corridor functioning. This is likely related to the presence of a well-developed leaf litter layer (Brown, 1978). No evidence was found of wood cricket establishing viable populations within semi-natural grassland or along hedge edges, both of which lack a suitable leaf litter layer. Along mature woodland edges bordering grassland or arable land, a situation common in fragmented agricultural landscapes, wood cricket was able to establish viable populations where leaf litter habitat was available (Site 1; Chapter 6). Furthermore, presence of a well-developed leaf litter layer was only found along mature woodland edges, indicating the considerable time that corridors possibly need to develop in order to meet the habitat requirements for wood cricket (Chapter 6). This has also been found for other ground-dwelling woodland-associated species. A nine year long study examining the natural spread of carabid species into newly developed linear tree plantations revealed that no specialised woodland species moved into these features (Gruttke, 1994), indicating their ineffectiveness as a corridor to facilitate dispersal. The main argument given for this result was also the immaturity of the woodland habitat represented within these features making it unsuitable for the specialist beetle species to live in (Gruttke, 1994).

When mature woodland edges are present with suitable edge habitat for wood cricket to move along, overall wood cricket showed a low tendency to disperse. It is likely that the majority of wood cricket will stay in areas where their basic habitat requirements in order to survive and reproduce are met, as was observed within the enclosures (Chapter 6) and in previous studies on wood cricket (Morvan & Campan, 1976; Morvan et al., 1977; 1978). At 'Site 2' (Chapter 6), over 60 days wood cricket was found to have not progressed further than 27 m along a South-facing mature woodland edge through suitable habitat. Furthermore, in two separate studies conducted in France, mark – re-sight experiments conducted within woodlands with suitable leaf litter habitat revealed that over 30 and 180 days, wood cricket did not disperse further than 40 – 60 m and 40 m respectively (Morvan & Campan, 1976; Morvan et al., 1978). Although the nymphal dispersal was not included in these observations, the total life-time distance that wood cricket individuals will disperse probably does not exceed a distance of 60 m. Therefore, I argue that individual patches of breeding habitat along corridors that are further apart than this distance are unlikely to be colonised. Additionally, males were found to be the primary dispersers attracting females in their wake (Dispersal ability, Figure 23). It is however not known if wood cricket females have a similar tendency to disperse and reach similar maximum dispersal distances as observed for males. This is particularly important in terms of actual dispersal success, where new populations can only be established if females show the same dispersal tendency and ability as males. This issue needs to be addressed in further research in order to get a full understanding of the dispersal ability of this species.

To summarise, these results indicate that dispersal of wood cricket can potentially be facilitated by creating woodland habitat networks. Woodland corridors and possibly woodland 'stepping stones' have the potential to be functional provided that suitable edge habitat is available at ground level at regular intervals (< 60 m apart). Furthermore, creating new woodland corridors and 'stepping stones' will increase the available woodland edge habitat over time. This particular habitat is favoured by many other woodland invertebrates (Bratton & Andrews, 1991; Warren & Key, 1991; Greatorex-Davies et al., 1994; Key, 1995; Diekotter et al., 2005), so creating woodland habitat networks will possibly benefit wood cricket and a range of additional species, given enough time to develop.

7.3.4 Transferability of the results (Chapter 4)

This thesis focused on woodland invertebrate species, with special reference to non-flying ground-dwelling species. However, the main body of work was conducted on a single species only (i.e. wood cricket). The main advantage of focusing on a single species, which was fully borne out by the results of this project, is the much greater depth of information that can be obtained. However, one of the main limitations of single-species studies relates to whether the results obtained are relevant for other species. When studying a single species, it preferably should represent this broader group of similar species (Ranius, 2006) in order to make useful generalisations. The systematic review was partially undertaken to identify a group of species for which wood cricket might be considered as representative (Chapter 4). The review revealed that the mean dispersal rate for dispersing wood cricket lies closest to that of ground-dwelling invertebrate species most strongly associated with woodland (Chapter 4; 'Group 1'). This level of habitat specialism was consistent with the habitat preferences found for wood cricket, and therefore wood cricket can be seen as representative of this particular group of woodland-associated invertebrates.

Additionally, Bowne & Bowers (2004) performed a review of the scientific literature similar to the systematic review performed in this study (Chapter 4). Their aim was to provide basic statistics on movement of species between habitat patches (Bowne & Bowers, 2004). As discussed in Chapter 4, in this and their review study, comparable movement rates for mobile butterflies and ground-dwelling beetles were obtained that were measured at different spatio-temporal scales. This result might indicate a potential link between absolute distances travelled within habitat on a daily basis and the fraction of a population dispersing between distinct habitat fragments during one life-cycle. Movement rates obtained at small spatio-temporal scales within continuous habitat might therefore reflect the dispersal ability of the species at larger scales between habitat fragments. In terms of woodland invertebrate dynamics within fragmented landscapes (metapopulation theory (Hanski & Gilpin, 1997)), this might be a very useful generalisation to use in conservation management and planning. However, this relationship needs to be explored in more depth for a wider range of woodland invertebrate species in order to justify this kind of generalisation.

7.4 Management implications

7.4.1 Population dynamics / metapopulation consideration

The current level of fragmentation and lack of connectivity between woodland fragments across the Isle of Wight suggests that for wood cricket within most areas a metapopulation structure (see Hanski & Gilpin, 1997) operating between woodlands is unlikely to exist. Similar to specialised beetle species (Driscoll, 2005), the results of this study suggests that for wood cricket, individual woodlands function as distinct islands operating as more-or-less closed systems within the agricultural matrix. Extinctions within fragments that are further away than 60 m from another populated fragment are therefore likely to be permanent. However, the landscape scale survey also suggests that in some areas where the level of fragmentation is low (i.e. woodlands are in close proximity to each other), interactions between fragments are occurring. This further suggests that in these specific areas a functional form of metapopulation dynamics between woodlands might still exist.

It is further thought that between distinct habitat patches within occupied woodlands also a form of metapopulation dynamics seems to apply. The species was typically observed in areas of open habitat where clearings and coppice/thinning activities had taken place. However, ground vegetation development was observed to be very vigorous and often covered these areas within one or two growing seasons after management interventions had taken place (Brouwers, pers obs). In these cases wood cricket populations were observed to disappear and/or retract to other temporary open habitat locations. The 'classic' metapopulation structure for wood cricket therefore does not seem to apply within woodland habitat (Hanski & Gilpin, 1997). In this case a nonequilibrium or habitat-tracking metapopulation structure seems to accurately describe the dynamics of this species within woodlands (Harrison & Taylor, 1997). This means that within the boundaries of the individual woodlands, wood cricket population dynamics are driven by the availability of suitable habitat. Distinct habitat patches in this particular metapopulation structure are only temporary, where in the case of wood cricket they become unsuitable after ground vegetation develops. This particular form of population dynamics driven by the succession of habitat was also observed for butterflies (Thomas, 1994). Thomas (1994) further reviewed that for many other (invertebrate) species, including butterflies living in woodland clearings and wide woodland tracks, this system is the main driver determining population dynamics and persistence. It is therefore important to maintain and create 'disturbance' habitats within woodlands in order to preserve wood cricket and other woodland dependant invertebrate species (Warren & Key, 1991).

7.4.2 Conservation scale

In order to direct conservation efforts for a particular species it is necessary to determine at what scale a species operates. Therefore, this investigation on wood cricket was undertaken at multiple scales. The results of the investigation indicate that processes determining wood cricket presence both operate between distinct woodland fragments and within woodlands (see previous paragraph; Nearest occupied neighbour distance, Chapter 2 & 3). The results suggest that interactions between woodland fragments do take place in areas where there is a low level of fragmentation. However, interactions between woodlands are already thought to be highly unlikely when they are separated more than 60 m from each other. Furthermore, wood cricket was also found to be persistent in actively managed woodlands that had a long history of being isolated within the agricultural matrix, indicating that without interactions with other populated woodlands, this species is also able to persist. Conservation for wood cricket can therefore focus on efforts carried out at relative small spatial scales equally within and between woodlands, preferably creating networks of suitable habitat areas no further than 60 m apart.

7.4.3 Wood cricket conservation management options

Wood cricket is a 'Species of Conservation Concern' in the UK (NBN Gateway, 2007). On the Isle of Wight wood cricket is therefore included in the local biodiversity action plan (Isle of Wight Biodiversity Action Plan Steering Group, 2000). To maintain viable populations and improve habitat conditions for wood cricket on the Isle of Wight and other wood cricket locations, a number of strategies can be adopted. Conservation aiming for the long-term persistence within the landscape of this species can focus on creating habitat networks in areas that include clusters of woodland fragments that are in relatively close proximity to each other and can focus on continuously providing and maintaining suitable habitat locations within woodland.

The current situation on the Isle of Wight (and in most of the UK) is that between most woodland fragments the intervening matrix stretches more than 60 m and does not provide suitable breeding habitat (i.e. well-developed leaf litter layer) making most woodland fragments for wood cricket effectively isolated from each other. Developing habitat networks under these circumstances could possibly provide the necessary gene flow for the overall long-term persistence of the species within the fragmented landscape. Corridors and 'stepping stones' could further prove useful as escape routes and habitat refuges, when habitat conditions within woodlands deteriorate, for instance with a decrease in management activity.

There are however a number of reasons why the creation of habitat networks, compared to other management options, arguably should not receive the highest priority for the conservation of this species. (1) The creation of habitat networks involves high costs with practically no financial return. Compared to traditional forestry activities that already take place in woodlands that are equally beneficial financially and for the persistence of this species, the habitat network approach seems less necessary. (2) Furthermore, one of the reasons behind the creation of habitat networks is to provide escape routes for species in terms of climate change/global warming. However, the necessity for this species to escape adverse conditions will be unlikely, as this species, together with other Orthoptera, particularly favours warm(er) conditions (Marshall & Haes, 1988). (3) Finally, there is still a large amount of uncertainty if wood cricket will be able and willing to use the corridor features and/or 'stepping stones' that recently have been developed within the framework of habitat network initiatives. These network features first need to mature sufficiently to provide the necessary woodland habitat characteristics that this and other woodland specialist species require. In the long run, habitat networks might prove to be important for the overall persistence of wood cricket within the landscape. However, the time lag that is involved before wood cricket will be able to benefit from these initiatives make them currently less effective than activities within woodland where the basic habitat requirements (i.e. well-developed leaf litter layer) are generally already present. Therefore, until woodland features within recently created habitat networks had time to develop and were tested to prove their effectiveness, conservation efforts for this species, particularly at this moment in time, should equally focus on providing continuous suitable habitat within woodlands.

Areas providing suitable edge habitat of only 100 m^2 are thought to already provide a firm basis to sustain viable wood cricket populations. The species demands early successional habitat conditions related to natural and anthropogenic disturbances within woodland habitat. Current management strategies incorporating regular felling and restoration activities within woodlands (e.g. Forestry Commission, 2007) are highly beneficial in terms of creating suitable habitat conditions for this species. It is advised to maintain at least 30% broadleaf, preferably oak (*Quercus* spp.), tree cover within the boundaries of the woodlands to provide and maintain the necessary leaf litter layer to secure successful reproduction. To maintain connectivity between populations and provide additional habitat within woodland, open tracks and rides should be maintained by preventing the tree canopy to close and yearly mowing/removal of the vegetation along the track edges will be equally beneficial. Providing larger areas characterised by permanent open habitat conditions maintained by regular management activities (e.g. public picnic areas and car parks; see circular source population in Figure 24) was further found to be highly beneficial for the persistence of this species within individual woodlands and should therefore be continued.

7.4.4 Additional management considerations

7.4.4.1 Grazing

A factor clearly affecting the habitat development within woodlands on the Isle of Wight is the absence of wild ungulates (i.e. deer) on the island (Pope et al., 2003). The development and natural regeneration of the ground vegetation after management activities such as coppice, felling and mowing of ride edges is therefore not hampered by browsing and grazing. As a result, ground vegetation development was observed to be very vigorous and often covered open areas within one or two growing seasons after management intervention had taken place (Brouwers, pers obs). This study revealed that this rapid successional development is highly unfavourable for wood cricket persistence. To prevent this adverse effect, annual active clearance of vegetation such as mowing of bramble could be one of the management options. However, an alternative management approach could also involve the introduction of some form of grazing regime within woodlands for instance by domesticated grazing animals. One of the main strongholds of wood cricket in the UK is the New Forest (Richards, 1952; Marshall & Haes, 1988; NBN Gateway, 2007). The long history of grazing in this location has had a major impact on habitat structure, creating a shifting mosaic of open and closed woodland habitats (Vera, 2000). In particular, herbaceous undergrowth is heavily affected by this grazing regime, reducing it to a minimum in most wooded areas. As wood cricket is highly persistent (Marshall & Haes, 1988) and widespread across the New Forest (NBN Gateway, 2007), the influence of (large) grazing animals on the habitat seems particularly favourable for this species. Therefore, the introduction of some sort of grazing regime within woodlands might be a feasible and possibly cheaper alternative compared to other management interventions.

7.4.4.2 Re-introduction

During the landscape scale survey, at least 50% of the woodlands that were surveyed where wood cricket was absent included areas of suitable habitat that were large enough to sustain viable wood cricket populations. Some of the surveyed woodlands, particularly those of secondary origin might never have been occupied. However, in other woodlands, the species might have gone extinct due to a lack of management activities or the replanting of these sites with coniferous tree species. Either way, a final consideration could involve re-introduction of the species within woodland areas where it is currently absent. This strategy is likely to succeed when suitable habitat is available (Brouwers, pers. obs; Marshall & Haes, 1988). The present lack of functional mature corridors between woodland fragments on the Isle of Wight largely prevents the species from spreading naturally. This might justify re-introduction of the species to increase their overall distribution and persistence at the landscape level. However, its current distribution and overall persistence within the individual managed woodlands on the Isle of Wight suggests that it seems unnecessary to resort to this conservation strategy.

7.5 Project appraisal

The following section focuses on a critical appraisal of the work I undertook during this project. The considerations were mainly a consequence of the time constraints that were related to the individual fieldwork seasons and the total duration of the project. (1) Possibly the main weakness of this study was the fact that the main body of work was conducted using a single species only. Although it is recognised that focussing on one species is often the only option for detailed dispersal studies (Turchin, 1998), the inclusion of another species similar to wood cricket in the larger scale studies might have strengthened the overall findings. Including another species in the landscape scale study (Chapter 2) and/or woodland scale investigation (Chapter 3) might have proved useful in making comparisons between species, ultimately adding to our understanding of how woodland species utilise these features within the landscape. Repeating these investigations using a different woodland-associated species to compare with the existing datasets could be a feasible option for further research initiatives.

(2) For a more accurate analyses of the landscape scale distribution of wood cricket and related woodland patch variables, preferably more woodlands should have been covered during the landscape scale survey of 2005 (Chapter 2). Furthermore, most woodlands were only visited once which might have resulted in wrongfully classifying woodlands as being unoccupied. In both cases, it is likely that the actual distribution of wood cricket on the island was underestimated. Future work could therefore focus on the following: to obtain the actual distribution of the species, additional surveys could be performed possibly focusing on the larger fragments with ancient woodland characteristics. Furthermore, to obtain a more accurate result in terms of the

relationships that were found (Chapter 2), preferably all remaining woodland fragments should be surveyed systematically from the North of the island to the South. The additional presence/absence data obtained could easily be added to the existing dataset and re-analysed.

(3) The models that were developed for predicting wood cricket presence within woodlands were not statistically tested for their robustness with external datasets (Chapter 2 & 3). Future investigations should include collecting these easily obtainable datasets to confirm the applicability of these models within woodlands at other geographical locations. This could further strengthen the findings and applicability of these models as an assessment tool of habitat suitability for wood cricket within woodlands.

(4) This study highlighted once more the complexity of dispersal studies and stressed the fact that using a range of scales and techniques is an absolute must in order to get a clear understanding of the dispersal ability of invertebrates and possibly many other species. The main difficulties that were encountered with the various dispersal experiments here were directly related to these factors (Chapter 5 & 6).
(a) For the detailed movement studies, the design of contrasting habitats and the spatial scale of the grids might have influenced the movement strategy of the individual wood crickets that were released (Chapter 5). This possible bias in the data is hard to detect and only attempts can be made to eliminate these by analysing each path individually (Turchin, 1998), as was done in this current investigation.
(b) A further possible bias in the data that was collected during the experiments was the estimate obtained for the proportion of the population moving for wood cricket populations released within the enclosures (Chapter 6). Particularly for the smaller enclosures, the number of individuals reaching the periphery of the enclosures over time might have been underestimated. The experimental set-up did not allow individuals to move any further than a fixed straight-line distance, which might have resulted in individuals reversing into the interior habitat after reaching the enclosure periphery, leaving their actual dispersal ability undetected. The initial strategy using pitfall traps was designed to prevent this bias in the data. Although suitable for ground beetles (see Baars, 1979; Nelemans, 1988; Vermeulen, 1994), this method was found to be unsuccessful for wood cricket. It was observed that in the case of nymphs they were able to sense the presence of the traps and were therefore able to prevent being caught. This strategy was therefore abandoned for the release experiment with the adults assuming similar sensory capabilities as found in previous studies (Morvan &

Campan, 1976; Beugnon, 1979). Developing a more sophisticated trapping system at the periphery of the enclosures could solve this particular problem in future investigations.

(c) The spatial scale of the experimental enclosure set-up, time-scale of observations, and inclusion of the maximum dispersal distances derived from separate datasets might have influenced the overall fit of the dispersal curves that were derived in this study (Chapter 6). In particular, the data points that represented the long-distance dispersal events were extracted from data that was gathered at different spatio-temporal scales and under different more heterogeneous habitat conditions compared to the data obtained within the enclosures. The long-distance dispersal events, as in so many other studies (Turchin, 1998), were very hard to establish particularly for adult wood crickets. This was mainly due to the level of detection that could be achieved for this species in relation to the un-manipulated set-up of the release experiments (Chapter 6). As a result no long-distance dispersal events for adults were recorded that could be related to a precise temporal scale. Furthermore, for adult males an indication of their life-time dispersal ability could be obtained, however for the non-stridulating females no such recordings were made. Therefore, the dispersal ability of females remains largely unknown. The actual dispersal success of the species is however completely dependant on females that disperse to suitable habitat locations and produce a fertile brood to secure the development of a new population that can move further in following generations.

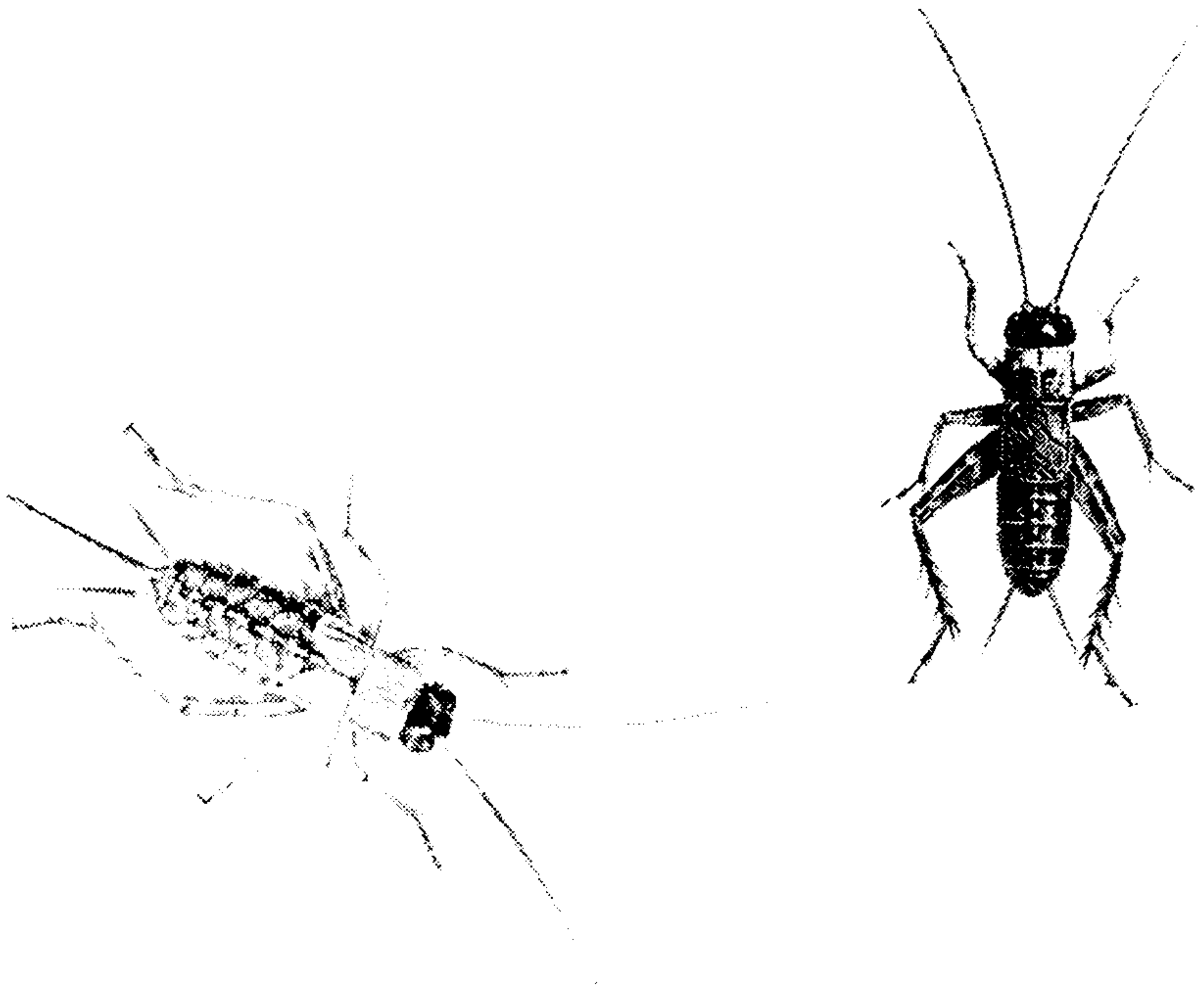
Future investigations should therefore focus on obtaining the actual dispersal ability of female wood cricket. This should be tackled by incorporating the ability of males to attract females. For males that were recorded to perform long-distance dispersal, females were unlikely to have been present, where they were heard performing their stridulation typical for a single male (Marshall & Haes, 1988). Therefore, first the attractive power of a stridulating male upon a female should be established, particularly to what maximum distance this attraction is still functional. Second, a natural spread experiment needs to be conducted using larger spatio-temporal scales than were used in this study. This could be achieved for instance by using larger circular enclosures and longer periods of monitoring. Preferably, the spread of the species should incorporate a complete life-cycle of the species. This is however practically impossible to accomplish in an experimental set-up, not only because of the logistics involved, but also because of the high risks of failure related to losses to predation and/or adverse weather conditions etc. A realistic alternative approach could be the introduction of the species in woodland areas/networks where they are currently absent as was done in a long-term study on Roesel's bush-cricket in Sweden (Berggren, 2001). Monitoring their natural spread over a long period of time (4-6 years) by simply surveying these areas on a yearly basis listening for multiple stridulating males could provide the basis to infer the overall dispersal ability and colonisation success of this species.

7.6 Knowledge contribution

This research project was designed to address the gaps in knowledge on: how woodland-associated taxa move through the landscape; how well they can disperse; and what factors and mechanisms influence their dispersal ability (Dolman & Fuller, 2003). Furthermore, this project was aimed to contribute to the evidence base of developing woodland habitat networks (Bailey, 2007) by investigating how woodland-associated species use corridors and how capable and willing they are to move outside their preferred woodland habitat. I performed an in-depth case study on wood cricket contributing to the gap in knowledge on how woodland-associated species that are restricted to movement over the ground move through the landscape. I further provided a useful review on the status of knowledge on woodland-associated invertebrates and their ability to move through the environment. The movement parameters gathered for wood cricket and other woodland-associated invertebrates presented in the review (Chapter 4) could further benefit modelling approaches, for instance to inform woodland habitat network design. Finally, although it is recognised that wood cricket should not be the sole indicator guiding conservation management and policy (James & McCulloch, 2002), the obtained knowledge provided a better understanding of the potential for corridor and woodland habitat network functioning within the wider landscape for this type of species.

7.7 Conclusion

This research project was designed to evaluate the relevance of conservation management and policy relating to future woodland creation initiatives that focus on the development of habitat networks. The results indicate that the overall success of woodland conservation lies in adopting a multi-scale and multi-management strategic approach (Lindenmayer & Franklin, 2002). Initiatives to increase woodland connectivity by creating habitat networks that target specific areas with a relative high amount of woodland fragments have a high potential to benefit invertebrate species persistence. However, restoration and re-instatement of traditional management activities within existing woodlands were found to be equally important for wood cricket and other woodland-associated invertebrates. Therefore, for non-flying invertebrate species both strategies should be applied to ensure that viable populations will be maintained within the landscape.



Appendix I: Publication plan

The chapters in this thesis (Chapters 2 – 6) were drafted as individual papers targeting specific scientific journals. These papers will be submitted for publication. The manuscript titles and target journals are listed below.

- The influence of habitat and landscape structure on the distribution of wood cricket (*Nemobius sylvestris*) on the Isle of Wight, UK. **Landscape ecology** (Chapter 2)
- Habitat requirements for the conservation of wood cricket (*Nemobius sylvestris*) on the Isle of Wight, UK. **Journal of insect conservation** (Chapter 3)
- Movement rates of woodland invertebrates: a systematic review of empirical evidence. **Ecological entomology** (Chapter 4)
- Movement strategy of wood cricket (*Nemobius sylvestris*) through different ground surface habitats. **Ecological entomology** (Chapter 5)
- Factors influencing dispersal of a woodland invertebrate: a case study of wood cricket (*Nemobius sylvestris*). **Ecological entomology** (Chapter 6)

Appendix II: Experimental designs

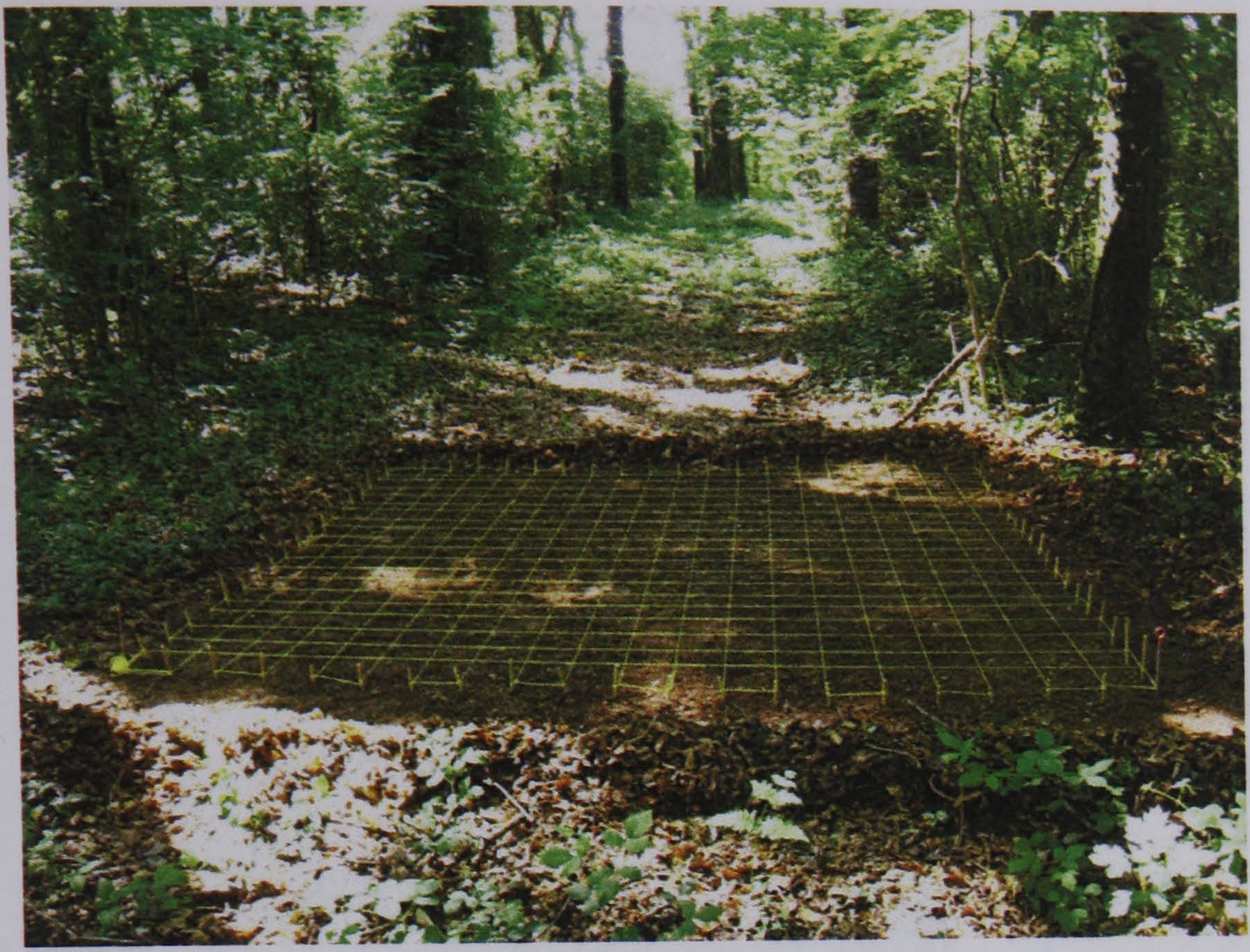
Experimental grids (Chapter 5)

Experiment 1

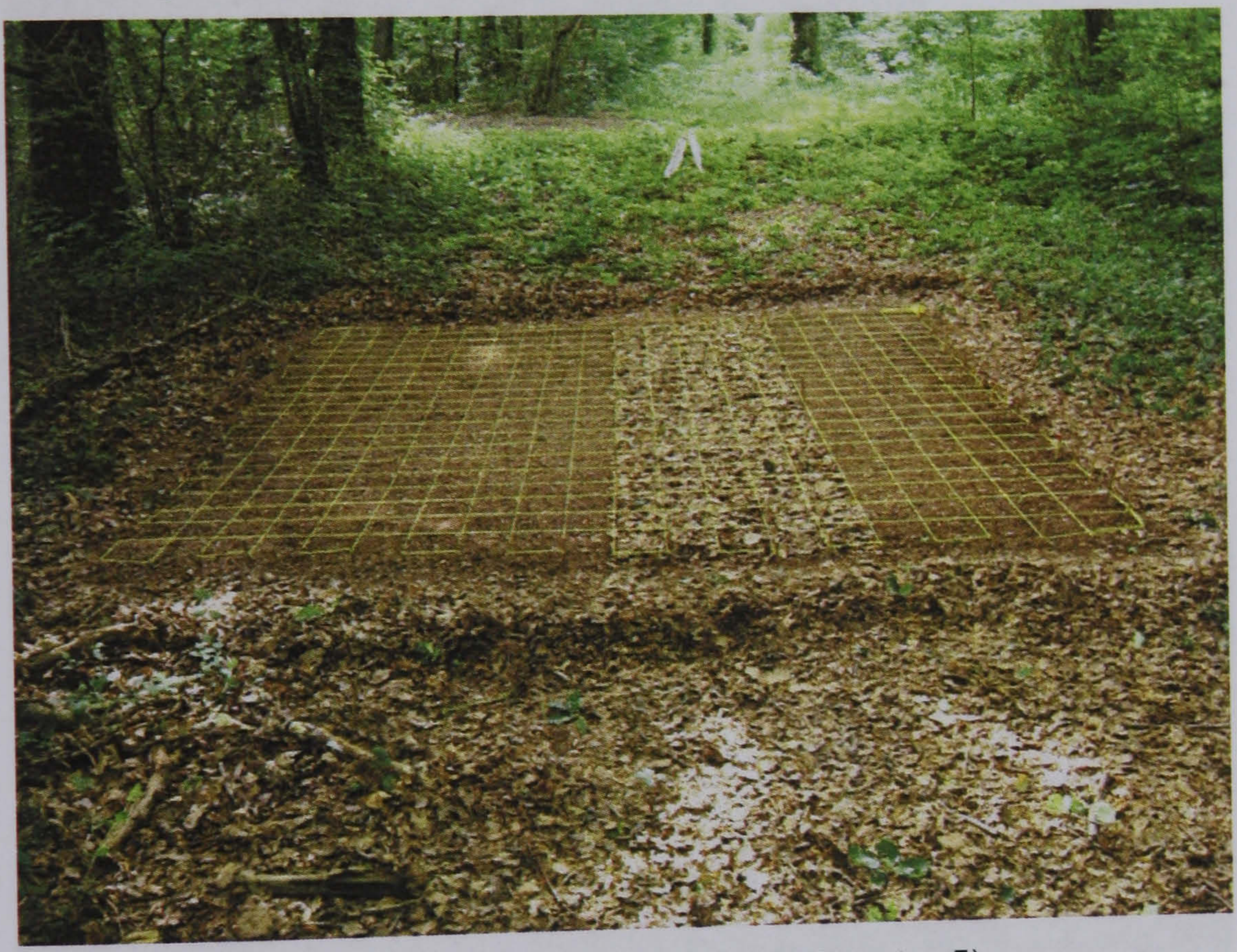
Release grid wood cricket nymphs (Leaf litter vs. Grass, Figure a; Chapter 5)

Release grid adults (Leaf litter vs. Grass, Figure b; Chapter 5)

Experiment 2



Release grid (Bare soil, Figure d; Chapter 5)



Release grid (Leaf litter vs. Bare soil, Figure f; Chapter 5)

Experiment 3

Release grid adults (Short grass vs. Tall grass, Figure c; Chapter 5)

Dispersal experiments (Chapter 6)

Experiment 1

Enclosures on woodland track (Radius: 5, 2 & 1 m)

Enclosures on woodland track (Radius: 3 & 4 m)

Pitfall trapping design within enclosures

Release site within enclosures with coloured nymphs (6-7th instar)

Release sites (Chapter 6)

Experiment 2, 3 and Surveys

Site 1

East facing edge

North facing edge

Site 2

Woodland edge

'JIGSAW' edge

Site 3

Woodland edge

Hedge edge (cut)

Improved release site

Site 4

Woodland edge

Hedge edge (cut)

Site 5

Woodland edge

Site 6

Woodland edge

Hedge edge

Site 7

Hedge edge

Site 8

'JIGSAW' edge

Woodland edge

Site 9

Hedge edge

Site 10

Barrier experiment (Chapter 6)

Experiment 4

Release island used for the wood cricket adults

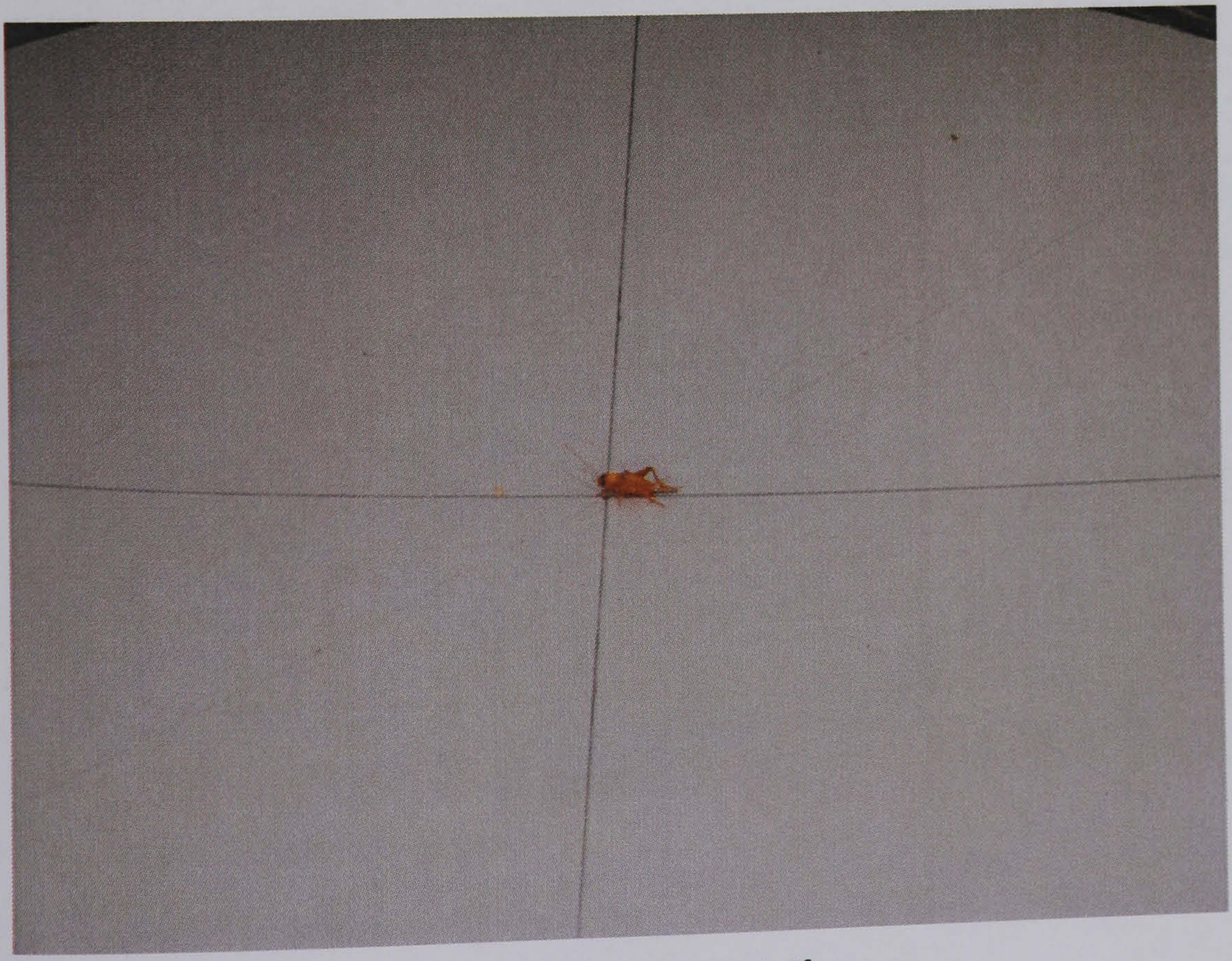
Orientation experiments (Chapter 6)

Experiment 5

‘JIGSAW’ planting and release platform

Experiment 6 – 8

Elevated release platform and transect



Coloured adult female in centre of release platform

Appendix III: Wood cricket biology pictures

Adult female (Body size: 11 mm)

Adult male (Body size: 9 mm)

Adult male

Nymph marked with orange powder (6-7th instar, body size: 7 mm)

Wood cricket habitat (Briddlesford, Isle of Wight)

Open woodland track

Open canopy woodland

Open canopy woodland

Railway embankment

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