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Title:

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

Niels C. Brouwers • Adrian C. Newton

N. C. Brouwers (Corresponding author) • A. C. Newton
School of Conservation Sciences
Bournemouth University
Talbot Campus, Fern Barrow, Poole, Dorset, BH12 5BB, UK
E-mail: ncbrouwers@hotmail.com
Phone: ++44 1202 965498 / Fax: ++44 1202 965255

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Abstract

1. A systematic review was conducted to gather empirical evidence on movement rates of invertebrates associated with woodland.
2. Eight scientific literature databases were systematically searched for relevant studies on invertebrates associated with woodland habitat.
3. Twenty-five studies were identified that met the search selection criteria, which provided estimates of movement rate for thirty invertebrate species associated with woodland habitat. These thirty species represented insect species only, including seventeen carabid (ground) beetle, eight butterfly, two bark beetle, two ant, and one moth species. From 2000 to 2007, only four studies were identified, indicating a current lack of dispersal-related studies for woodland invertebrates.
4. A meta-analysis of studies on ground-dwelling species indicated that carabid beetle species that were strongly associated with woodland habitat were found to move more slowly than more generalist species (median: 2.1 m day^{-1} vs. 11.0 m day^{-1}). Furthermore, for carabid beetles it was found that body size was positively correlated with movement rate.
5. The lack of field measurements of movement and dispersal ability for all but a tiny minority of woodland invertebrates indicates a substantial knowledge gap that should be addressed by future research, which might usefully test whether the patterns identified for carabid beetles are generally applicable.

Keywords: movement rate; dispersal; systematic review; woodland; forest; invertebrate; insects; meta-analysis; carabid beetles; habitat specialisation.

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 (Niemelä, 2001; Tscharntke *et al.*, 2002; Bailey, 2007). Furthermore, this group of species is of particular importance, as many have highly restricted distributions and are considered as priorities for conservation action (Ranius, 2002; Buse *et al.*, 2007; Matern *et al.*, 2007; Hedin *et al.*, 2008). 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).

Species showing low dispersal ability generally are found in relatively stable long-lived high-quality habitats (Hedin *et al.*, 2008), whereas species showing a higher dispersal ability are often associated with ephemeral and/or highly disturbed habitats (Denno *et al.*, 1996; Travis & Dytham, 1999). Furthermore, species that show a high degree of habitat specialisation (i.e. by being specific in their habitat requirements), are often linked with stable habitats and therefore generally show low rates of dispersal (e.g. Ranius & Hedin, 2001; Hedin *et al.*, 2008). Within woodland invertebrates, habitat-specialist species have been found to be more vulnerable to habitat loss (Tscharntke *et* *al.*, 2002) and fragmentation effects (Niemelä, 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 (Niemelä, 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 (Niemelä, 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). The limited dispersal ability of woodland-associated invertebrates is supported by other research. For example, for a woodland specialist beetle species living in trees, the dispersal rate between trees within a forest stand was estimated to be 15% per generation (Ranius & Hedin, 2001; Hedin *et al.*, 2008). Furthermore, because of the long-lived nature of its habitat and degree of habitat specialisation, dispersal between woodland stands was assumed to be very rare for this species (Ranius, 2006; Hedin *et al.*, 2008). This suggests that woodland-specialist invertebrates might be particularly vulnerable to habitat fragmentation effects (Hedin *et al.*, 2008).

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 (Niemelä, 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, 1990b; a; Thomas, 2000) and body size (den Boer, 1990b; Drach

& Cancela da Fonseca, 1990). 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 measures of movement rate (as a measure for dispersal ability) for woodland invertebrate species; and (2) to examine whether ground-dwelling woodland invertebrates could be grouped based on movement rate (m day^{-1}) and habitat specialisation, and (3) to examine the relationships between movement rate, body size, and habitat specialisation. 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.

Methods

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 (1970-2007/01), AGRIS (1975-2007/01), Biological abstracts (1969-2007/01), CAB abstracts (1910-2007/01), Current Content (1996-2007/02/22), Scopus (1960-2007/01), ISI Web of Science (including Science Citation Index Expanded (SCI-EXPANDED) (1945-2007/01); Social Sciences Citation Index (SSCI) (1956-2007/01); Arts & Humanities Citation Index (A&HCI) (1975-2007/01)).

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 the temperate zones, references including *tropica* or *rain forest* or *seed* in either the journal title, title, keywords or abstract, were selected and checked if they were conducted in countries lying within the temperate zones. Studies that were not, were deleted. 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.

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.

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)).

Meta-analysis

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 specialisation (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.

To standardise the results found in the individual studies, the reported rates were weighted based on the number of observations (N) made. Rate estimates based on a high number of observations were considered more accurate than estimates based on relatively few observations. Therefore, within each 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.).

Statistical analysis

Statistical tests were performed to investigate whether movement rate differed between the habitat specialisation groups (Kruskal-Wallis and Mann-Whitney *U* tests), if body size differed between the specialisation 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.

Results

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 1). 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 1). The second table presents standardised straight-line movement rates for woodland invertebrate species that moved over the ground (Table 2). The studies that were found were conducted in the period 1964 – 2005, and were mainly undertaken in Europe (16), including four studies from the UK, with an additional seven studies from North America and two from Asia (Table 1). All studies that were found were performed on insect species. 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 1). Within the 25 studies, rates were reported for 34 separate invertebrate species of which 30 were associated with woodland habitat (Table 1). 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).

Factors influencing rate

All studies included in Table 1 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 1 approx here #

 # Table 2 approx here #

Meta-analysis

 # Fig. 1. approx here #

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 2). 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 2). Rates found for the woodland species varied between 0.6 and 18.4 m day^{-1} (Table 2, Fig. 1). Based on habitat preference, ‘Group 1’ included nine rates for four species (body size: range 12.0 – 36.0 mm, mean = 22.6 mm, SD = 8.8) with rates varying between 0.6 and 8.5 m day^{-1} (Table 2, Fig. 1) 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 mm, SD = 1.6) ranging from 1.0 to 2.6 m day^{-1} (Table 2, Fig. 1) 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 2, Fig. 1) with a mean rate of 11.4 (SD = 6.5) m day^{-1}.

 # Fig. 2 approx here #

A significant difference was found for median rate between the individual habitat specialisation 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; Fig. 2). 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 Fig. 2) 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 when considered 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 2: $n_{Gb} = 20$, median = 2.32 (inter-quartile: 4.1) vs. Woodland butterfly species with straight-line movement rates in m day^{-1} Table 1: $n_{Bf} = 4$, median = 52.2 (inter-quartile: 19.3); Mann-Whitney: $z = -3.10$, $P = 0.002$).

Discussion

The systematic review revealed only a limited number of studies that provided measures of movement rate for woodland invertebrates. Furthermore, movement rates were only found for insects, indicating a lack of studies on other types of invertebrate species. The majority of the studies found (18) were conducted between 1985 and 2000, mainly focussing on carabid beetles. Interestingly, between 2000 and 2007/01 only four studies reporting a rate movement were identified. An additional search for studies that were published after the initial review between 2007/01 and 2008/08 revealed only two more studies that reported movement rates; one for stag beetles (*Lucanus cervus*) (males 73.9 m day^{-1}; females 8.3 m day^{-1}) (Rink & Sinsch, 2007) and one for three woodland related nematode species moving 20 cm year^{-1} (Dillon *et al.*, 2008). This highlights the general lack of information on movement rates for woodland invertebrates.

This review focused on studies reporting a rate of movement for woodland-associated invertebrates, including only rates estimated by measuring distance covered over time. With the movement rates that were gathered, predictions can be made on how fast and far a species can move through a habitat or landscape (Walters *et al.*, 2006). Therefore, the reported movement rates can be used as a measure of dispersal ability, and provide insights into the influence of dispersal on patterns of species across different spatial and temporal scales (Tscharntke *et al.*, 2002; Ranius, 2006). However, movement rates should be interpreted with reference to the characteristics of the species concerned. For example, saproxylic species able to walk and fly often only disperse during a short period of their life-cycle (Rink & Sinsch, 2007; Hedin *et al.*, 2008). Such species demonstrate different modes of dispersal depending on factors such as weather conditions, sex, and habitat persistence, quality and availability (Rink & Sinsch, 2007; Hedin *et al.*, 2008). High habitat stability and/or lack of alternative habitat nearby can result in only a few individuals within a population tending to disperse during their lifetime (Hedin *et al.*, 2008). Estimates for movement rate as an indication of dispersal ability for such species should therefore be interpreted with caution. The current study revealed a bias in the literature towards particular invertebrate groups, namely ground beetles and butterflies. These insects typically show a more continuous modus of movement during their active life-stages (e.g. Lövei & Sunderland, 1996) and therefore a generalised rate can be used more readily as a measure of dispersal ability and potential dispersal success. The results of this review are therefore particularly relevant to these groups, but also highlight the current lack of research on movement of other woodland-associated invertebrates.

Relatively few of the studies found in this review used advanced techniques such as telemetry (1) and harmonic radar (4) to derive movement rates. In the last decade, technological advances have been rapid in these techniques and substantial improvements have been made, for example 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 these methods to obtain movement rates for woodland species. Only two recently published studies on woodland-associated saproxylic beetle species were found that used radio-telemetry for tracking individuals (Rink & Sinsch, 2007; Hedin *et al.*, 2008), where only one reported a movement rate for the species (Rink & Sinsch, 2007). This indicates that 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 such as mark-recapture are still generally preferred.

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 conventional literature review by Bowne & Bowers (2004), found similar differences between movement rates of butterfly and carabid species moving between habitat patches. Their aim was to provide basic statistics on movement of species between habitat patches, which was addressed by calculating rates of inter-patch movement as the proportion (%) of the population moving per generation. However, unlike the study presented here, Bowne & Bowers (2004) considered movement rates of invertebrates at relatively large spatial and temporal scales. 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 larger spatial scales.

Systematic review approach

The systematic review approach is 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, Bowne & Bowers (2004) similarly used a two-stage search strategy, 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).

Meta-analysis

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 specialisation and with physical attributes such as body size. Body size is often assumed to be positively related to 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, included data for only 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 develop 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 specialisation/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 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; b) 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 (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 (den Boer, 1990b).

In the current study, ground-dwelling woodland invertebrates (i.e. carabid beetles) were grouped according to the degree of habitat specialisation 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 specialisation, 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 specialisation for ground-dwelling woodland carabid species (i.e. 'Group 1 & 3', this study), and *vice versa*.

Conservation implications

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 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) suggested 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. 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.

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Table 1. 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
Hågvar, 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 2. 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 specialisation; (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: average 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	20.0	Charrier et al., 1997
Abax ater	1.8	420	Capture-Recapture	WT	1	20.0	Loreau and Nolf, 1993
Abax ater	2.3	50	Capture-Recapture	WT	1	20.0	Drach and Cancela da Fonseca, 1990
Abax ater	2.3	85	Capture-Recapture	WT	1	20.0	Petit, 1994
Amara equestris	1.8	259	Enclosure experiment	HM	2	9.3	Vermeulen, 1994b
Calathus ambiguous	2.4	116	Enclosure experiment	HM	2	10.0	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	36.0	Riecken and Raths, 1996
Carabus nemoralis	5.0	15	Capture-Recapture	WT/HM/M	3	24.0	Kennedy, 1994
Carabus nemoralis	18.4	14	Harmonic radar	WT/HM/M	3	24.0	Kennedy, 1994
Carabus problematicus	15.4	63	Capture-Recapture	WT/HM/M	3	24.0	Rijnsdorp, 1980
Harpalus servus	1.0	360	Enclosure experiment	HM	2	8.0	Vermeulen, 1994b
Nebria brevicollis	1.3	598	Enclosure experiment	WT/M	1	12.0	Nelemans, 1988
Nebria brevicollis	1.5	83	Capture-Recapture	WT/M	1	12.0	Joyce et al. 1999
Nebria brevicollis	2.1	301	Capture-Recapture	WT/M	1	12.0	Greenslade, 1964
Orinocarabus nemoralis	6.7	8	Capture-Recapture	WT/HM/M	3	24.0	Drach and Cancela da Fonseca, 1990
Procrustes purpurascens	8.5	11	Capture-Recapture	WT/M	1	25.0	Drach and Cancela da Fonseca, 1990
Pterostichus lepidus	1.9	408	Enclosure experiment	HM/SD	2	12.0	Vermeulen, 1994b
Pterostichus lepidus	2.6	118	Capture-Recapture	HM/SD	2	12.0	Vermeulen, 1994a

Fig. 1. Frequency distribution for the mean movement rates of ground-dwelling woodland invertebrate species as presented in Table 2. The different shading of the bars indicates to what habitat specialisation group the species belongs. Group: indicates the group for each species based on habitat specialisation; '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).

Fig. 2. 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 specialisation; '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 specialisation groups. The stars and circles indicate extreme values and outliers respectively. For more information on boxplots see Pallant (2007).

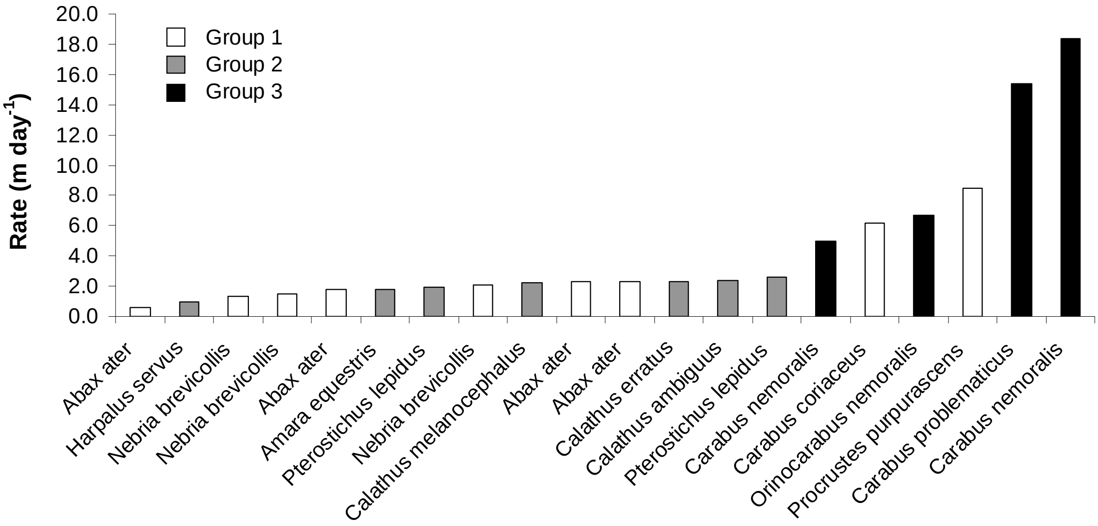

Fig. 1. (see attached file Fig 1.tiff)

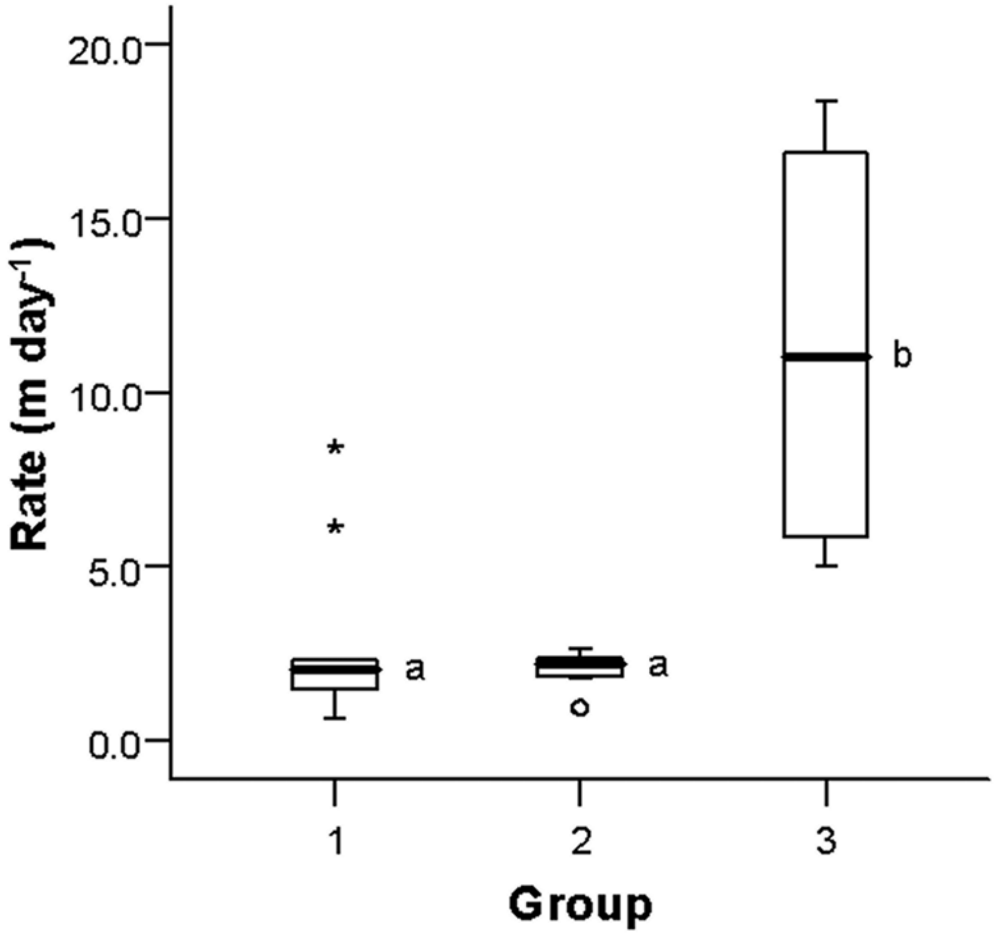

Fig. 2. (see attached file Fig 2.tiff)

References

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355-366.

Bailey, S. (2007) Increasing connectivity in fragmented landscapes: an investigation of evidence for biodiversity gain in woodlands. *Forest Ecology and Management*, **238**, 7-23.

Barton, B.J. & Bach, C.E. (2005) Habitat use by the federally endangered Mitchell's satyr butterfly (*Neonympha mitchellii mitchellii*) in a Michigan prairie fen. *American Midland Naturalist*, **153**, 41-51.

Bowne, D.R. & Bowers, M.A. (2004) Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology*, **19**, 1-20.

Buckland, P. (2007) *The development and implementation of software for palaeoenvironmental and palaeoclimatological research: the Bugs Coleopteran Ecology Package (BugsCEP)*.Doctoral thesis, Umeå University, Umeå, Sweden.

Buckland, P.I. & Buckland, P.C. (2006) Bugs Coleopteran Ecology Package.

Bullock, J.M., Kenward, R.E. & Hails, R.S., eds. (2002) *Dispersal ecology*. Cambridge University Press, Cambridge, UK.

Buse, J., Schroder, B. & Assmann, T. (2007) Modelling habitat and spatial distribution of an endangered longhorn beetle: a case study for saproxylic insect conservation. *Biological Conservation*, **137**, 372-381.

Davies, Z., Tyler, C., Stewart, G. & Pullin, A. (2008) Are current management recommendations for saproxylic invertebrates effective? A systematic review. *Biodiversity and Conservation*, **17**, 209-234.

Davies, Z.G. & Pullin, A.S. (2007) Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. *Landscape Ecology*, **22**, 333-351.

del Barrio, G., Harrison, P.A., Berry, P.M., Butt, N., Sanjuan, M.E., Pearson, R.G. & Dawson, T. (2006) Integrating multiple modelling approaches to predict the potential impacts of climate change on species' distributions in contrasting regions: comparison and implications for policy. *Environmental Science & Policy*, **9**, 129-147.

den Boer, P.J. (1990a) Density limits and survival of local populations in 64 carabid species with different powers of dispersal. *Journal of Evolutionary Biology*, **3**, 19-48.

den Boer, P.J. (1990b) The survival value of dispersal in terrestrial arthropods. *Biological Conservation*, **54**, 175-192.

Denno, R.F., Roderick, G.K., Peterson, M.A., Huberty, A.F., Dobel, H.G., Eubanks, M.D., Losey, J.E. & Langellotto, G.A. (1996) Habitat Persistence Underlies Intraspecific Variation in the Dispersal Strategies of Planthoppers. *Ecological Monographs*, **66**, 389-408.

Dillon, A.B., Rolston, A.N., Meade, C.V., Downes, M.J. & Griffin, C.T. (2008) Establishment, persistence, and introgression of entomopathogenic nematodes in a forest ecosystem. *Ecological Applications*, **18**, 735-747.

Dolman, P.M. & Fuller, R.J. (2003). The processes of species colonisation in wooded landscapes: a review of principles. *The restoration of wooded landscapes* (ed. by J. Humphrey, A. Newton, J. Latham, H. Gray, K. Kirby, E. Poulsom & C. Quine), pp. 25-36. Forestry Commission, Edinburgh, UK.

Drach, A. & Cancela da Fonseca, J.P. (1990) Approche experimentale et theorique des desplacements de carabiques forestiers. *Revues d'Ecologie et de Biologie du Sol*, **27**, 61-71.

Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**, 65-74.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487-515.

Freemark, K., Bert, D. & Villard, M.-A. (2002). Patch-, landscape-, and regional-scale effects on biota. *Applying landscape ecology in biological conservation* (ed. by K.J. Gutzwiller), pp. 58-83. Springer Verlag, New York, USA.

Haddad, N.M. (1999) Corridor use predicted from behaviors at habitat boundaries. *American Naturalist*, **153**, 215-227.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41-49.

Hanski, I.A. & Gilpin, M.E., eds. (1997) *Metapopulation biology. Ecology, genetics, and evolution*. Academic Press, New York, USA.

Hedin, J., Ranius, T., Nilsson, S.G. & Smith, H.G. (2008) Restricted dispersal in a flying beetle assessed by telemetry. *Biodiversity and Conservation*, **17**, 675-684.

Lambeck, R.J. (1997) Focal species: a multi-species umbrella for nature conservation. *Conservation Biology*, **11**, 849-856.

Lövei, G.L. & Sunderland, K.D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, **41**, 231-256.

Matern, A., Drees, C., Kleinwachter, M. & Assmann, T. (2007) Habitat modelling for the conservation of the rare ground beetle species *Carabus variolosus* (Coleoptera, Carabidae) in the riparian zones of headwaters. *Biological Conservation*, **136**, 618-627.

Newton, A.C., ed. (2007) *Biodiversity loss and conservation in fragmented forest landscapes. The forests of montane Mexico and temperate South America*. CABI Publishing, Wallingford, Oxford, UK.

Niemelä, J. (1997) Invertebrates and boreal forest management. *Conservation Biology*, **11**, 601-610.

Niemelä, J. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review. *European Journal of Entomology*, **98**, 127-132.

O'Neal, M.E., Landis, D.A., Rothwell, E., Kempel, L. & Reinhard, D. (2004) Tracking insects with harmonic radar: a case study. *American Entomologist*, **50**, 212-218.

Pallant, J. (2007) *SPSS survival manual*, Open University Press, Berkshire, UK.

Petit, S. (1994). Diffusion of forest carabid beetles in hedgerow network landscapes. *Carabid beetles: ecology and evolution* (ed. by K. Desender, M. Dufrêne, M. Loreau, M.L. Luff & J.-P. Maelfait), Vol. 51, pp. 337-341. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Petit, S. & Burel, F. (1998) Connectivity in fragmented populations: *Abax parallelepipedus* in a hedgerow network landscape. *Comptes Rendus de l'Academie des Sciences - Series III - Sciences de la Vie*, **321**, 55-61.

Pichancourt, J.-B., Burel, F. & Auger, P. (2006) A hierarchical matrix model to assess the impact of habitat fragmentation on population dynamics: an elasticity analysis. *Comptes Rendus Biologies*, **329**, 31-39.

Pullin, A.S. & Knight, T.M. (2001) Effectiveness in conservation practice: pointers from medicine and public health. *Conservation Biology*, **15**, 50-54.

Pullin, A.S. & Stewart, G.B. (2006) Guidelines for systematic review in conservation and environmental management. *Conservation Biology*, **20**, 1647-1656.

Ranius, T. (2002) Population ecology and conservation of beetles and pseudoscorpions living in hollow oaks in Sweden. *Animal Biodiversity and Conservation*, **25**, 53-68.

Ranius, T. (2006) Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. *Population Ecology*, **48**, 177-188.

Ranius, T. & Hedin, J. (2001) The dispersal rate of a beetle, *Osmoderma eremita*, living in tree hollows. *Oecologia*, **126**, 363-370.

Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., Osborne, J.L., Williams, I.H., Carreck, N.L. & Poppy, G.M. (1996) Tracking bees with harmonic radar. *Nature*, **379**, 29-30.

Rink, M. & Sinsch, U. (2007) Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. *Journal of Zoology (London)*, **272**, 235-243.

Ross, J.A., Matter, S.F. & Roland, J. (2005) Edge avoidance and movement of the butterfly *Parnassius smintheus* in matrix and non-matrix habitat. *Landscape Ecology*, **20**, 127-135.

Sutherland, W.J., ed. (2006) *Ecological census techniques: a handbook*. Cambridge University Press, Cambridge, UK.

Szyszko, J., Gryuntal, S. & Schwerk, A. (2004) Differences in locomotory activity between male and female *Carabus hortensis* (Coleoptera: Carabidae) in a pine forest and a beech forest in relation to feeding state. *Environmental Entomology*, **33**, 1442-1446.

Thomas, C.D. (2000) Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society Biological Sciences Series B*, **267**, 139-145.

Travis, J.M.J. & Dytham, C. (1999) Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 723-728.

Tscharntke, T., Steffan Dewenter, I., Kruess, A. & Thies, C. (2002) Characteristics of insect populations on habitat fragments: a mini review. *Ecological Research*, **17**, 229-239.

Vermeulen, R. (1994). The effect of different vegetation structures on the dispersal of carabid beetles from poor sandy heaths and grasslands. *Carabid beetles: ecology and evolution* (ed. by K. Desender, M. Dufrêne, M. Loreau, M.L. Luff & J.-P. Maelfait), Vol. 51, pp. 387-392. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Vos, C.C., Verboom, J., Opdam, P.F.M. & Ter Braak, C.J.F. (2001) Toward ecologically scaled landscape indices. *The American Naturalist*, **157**, 24-41.

Walters, R.J., Hassall, M., Telfer, M.G., Hewitt, G.M. & Palutikof, J.P. (2006) Modelling dispersal of a temperate insect in a changing climate. *Proceedings of the Royal Society B*, **273**, 2017-2023.

Watts, K., Humphrey, J.W., Griffith, M., Quine, C. & Ray, D. (2005). *Evaluating biodiversity in fragmented landscapes: principles*, Forestry Commission, Edinburgh.