# The value of the trackway system within a lowland plantation forest for ground-active spiders

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**Abstract**

European forest management guidelines include conservation and enhancement of biodiversity. Within plantation forestry, trackways provide contiguous permanent open-habitat with potential to enhance biodiversity. We examined the ground-active spider assemblage in the trackway network of Thetford Forest, Eastern England, the largest lowland conifer forest in the UK, created by afforestation of heathland and farmland. Results are relevant to other forests in heath regions across Europe. We used pitfall trapping to sample the spider assemblage of trackways within thicket-aged stands (n=17), mature stands (n=13) and heathland reference sites (n=9). A total of 9314 individuals of 71 species were recorded. Spider assemblages of the trackway network were distinct from those of the heathland reference sites; however trackways were found to support specialist species associated with grass-heath habitats, including nationally scarce species. Richness of grass-heath species was similar for trackways in thicket-aged forest and heathland reference sites, although the abundance of individuals was three times greater in the reference sites. Trackways in mature stands had lower grass-heath species richness and abundance than both thicket trackways and heath reference sites. Wide trackways within thicket stands contained greater richness and abundance of specialist xeric species than narrower trackways. However, fewer xeric individuals were found in trackways compared to heathland reference sites. Either inferior habitat quality in trackways or poor dispersal ability of specialist xeric species may largely restrict these to relict areas of heathland. Targeted widening of trackways to allow permanent unshaded habitat and creating early successional stages by mechanical disturbance regimes could improve trackway suitability for specialist species, helping to restore connectivity networks for grass-heath biodiversity.

**Key words:** Forest management, heathland, ecological networks, connectivity, arachnid.

## Introduction

Heathland ecosystems in Western Europe support important biodiversity (European Community 1992; Webb 1998, 2009) but have been considerably reduced in extent through changing land-use, particularly afforestation and agriculture (Gimingham 1972; Granstrom 1988; Farrell 1993). Remaining heathland is highly fragmented and efforts to recreate, buffer and connect heathland are key to conserving its biodiversity in the longer term (Hopkins & Webb 1984; Aerts et al. 1995; Lawton et al. 2010). Restoration programmes have often focussed on the removal of plantation forest in former heathland regions as soils under coniferous plantations have not been modified by agricultural fertiliser and may contain viable heathland seed-banks (Granstrom 1988; Pywell et al. 2002; Eycott et al. 2006). However, permanent open space within a plantation landscape, such as that provided by extensive trackway networks, may already have potential to support open habitat species (Warren 1985; Greatorex-Davies et al. 1994) including elements of heathland biodiversity (Eycott et al. 2006; Lin et al. 2007; Bertoncelj 2010).

Furthermore, open space can greatly enhance the biodiversity within plantations (Day et al. 1993; Butterfield et al. 1995), the need for which is increasingly recognised (Kuusipalo & Kangas 1994; Spellerberg & Sawyer 1996). Previous studies have focussed on increased species richness to enhance forest biodiversity (Warren 1985; Greatorex-Davies et al. 1993; Oxbrough et al. 2006). However, for heathland assemblages, species richness is generally lower than the surrounding areas and is therefore not an appropriate criterion for assessment (Webb & Hopkins 1984). In addition to enhancing heterogeneity, complexity and overall richness, conservation goals should aim to assess the suitability of forested landscapes for species of relevant pre-plantation habitats, such as lowland heathland, dune, or upland moorland, as well as rare and threatened species that are a focus of regional conservation priority.

Within plantation forests managed by clearfelling and replanting of even-aged stands, the temporal dynamics of the mosaic growth stages may make individual trackways ephemeral in their suitability to shade intolerant open-habitat species. Therefore, dispersal will be essential for population survival. Previous invertebrate research within the open space of plantation forests has often focussed on the influence of shade on Lepidoptera species richness in trackways (Warren 1985; Greatorex-Davies et al. 1993; Sparks et al. 1996). The ability of butterflies to disperse aeronautically enables them to bypass unsuitable or low quality habitat in search of mates, food plants and nectar sources, described as stepping stone dispersal (Schultz 1998; Haddad & Tewksbury 2005). Management guidelines lack an understanding of less mobile ground-active invertebrate community in the open space within a plantation.

This study examined the ground-active spider community in the trackway network of a large lowland coniferous forest planted on a heathland region of Breckland, East Anglia, UK. The region is of high biodiversity importance for assemblages of continental heath, steppe, coastal and Mediterranean species not found elsewhere in Britain, that require open heathland or ruderal habitats (Dolman et al. 2010). Within the forest (185 $km^2$) there are approximately 1290 km of trackways (average width 14 m) providing a potential open habitat resource of 18 $km^2$, equivalent to a fifth (21 %) of the designated extent of grass-heath remaining in the region (83 $km^2$). Much of the remaining grass-heath is in close proximity to the forest with some sites bordering the forest. This extensive trackway network has potential to contribute greatly to the available grass-heath habitats in the region and also to provide connectivity, among permanent open and ephemeral areas within the forest landscape and also linking across the forest to connect between external heathland patches.

Heathland and disturbed ruderal sites within the region support over 600 nationally rare and/or restricted species (Dolman et al. 2010). Spiders are among the top macroinvertebrate predators, occupying an important position in terrestrial food webs (Wise 1993). Changes in spider assemblages reflect changes in environmental conditions such as habitat structure (Duffey 1968; Robinson 1981) and fragmentation (Hopkins & Webb 1984), making spiders an effective group to examine open habitat networks. Furthermore, dry grass-heath in the region contains a very distinct spider community which includes stenotopic species adapted to living in arid places including coastal dune species rarely found inland in the UK (Duffey et al. 1957). The majority of this specially adapted community are ground hunting spiders.

The aim of this study was to assess the ground-active spider assemblage in the forest trackway network; firstly by comparing the forest trackway assemblages to those of reference grass-heaths in the region, and secondly by examining different trackway types and elements in terms of age structure of the surrounding forest, width of the trackway and track component (verge and vehicle tracks). Finally, we discuss the trackway network in terms of its ability to provide connectivity through the forest for open habitat spider communities.

**Methodology**

*Study site*

Thetford Forest is the largest lowland coniferous plantation forest in the United Kingdom; planted in the early 20th century on heathland and marginal agricultural land it occupies 185 $km^2$ of the Breckland region in eastern England (0°40'E, 52°27'N). Breckland is characterised by a semi-continental climate, sandy, nutrient-poor soil and a long history of human land-use that has included extensive and intensive grazing and episodic cultivation (Dolman & Sutherland 1992). This historic anthropogenic disturbance enabled specialist xerophilic invertebrates to persist in open-sand habitats in the region. Many of these species are now rare and threatened at national or European scales, due to both habitat degradation and destruction (Dolman et al. 2010). The Breckland Forest Site of Special Scientific Interest (SSSI) is notified under UK conservation legislation, imposing a requirement to maintain populations of nationally scarce and rare invertebrates in favourable condition (English Nature 2004).

The forest is dominated by conifer plantations, of which approximately 80% comprise Corsican (*Pinus nigra*) and Scots pine (*P. sylvestris*). The plantation is managed by clear-felling and replanting of large, even-aged stands (range 2-16 ha) which create a mosaic of even-aged growth stages (Eycott et al. 2006). Stands are typically harvested 60-80 years after planting. Stands are subdivided by a network of forestry trackways that enable access for management operations. Trackways consisted of two elements: a central vehicle track with disturbed wheelings, sparse vegetation and exposed substrate, flanked on either side by vegetated verges, that include elements of heathland vegetation, but generally lack bare substrate (Eycott et al. 2006). Trackways are currently cut or forage-harvested approximately once a year to maintain vehicle access and facilitate deer management. Trackways vary in width (mean 13.7 m ± 5.8 SD, range 5-50 m, from a sample of n=93), surface structure (sand, gravel), vegetation and amount of shade due to varying age of adjacent forest stands.

*Spider sampling in trackways*

Thirty forestry trackways (the basic unit of replication) were sampled, 13 with mature trees (>30 years) adjacent (subsequently referred to as mature trackways) and 17 with thicket stands (11-20 years following Hemami *et al.* (2004)) adjacent (subsequently referred to as thicket trackways) (Table 1). Trackways within clear-felled, recently restocked (0-5yr) or pre-thicket (5-10yr) stands were not sampled as trackways assemblages will not be distinct from those of adjacent open forest habitat. Of the 17 thicket trackways, seven were wider than the remainder (Table 1) and consequently experience less shading. To reduce confounding variation, only trackways located on predominantly acidic soil types (brown earths and podzols) within central blocks of Thetford Forest (covering 99.8km$^2$; Fig. 1) were sampled. Analysis of variance on easting and northing confirmed the age classes of sampled trackways were not aggregated within the sampled landscape (Northing; $F_{1,29}$=1.526 $P$=0.231, Easting; $F_{1,29}$=0.848 $P$=0.480). Each trackway was sampled by two pitfall transects, one on the vehicle track and the other in the least shaded trackway verge. Of the 30 trackways, 16 were oriented approximately north-south and 14 were east-west. In trackways oriented north-south the widest of both verges was sampled (four west and 12 east verges) and on trackways oriented east-west the northern (insolated) verge was sampled. Transects were set a minimum of 50m away from the corners of trackways and away from any open areas or cleared tree stands, hence each sample represented the spider community of that trackway and not other open habitat.

Each trackway was sampled on three occasions, to span the phenology of ground-active invertebrates, with pitfall traps set in mid-May, end of July and the end of August 2005. At each site, paired transects were set along the centre of the verge ('verge' transect) and between the central vehicle wheelings ('track' transects). Transects comprised five traps (each 7.5cm deep, 6.5cm in diameter, filled with 50ml of 70% ethylene glycol), with traps being open for five consecutive days in each sampling period. Traps in each transect were set approximately 22 m apart and were staggered alternately between track and verge leaving at least 11 m between adjacent traps in the paired transects. The five traps in each transect were combined to give one sample for the track and one sample for the verge for each trackway site; these were subsequently combined in analysis that considered the trackway as the basic unit of replication (see below). All analyses were conducted on aggregate samples that pooled across the three trapping periods. During the trapping season many females Lycosids (wolf spiders) were observed with eggsac and also carrying spiderling, indicating breeding populations within the forestry trackways.

*Heathland sampling*

The ground-active spider assemblage was also sampled nine heathland and ruderal reference sites considered important for specialist and rare invertebrates (Table 2), of which eight were designated SSSIs (including two National Nature Reserves). Within each of these, three transects were set, at least 50 m apart, providing a total of 27 sampling locations. Each comprised six pitfall traps (of the same dimensions as those used in forest trackways) and remained open for seven consecutive days over three trapping periods in 2009; mid-May, mid-June and the beginning of August. Pitfall traps where placed 15 m apart, similar to the 11 m spacing in the paired forest trackway transects. Again, aggregate samples pooled across the three trapping periods were used in analyses.

Both the 2005 forest trapping and the 2009 heathland trapping were elements of larger experiments taking place at the respective times and hence the differences in methodology. We acknowledge that sampling of reference transects may have differed slightly in effectiveness compared to forest trackways, due to the use of six not ten traps that were open for seven not five days during each trapping period (total 42 versus 50 trap-days per trapping period, respectively). In analysis of abundance we control for trapping effort (see below). Furthermore, activity and trapability may have been influenced by inter-annual differences in weather. However, the major differences in composition between forest trackway classes and heath reference sites are unlikely to have been an artefact of differences in weather between sampling years.

*Identification*

Adult spiders were identified to species using a 50x magnification microscope following Roberts (1987, 1996); juvenile and sub-adult specimens were not identified due to the lack of developed reproductive structures.

*Analysis*

Species were assigned to one of five habitat associations (Table 3), with reference to habitat descriptions in Harvey *et al.* (2002) and Roberts (1996). Habitat associations were defined hierarchically so that upper broader categories contain any species associated with woodland and or mesic habitats irrespective of whether they may also be found in open habitat types lower in the classification, while the lowest categories solely comprise specialist (stenotopic) species restricted to a narrow range of dry open habitats. Conservation status of species followed Harvey *et al.* (2002): Notable A (Na; nationally scarce, occurring in 30 or fewer UK 10 km squares) and Notable B (Nb; nationally scarce, occurring in 31-100 of the UK 10km squares). Linyphiidae spiders where not used in the analysis due to the scarcity of heathland spiders in the assemblage. Only one species associated with xeric habitats and two associated with grass-heath were recorded. The assemblage strongly consisted of eurytopic and mesic species.

For most habitat association groups, abundance and species richness was similar between the paired track and verge samples (paired t-tests: $P > 0.1$), with the exception of xeric species (richness: track > verge, $t_{29}$=1.989 $P$=0.056; abundance: track > verge, $t_{29}$=1.964 $P$=0.059) and eurytopic species richness (track > verge, $t_{28}$=1.814 $P$=0.080). Track and verge samples were pooled and aggregate samples for each trackway site were used in all subsequent analyses.

Species accumulation with increasing sampling effort was examined separately for trackway and heathland reference samples, using sample based rarefaction performed in EstimateS (Colwell 2009) and also rescaled to examine the number of individuals sampled (to control for differential trapping effort).

Assemblage composition across samples was examined using Multidimensional Scaling (MDS) performed on a similarity matrix of Bray-Curtis coefficients of spider abundance data (standardised per trap-days and square root transformed) using PRIMER 5 (Clarke & Gorley 2001). Stress values for MDS ordinations indicate the level of accuracy in representation; < 0.05 excellent, < 0.1 good, < 0.2 potentially useful, > 0.3 points close to being arbitrarily placed (Clarke & Warwick 1994).

Species richness and abundance of each habitat association group was compared among site categories (e.g. heathland reference transect, thicket trackway, mature trackway) using generalised linear models (GLM), with abundance data standardised by the number of trap-days per sample. The error term (normal, poisson, negative binomial) for each analysis was selected by examining the deviance/degree of freedom ratio. Differences among group means were examined by sequential sidak pairwise comparisons.

For thicket trackways alone, species richness and abundance of each habitat association group, and the abundance of each of the three most numerous species, were compared between trackways of different widths using T-tests. Statistical analyses were performed in SPSS v.16 (SPSS Inc, Chicago, IL, U.S.A).

## Results

We collected and identified 3746 spiders from 54 species in the 30 forestry trackways, while from the 27 heathland reference transects 5568 spiders from 50 species were identified. Overall, a total of 71 species were recorded, of which 21 were unique to the trackways and 17 were unique to the heathland reference sites. Pitfall trapping of ground-active spiders in this study effectively captured the assemblage composition in both the forest trackways and heathland reference sites, as sample based rarefaction approached the asymptote in each case (Fig. 2).

*Ground-active spider composition in Thetford Forest trackways*

The majority of spiders captured in trackways were eurytopic species (41% of the total). The family Lycosidae (wolf spiders) were the most numerous, with 2725 individuals (73% of the total sample) from eleven species. The three most numerous species caught were all Lycosidae, *Pirata hygrophilus* Thorell (n = 1012, woodland associated), *Pardosa pullata* (Clerck) (n = 900, eurytopic associated) and *Pardosa monticola* (Clerck) (n = 540, grass-heath associated).

Of the 54 species, thirteen were associated with grass-heath habitats and three with xeric habitats, comprising 26% and 1% of the total individuals found in the trackways respectively. Of the 54 species recorded, four were Nationally Scarce (Nb), including three grass-heath species: *Trachyzelotes pedestris* (C.L. Koch), *Xerolycosa nemoralis* (Westring), and *Aelurillus v-insignitus* (Clerck) and a woodland species *Micaria subopaca* (Westring).

*Ground spider composition in heathland reference sites*

In contrast to the forest trackways sampled, the majority of individuals sampled on heathland reference sites were grass-heath species (73%), while xeric species made up 3% of the total catch. The most numerous species caught were *P. monticola* (Clerck) (n = 3490, grass-heath associated), *Pardosa palustris* (Linnaeus) (n = 417, open-mesic associated) and *Steatoda phalerata* (Panzer) (n = 250, grass-heath associated).

Eight of the species recorded were Nb including two grass-heath species recorded in forest trackways *T. pedestris* and *X. nemoralis,* one additional grass-heath species *Micaria silesiaca* L. Koch, and a further three xeric species: *Ozyptila scabricula* (Westring)*; Sitticus saltator* (O.P.-Cambridge) and *Steatoda albomaculata* (Degeer), as well as one woodland and one open-mesic species, *Marpissa muscosa* (Clerck) and *Pardosa agrestis* (Westring) respectively.

*Community composition of trackway and heathland reference assemblages*

MDS successfully represented the assemblage structure with a low stress value (Fig. 3) (Clarke & Warwick 1994). Spider assemblages differed among the mature trackways, thicket trackways and heathland reference transects with strong separation along axis one of the ordination, mature trackways and heathland transects showed the greatest separation (Fig. 3a, Table 4). Of the outliers, three transects from a single heathland reference site with closed sward vegetation were grouped together at the top of the plot. The heathland reference transects located lowest in the ordination were obtained from the most physically disturbed sites, including heavily rabbit-grazed warrens and recently ploughed areas.

The relative abundance of the three most frequently recorded species within the ordination *Pardosa monticola* (grass-heath), *Pardosa pullata* (eurytopic) and *Pirata hygrophilus* (woodland), indicated a moisture gradient across the site classes (Fig. 3). *P. monticola* was most abundant in the heathland transects, scarcer in thicket trackways and was almost absent in the mature trackways (Fig. 3b). *P. pullata* was most numerous in the thicket trackways and closed sward heaths but was also abundant in the mature trackways (Fig. 3c), while small numbers of *P. pullata* were also present in approximately half of the heathland reference transects. *P. hygrophilus* is dominant in the mature trackways with smaller numbers in some of the thicket trackways (Fig. 3d) but was absent from the heathland transects.

*Community comparison: habitat association*

Trackways adjacent to mature stands were dominated by eurytopic and woodland spiders, both in terms of species richness and relative abundance (Fig. 4). Very few species restricted to xeric and grass-heath habitats were found in the mature trackways. In contrast, trackway samples in thicket stands contained significantly fewer woodland species and individuals, although were similar in richness and relative abundance of eurytopic species (Fig. 4, Table 4). Thicket trackways provided more individuals associated with xeric and grass-heath habitats than were trapped in mature trackways (Fig. 4, Table 4).

Heathland reference transects were strongly dominated by individuals of species associated with grass-heath habitats, comprising approximately three quarters of the total catch (Fig. 4,

Table 4). Heathland transects contained significantly fewer woodland and eurytopic spiders than forest trackways of either class (Table 4). Although the abundance of grass-heath species was significantly greater in heathland reference transects than in thicket trackways, the species richness of xeric, grass-heath and open-mesic species was similar (Table 4).

*Influence of trackway width*

Within thicket stands, narrow trackways had significantly greater abundances of eurytopic and open-mesic spiders and also a greater species richness of woodland spiders (Table 5). Conversely, the species richness and abundance of spiders restricted to xeric habitats was greater in wider thicket trackways.

## Discussion

### *Heathland spider communities in forestry trackways*

The trackway network supported important elements of open habitat assemblages, particularly heathland species of which a number were nationally scarce. Trackways in thicket-aged stands supported similar numbers of grass-heath and xeric species as heathland sites. These results show that trackway elements within the forest landscape can be important for open habitat species and can contribute to the overall biodiversity of the landscape. Furthermore, wide trackways (those greater than 25m) in thicket stands supported greater numbers of xeric species than narrow trackways and lower abundances of woodland and eurytopic species; thus increasing the width of forestry trackways would benefit open habitat assemblages.

### *Effects of forest growth stage on trackway assemblage*

Although trackways supported characteristic and rare heathland spider species, the trackway assemblage still differed considerably from that found in heathland sites; heathland reference sites were dominated by grass-heath species, whereas trackways in thicket stands contained far more eurytopic species. Furthermore, only the trackways in thicket-aged stands showed any resemblance to the assemblage found in heathland sites; trackways in mature stands were dominated by woodland and eurytopic species.

Shading by mature trees in trackways is likely to increase moisture and decrease temperature and light availability, creating unsuitable habitat for grass-heath and xeric species. This is shown by the relative distribution of the dominant Lycosidae species; the damp habitat species, *P. hygrophilus*, was confined to the mature trackways whereas the grass-heath species, *P. monticola*, dominant in the heathland reference sites was also present in thicket trackways. *P. monticola* in this study shows similar patterns of shade intolerance as open habitat butterfly species reported in other studies (Warren 1985; Greatorex-Davies et al. 1993).

### *Influence of trackway width on the spider community*

Increased trackway width in the thicket stands had significant effects on the assemblage composition. Wide trackways contained fewer eurytopic individuals and woodland species and more xeric species and individuals than narrow thicket trackways, likely due to reduced shading causing changes in the microhabitat and soil moisture. Although other studies have advocated trackway widening for open habitat species (Warren 1985; Greatorex-Davies et al. 1994; Mullen et al. 2003), this study provides direct evidence that increasing trackway width can benefit specialist ground-active invertebrate species associated with xeric habitats. For example, *Arctosa perita*, a specialist species of frontal dune and dry heathland habitats was only found in the wide trackways (where it was represented by five individuals).

As well as changes in microhabitat, competition from eurytopic and woodland species from the surrounding forest may potentially also restrict xeric species in trackways. Hopkins and Web (1984) speculate that this may occur on small heathland fragments where vagrant species may outcompete heathland species. The current study showed wide trackways have lower densities of eurytopic individuals and fewer woodland species, which could alleviate competition pressures to benefit persistence of xeric species in the forested landscape.

Wide trackways sampled were two to three times the width of the average trackway in the forest. This corresponds with current conservation guidelines that suggest that to maintain open habitat communities, forest trackways need to be at least as wide, and preferably 1.5 times as wide as the height of the surrounding trees (Warren & Fuller 1993). For thicket stands where trees are approximately 10 metres tall, trackways need to be 10-15m wide. However, to allow unshaded open habitat conditions to persist throughout the forest growth cycle would require trackway widths of 30-45 m within mature stands, where trees are 20-30m in height. Whether connectivity requires a permanent network of unshaded trackways or can be achieved by a shifting pattern of more short lived elements, dependent on the forest management and growth cycle, depends on the relative mobility and vagility of the ground-active invertebrate fauna that forms the conservation concern.

*Connectivity and dispersal*

Given that the forest is planted in a patchwork of growth stages, trackway suitability will be both spatially and temporally sporadic. Open habitat species with relatively good cursorial dispersal abilities, such as reported for various *Pardosa* species (Morse 1997; Kiss & Samu 2000; Bonte et al. 2007), may be able to sustain metapopulations in this changing environment. However, the restricted distribution of many specialist heathland invertebrates has in part been attributed to their poor dispersal ability (Hopkins & Webb 1984; Bonte et al.

2003). For less mobile specialist xeric species a patchy mosaic of suitable habitat may not be sufficient to allow colonisation and persistence in the forested landscape.

*Management implications*

To create and maintain grass-heath biodiversity in the trackway network of plantation forests established on former heathland areas, management needs to focus on: widening existing trackways, reducing the dominance of dense grass-swards in track verges and increasing the patchiness of growth stages within the forest.

Widening trackways to create permanently unshaded habitat could facilitate dispersal and colonisation from adjacent grass-heath into the forest trackway network, linking fragmented remnants of heath across the forest and providing movement pathways through the forest for specialist xeric invertebrates. Many specialist species with poor dispersal abilities will benefit from having connectivity of wide permanently unshaded trackways that could support persistent resident populations as well as being used as dispersal corridors.

Where ground vegetation is dominated by thick-dense swards in the trackways, some form of physical disturbance may also be required to created early successional habitats with exposed substrates and reduced vegetation density. The need for disturbance to enhance grass-heath biodiversity is well known (Dolman & Sutherland 1992, 1994; Romermann et al. 2009), but little work has been carried out to compare the benefits of different techniques.  Early successional stages in many heathland reference sites are maintained by large rabbit populations, but as this is incompatible with forestry management, similar vegetation structures in the trackways may require physical mechanical disturbance.

Large-congregated restocks may impede dispersal along trackways for less mobile habitat specialist when trees mature. Although trackway widening may not be feasible throughout the forest to alleviate this, we advocate an increase in patchiness of growth stages (by reducing coupe area), allowing greater proximity between ephemeral patches of open habitat to be as close as possible for dispersal limited species.

## Conclusion

Trackways support a significant amount of the heathland spider composition. However, management in trackways may further increase the abundance of grass-heath species while reducing the influence of woodland and eurytopic species. Restoring open habitat networks would enhance the biodiversity of the forest as well as support specialist xeric species. Management options should be tested to find cost effective methods. There is great potential for trackways to enhance the biodiversity of plantation forests whilst also improving the cohesion of fragmented grass-heath habitats in the region.

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**Table 1** Characteristics of four trackway categories showing mean (± standard deviation) age of adjacent trees and trackway width

| | Number of sites | Average tree age on southern side (years) | Average tree height on southern side (m) | Average width (m) |
|---|---|---|---|---|
| Mature tracks | 13 | 53.2 ± 23.3 | 17.3 ± 4.1 | 9.8 ± 2.1 |
| Thicket tracks | 17 | 17.8 ± 4.7 | 8.4 ± 3.0 | 17.3 ± 10.6 |
| Narrow | 10 | 15.7 ± 4.3 | 7.2 ± 2.6 | 10.7 ± 2.7 |
| Wide | 7 | 20.7 ± 3.6 | 10.0 ± 3.0 | 26.9 ± 10.4 |

**Table 2** Heathland and ruderal reference sites sampled for ground-active spiders, giving grid references (UK Ordnance Survey) of transect locations

| Site | Notes |
|---|---|
| Deadman's Graves SSSI<br>TL 775744, TL 776743,<br>TL 776742 | All three transects were located in short sparse vegetation with large areas of exposed sand on a heavily disturbed rabbit warren. |
| Eriswell Low Warren SSSI<br>TL 739793, TL 740793,<br>TL 739793 | A sheep grazed site with a series of old plough cleaning lines, that are re-ploughed as needed to create disturbance for rare vegetation, most recently in 2003. Rabbit grazing and burrows along the lines has maintained exposed substrate. Transects were placed along the ridge of the plough lines in broken short vegetation. |
| Icklingham Plains SSSI<br>TL 759734, TL 759735,<br>TL 758735 | All three transects were positioned in lichen dominated grass-heath affected by heavy rabbit activity that has maintained short vegetation and exposed sand. |
| Maidscross Hill SSSI<br>TL 729825, TL 730825,<br>TL 726823 | One transect was placed along the south facing slope of former gravel-pit with sparse vegetation and exposed substrate, the remaining two were on short rabbit-grazed turf. |
| Wangford Warren SSSI<br>TL 757840, TL 758841,<br>TL 757842 | Mechanically disturbed areas at the site are ploughed approximately annually to maintain open sand. One transect was positioned in ploughed unvegetated open sand, the remaining two in lichen dominated grass-heath. |
| Runway Field<br>(adjacent to Wangford Warren)<br>TL 757840, TL 757839,<br>TL 756837 | Reverted from arable after inundation by windblown sand, the site includes areas of heavy rabbit activity and one annually ploughed strip bordering Wangford Warren. One transect was positioned along the ploughed strip and the other two within areas of short rabbit-grazed turf. |
| Thetford Heath SSSI<br>TL 854795, TL 849795,<br>TL 846795 | All transects were placed in closely sheep and rabbit grazed grass-heath, with short and in places broken sward. |

| | |
|---|---|
| Brettenham Heath NNR<br>TL 916861, TL 915860, TL 916859 | The area is cut annually to reduce bracken dominance. The area sampled was vegetated by a dense grass sward with substantial amounts of bracken and no exposed substrate. |
| Weeting Heath NNR<br>TL 757883, TL 758882, TL 757880 | Two transect were placed in a rabbit grazed area of deep sand and the third along the fence line of a rabbit grazed area of lichen dominated grass-heath. Both areas have short rabbit grazed swards with patches of exposed substrate. |

**Table 3** Classification of habitat associations of spider species, based on species accounts in Harvey et al (2002) and Roberts (1996)

| Habitat | Description |
|---|---|
| Eurytopic | Species described as eurytopic (living in most habitats), or that are associated with most of the habitats considered below. |
| Woodland | All species (other than eurytopic species) associated with woodland, including those also associated with open-mesic, grass-heath or xeric habitats. |
| Open-mesic | Species associated with grassland, moorland (upland dwarf shrub heath on peat soils), and/or marshy damp habitats; long and short vegetation; may be damp or dry but not associated with woodland. |
| Grass-heath | Species associated with dry lowland calcareous and/or acidic grassland, lowland heathland, sparse and/or short vegetation and not also associated with the habitats above. |
| Xeric | Dry heathland; sandy or dune habitats; sand or gravel pits, bare ground, lichen, coastal, scree and shingle |

**Table 4** Means, standard errors and results of General Linear Models ($\chi^2$ and p-value) comparing MDS axis scores, species abundance (standardised for number of trap days) and species richness of the spider habitat association groups among the mature tracks, thicket tracks and heathland reference sites. Sequential Sidak pairwise comparisons were used to define homogenous sub-sets (a-c ranked highest to lowest); means that share a superscript do not differ significantly (P<0.05).

| | Variable | Mature n = 13 Mean ± s.e | Thicket n = 17 Mean ± s.e | Heath/ruderal n = 27 Mean ± s.e | Chi square | P-value | Mature | Thicket | Heath |
|---|---|---|---|---|---|---|---|---|---|
| Individual abundance | MDS axis 1[1] | -1.27 ± 0.08 | -0.33 ± 0.10 | 0.82 ± 0.06 | 352.041 | <0.001 | c | b | a |
| | MDS axis 2[1] | 0.00 ± 0.08 | -0.14 ± 0.06 | 0.09 ± 0.10 | 3.515 | 0.172 | a | a | a |
| | Grass-heath[2] | 1.02 ± 0.44 | 4.98 ± 1.26 | 17.90 ± 2.77 | 57.326 | <0.001 | c | b | a |
| | Xeric[2] | 0.01 ± 0.01 | 0.15 ± 0.04 | 0.78 ± 0.15 | 34.871 | <0.001 | b | b | a |
| | Open mesic[2] | 0.15 ± 0.06 | 0.51 ± 0.07 | 3.37 ± 0.98 | 32.120 | <0.001 | b | b | a |
| | Woodland[2] | 7.32 ± 1.72 | 0.93 ± 0.39 | 0.02 ± 0.01 | 107.175 | <0.001 | a | b | c |
| | Eurytopic[2] | 4.58 ± 0.62 | 5.45 ± 0.70 | 2.49 ± 0.85 | 20.169 | <0.001 | a | a | b |
| Species richness | Grass-heath[2] | 2.23 ± 0.47 | 6.00 ± 0.35 | 6.00 ± 0.36 | 11.396 | 0.003 | b | a | a |
| | Xeric[2] | 0.08 ± 0.08 | 0.71 ± 0.17 | 2.04 ± 0.29 | 12.123 | 0.002 | b | a/b | a |
| | Open mesic[2] | 1.00 ± 0.30 | 3.24 ± 0.29 | 3.74 ± 0.36 | 12.075 | 0.002 | b | a | a |
| | Woodland[3] | 2.38 ± 0.24 | 0.94 ± 0.18 | 0.15 ± 0.07 | 31.467 | <0.001 | a | b | c |
| | Eurytopic[2] | 6.46 ± 0.43 | 6.71 ± 0.33 | 3.04 ± 0.34 | 11.269 | 0.004 | a | a | b |

Variable superscript indicates which model type used; 1 = linear normal, 2 = square root linear, 3 = poisson

**Table 5** Mean ± S.E of spider abundance and species richness of spider habitat groups in thicket tracks. Differences from T-tests between the narrow and wide tracks for each spider habitat group are shown, p values < 0.05 are shown in bold.

| | Species variable | Thicket narrow n = 10 mean ± s.e | Thicket wide n = 7 mean ± s.e | T statistic; DF | p-value |
|---|---|---|---|---|---|
| Abundance | Grass-heath | 55.90 ± 20.76 | 41.00 ± 9.00 | 0.570, 15 | 0.577 |
| | Xeric | 0.50 ± 0.31 | 3.00 ± 0.62 | -3.626, 9 | **0.006** |
| | Open mesic | 6.40 ± 0.90 | 3.29 ± 0.42 | 3.144, 13 | **0.008** |
| | Woodland | 13.50 ± 6.26 | 3.29 ± 2.39 | 1.525, 15 | 0.154 |
| | Eurytopic | 66.10 ± 7.42 | 38.00 ± 11.18 | 2.187, 15 | **0.045** |
| | *P. monticola* | 38.20 ± 17.92 | 21.43 ± 5.76 | 0.757, 15 | 0.461 |
| | *P. pullata* | 44.60 ± 6.11 | 25.57 ± 9.96 | 1.723, 15 | 0.105 |
| | *P. hygrophilus* | 12.70 ± 6.13 | 3.14 ± 2.41 | 1.247, 15 | 0.231 |
| | | | | | |
| Species richness | Grass-heath | 5.90 ± 0.55 | 6.14 ± 0.40 | -0.329, 15 | 0.747 |
| | Xeric | 0.40 ± 0.22 | 1.14 ± 0.14 | -2.546, 15 | **0.022** |
| | Open mesic | 3.60 ± 0.43 | 2.71 ± 0.29 | 1.563, 15 | 0.139 |
| | Woodland | 1.30 ± 0.21 | 0.43 ± 0.20 | 2.840, 15 | **0.012** |
| | Eurytopic | 7.20 ± 0.47 | 6.00 ± 0.31 | 1.941, 15 | 0.071 |

**Fig. 1** Central Thetford Forest blocks (99.8 $km^2$) showing the mosaic of open space, mature (planted before 1986) and younger (planted after 1985) tree stands.  Trackways are shown as thick black lines

**Fig. 2** Sample-based rarefaction curves (Mao Tau function) with 95% confidence interval lines of spider species collected from 30 trackways sampled in Thetford Forest and 27 heath reference sites

**Fig. 3** MDS ordination plots of spider assemblages showing the two forestry trackway categories (mature and thicket) and the heathland reference transects. Plot a) shows the forest trackway samples (pooled track and verge samples) and the heathland reference transects. Bubble plots show the abundance of the three most dominant species recorded; b) *Pardosa monticola,* a grass-heath species, c) *Pardosa pullata,* a eurytopic species and d) *Pirata hygrophilus,* a damp habitat/woodland species.  Numbers in bubble plots indicate the abundance of each species per site (corrected for trap/day)

**Fig. 4** Mean numbers of a) individual spiders (standardised for trap-days), b) species for each habitat association category compared among the three site types; mature forestry tracks, thicket forestry tracks and transects from heathland reference sites