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Manuscript title:

The influence of barriers and orientation on the dispersal ability of wood cricket (*Nemobius sylvestris*) (Orthoptera: Gryllidae)

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Abstract

Dispersal is an important process determining species spread and survival in fragmented landscapes. However, information on the dispersal ability of woodland-associated invertebrate species is severely lacking. A study was conducted examining the ability of wood cricket (*Nemobius sylvestris*) (Orthoptera: Gryllidae) to cross small watercourses and to orientate themselves towards habitat edges. A series of experiments were conducted where juvenile (i.e. nymph) and adult wood crickets were released and observed over time. The results of this investigation indicated that (i) nymphs and adults were equally able to swim across a small (≤ 35 cm) watercourse; and (ii) within grassland adult wood cricket were able to positively orientate themselves towards a mature woodland edge at a visual angle of ≥ 19°, less than 50 m away. Together, this investigation suggests that these traits likely facilitate the ability of this species to disperse within fragmented wooded landscapes, however further study is needed to strengthen the significance of these findings for this and similar species.

Keywords: dispersal; perceptual range; orientation; watercourse; forest; insect; fragmentation

Introduction

Dispersal is widely considered to be a key process influencing the survival of species populations within fragmented landscapes (Turner et al. 2001). An important aspect of dispersal success is the ability of a species to move through the landscape (Merckx and Van Dyck 2007; Schtickzelle et al. 2007; Dover and Settele 2009). However, key factors influencing the dispersal ability of many groups of species are poorly known (Dolman and Fuller 2003; Holyoak et al. 2008).

The dispersal ability of species within real landscapes is primarily determined by morphological and physiological traits. These traits are key in understanding the potential of a species to disperse within fragmented landscapes. The ability to orientate towards habitat (Coyne et al. 1987; Harrison 1989; Zollner and Lima 1997; Zollner 2000; Dover and Fry 2001; Merckx and Van Dyck 2007; Schtickzelle et al. 2007), and the ability to cross physical barriers within the landscape (Dover and Fry 2001; Strong et al. 2002; Dover and Settele 2009) are two important traits that determine the level of dispersal that can be achieved by a species. However, the results of studies on, for instance, the ability to use visual cues to move through natural landscapes has been found to vary considerably between species (Coyne et al. 1987; Harrison 1989; Zollner and Lima 1997; Zollner 2000; Dover and Fry 2001; Merckx and Van Dyck 2007; Schtickzelle et al. 2007; Dover and Settele 2009). Choosing between corridors or stepping stones as a means to preserve and enhance biodiversity can be informed by studying these traits (Dover and Settele 2009) and consequently influence the effectiveness of conservation initiatives such as the agri-environmental schemes adopted in the UK (Merckx et al. 2009a; Merckx et al. 2009b). Studies examining these specific traits, particularly for invertebrates, are however still lacking (Holyoak et al. 2008).

Few studies have examined relatively immobile woodland-associated invertebrate species that are ground-dwelling and predominately move by walking (Diekotter et al. 2005; Brouwers and Newton 2009c). Compared to flying invertebrates, such species move over finer scales, and can therefore be considered more vulnerable to habitat fragmentation (Diekotter et al. 2005). Furthermore, these species are likely to benefit most from recent developments in conservation focussing on creating woodland habitat networks (Bailey 2007; Quine and Watts 2009). Therefore we examined two factors that are important in moving through a fragmented wooded landscape, (i) the ability to use orientation and (ii) cross watercourses, for a flightless woodland insect, the wood cricket (*Nemobius sylvestris* (Bosc, 1792)) (Orthoptera: Gryllidae), on the Isle of Wight, UK.

In the UK, wood cricket has the status of a 'Species of Conservation Concern' (NBN Gateway 2009). The species is strongly associated with deciduous woodland often dominated by oak (*Quercus spp.*) (Richards 1952; Brouwers and Newton 2009b). The species lives on the ground and requires a well-developed leaf litter layer, which serves as shelter, food and breeding ground (Richards 1952; Brouwers and Newton 2009b). The species prefers warm but sheltered conditions, and within woodlands can be found in open areas such as clearings and in edge habitat along woodland tracks, footpaths, railway lines and woodland peripheries (Richards 1952; Brouwers and Newton 2009b). The species is typically found in relatively large woodlands that lie in close proximity to each other within the landscape (Brouwers and Newton 2009a). This is mainly due to their limited dispersal ability, being small (~1 cm) and flightless, both in the UK and mainland Europe (Brown 1978).

Factors influencing the dispersal of ground-dwelling invertebrates, such as wood cricket, have been little studied (Dolman and Fuller 2003; Holyoak et al. 2008; Brouwers and Newton in press). In a study conducted in France, wood crickets were found able to cross forest tracks (Morvan and Campan 1976), showing that these features do not act as dispersal barriers for this species. However, no other landscape features generally present within woodlands were tested in this respect. Observations made in earlier studies showed a likely negative effect of small watercourses on the presence of wood cricket within the landscape and individual woodlands (Brouwers and Newton 2009a; Brouwers and Newton 2009b). In many woodland areas, small watercourses are present, and therefore potentially represent a substantial barrier for dispersal; however, the influence of small watercourses acting as possible barriers was never tested for this species. They were further found to show an ability to orientate towards distinct terrestrial features (Beugnon 1979), and able to disperse away from woodland habitat through other vegetation types like grassland (Brouwers personal observation). This indicated that their dispersal success between individual woodlands might be influenced by their ability to orientate towards distinct woodland edges. Investigations on the perceptual abilities of invertebrates in fragmented landscapes are still lacking (Bonte et al. 2004; Merckx and Van Dyck 2007; Holyoak et al. 2008), and to our knowledge no such investigations have been undertaken previously for flightless woodland-associated species.

The specific aims of this study were to investigate if wood crickets were able to (1) cross small watercourses, and (2) to derive their perceptual range by examining their ability to orientate towards distinct woodland edges within the landscape. Based on preliminary field observations and earlier findings for wood cricket (Beugnon 1979; Brouwers and Newton 2009a; Brouwers and Newton 2009b; Brouwers personal observation) it was hypothesised that: (i) neither nymphs nor adults would be able to cross a small watercourse, and (ii) adult wood crickets would show a positive orientation towards distinct woodland edges, but that this is affected by distance from them.

Materials and Methods

In 2007, two experiments were conducted using wood cricket nymphs (6-7th instar) and adult males and females respectively. The experiments were carried out in the Briddlesford area, Isle of Wight, UK (50° 42' 41.00" N, 1° 13' 30.50" W). For the experiments, both nymphs and adults were caught using a custom designed pooter, and kept in a plastic container with ample supplies of food (bread, various fungi and oak leaf litter). All experiments were performed under similar meteorological conditions where mean average daytime temperature did not go below 15 °C.

Watercourse experiment

To test whether wood crickets were able to cross a watercourse, an island (75x50 cm) was created on a woodland track surrounded by a 35 cm wide and 2 cm deep watercourse. The island was designed to mimic their natural preferred habitat, based on their known habitat preferences (see Brouwers and Newton 2009b), including a 3 cm thick leaf litter layer. Fifteen nymphs and 20 adults (sex ratio: 0.5) were released on the 21st of June and 2nd of August, respectively. These densities are similar to the densities that can be observed under natural circumstances (up to 196 individuals per m^2) (Gabbutt 1959; Brouwers personal observation). The release was achieved by inverting a circular transparent plastic container (9x10 cm), including the wood crickets and a small amount of leaf litter, in the centre of the island and releasing the specimens after 15 seconds. Activities of the released individuals were observed continuously for the first hour. Then surveys were made at 2, 3, 4, 5, 24 and 48 hours after the initial release. Time of escape attempt, direction, and sex were recorded. For both life-stages, chi-square 'goodness of fit' tests were performed to test for their ability to cross the watercourse and a Fisher's exact probability test was performed to test for differences between the sexes, both using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA).

Orientation experiment

To test the ability of wood cricket adults and to what extent they were able to orientate towards a woodland edge, an experiment was conducted following the method of Beugnon (1979). For this experiment, an elevated cardboard release platform (diameter: 50 cm) was used. This platform was raised 60 cm above ground level to provide a clear view of the woodland edge. Releases were replicated twice and performed on the 24th and 26th of August around noon. To avoid directional bias related to the sun, releases were made under overcast conditions. Releases were made within a grazed grassland at distances between 15 and 50 meters from woodland edges dominated by oak (*Quercus spp*.) that had an average height of 18 meters. At each distance, individual wood crickets (sex ratio: 0.5) were released in the centre of the platform with a circular transparent plastic container (3.5 x 7 cm). Release direction was randomised by releasing each individual after 10 seconds. Individuals were drawn from a pool of 50 individuals with replacement. For each released individual, the movement path and exit location relative to the habitat edge were recorded. Furthermore, the height of the habitat edge, and for each release location, the visual angle (in degrees) to the top of the nearest edge was measured using a clinometer (ClinoMaster, Silva Sweden AB). To analyse the data, chi-square 'goodness of fit' tests were performed using SPSS.

Results

Watercourse experiment

Both nymphs and adults were able to cross the watercourse, rejecting the initial hypothesis. They were observed actively leaping in the water and swimming across, staying afloat by the water tension. Overall, nymphs crossed the watercourse more readily than adult wood crickets. Within the first 5 hours, 13 out of 15 nymphs (87%) had crossed the watercourse. The adults took 48 hours to match this number with 9 males and 8 females (85%) that made the crossing, showing no differences between the sexes (Table 1).

 # Table 1 approx here #

Orientation experiment

Wood crickets showed a positive orientation towards distinct woodland edges when the visual angle was ≥ 19° (Table 2), confirming the initial hypothesis. This translated into a positive orientation up to 40 m distance from a mature woodland edge with an average height of 18 meters (Table 2).

 # Table 2 approx here #

Discussion

Within the limits of the experiments, this study provided novel information on factors influencing the ability of a flightless woodland invertebrate to disperse within a heterogeneous agricultural landscape. Wood cricket males have been found moving away from colonies through suboptimal habitat, where contrary to forest carabid species, woodland edges were found to act as conduits rather than barriers for wood crickets (Richards 1952; Strong et al. 2002; Brouwers and Newton 2009b). Dispersal was observed to be mainly driven by suitable habitat becoming unsuitable (Brouwers and Newton 2009b), and possibly also through density dependant territorial behaviour (Richards 1952). Together with earlier findings on their ability to cross forest roads

(Morvan and Campan 1976), this study suggests that common landscape features within woodlands such as small watercourses do not act as barriers for dispersing wood crickets. Furthermore, wood crickets were found to have a relative long perceptual range. Together with their ability to traverse through non-woodland vegetation (i.e. grassland) (Brouwers personal observation), this suggests that these traits likely facilitate the ability of this species to disperse within wooded landscapes, however further study is needed to strengthen the significance of these findings for this and similar species.

The ability to use visual orientation to detect and move towards habitat is not universal among invertebrates. For example, the ability to orientate towards terrestrial cues was found to be minimal for the dune wolf spider species, *Pardosa monticola* (Bonte et al. 2004) and *Drosophila* flies (Coyne et al. 1987). However, butterfly species were found to be more able to use this trait within fragmented landscapes (e.g. Harrison 1989; Schtickzelle et al. 2007; Dover and Settele 2009). For woodland-associated species, this type of investigation has been conducted for various small mammals (Zollner and Lima 1997; Zollner 2000), and the speckled wood butterfly (*Pararge aegeria*) (Merckx and Van Dyck 2007). These studies showed a high variability between and within species in their ability to orientate towards woodland habitat (Zollner and Lima 1997; Zollner 2000; Merckx and Van Dyck 2007). This highlights that the effectiveness of current conservation approaches like the creation of corridors and stepping stones to increase connectivity will be highly species specific (Dover and Settele 2009). Several recent studies specifically highlight the importance of the perceptual ability of invertebrates as a dispersal trait in fragmented landscapes (Merckx and Van Dyck 2007; Dover and Settele 2009). These type of studies are therefore highly important in filling the gap in knowledge in understanding species specific attributes that influence dispersal (Holyoak et al. 2008). However, there is still a great need for studying the dispersal ability of this and similar species to derive the key factors influencing successful dispersal in fragmented anthropogenic landscapes.

The findings on the perceptual range of wood cricket seem to support earlier studies that indicate an apparent threshold distance for dispersal of wood cricket around 50 meters. Morvan et al. (1978) found a maximum dispersal distance for wood cricket between 50 and 60 meters. A landscape scale fragmentation study found that the species was primarily present in clusters of woodlands that were situated in close proximity (50 m) to each other (Brouwers and Newton 2009a). Within woodlands the species was also found to be absent when more than 54 meters away from a source population (Brouwers and Newton 2009b), and the species was observed to be able to traverse up to 55 m away from woodland habitat through grassland (Brouwers personal observation). Together with these findings, the current study supports the suggestion that wood crickets are able to disperse between woodlands when they are less than 50 meters apart. More importantly, these findings give an indication of when woodland fragments within the landscape can be considered functionally disconnected for wood crickets (Crooks and Sanjayan 2006). This further indicates that for the conservation of this species, increasing connectivity by creating habitat networks is likely to be necessary and useful in areas where woodlands are further away than 50 meters from each other.

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Table 1 Watercourse crossing success for wood cricket. Chi-square 'goodness of fit' tests for wood cricket nymphs (after 5 h) and adults (after 48 h), and Fisher's exact test between sexes. Crossed/Remained = number of individuals that crossed the watercourse or remained on the release site.

Life-stage	Crossed	Remained	χ^2	df	*P*
Nymphs	12	3	5.400	1	0.020
Adults	17	3	9.800	1	0.002
Males	9	1	Fisher's test		0.999
Females	8	2			

Table 2 Orientation preference for wood cricket. Chi-square ‘goodness of fit’ tests for orientation direction of wood cricket. Distance: release distance from a woodland edge in meters. Angle = angle (in degrees) measured from the release location to the top of the woodland edge (av. height 18m). *n* edge/field = number of wood cricket exiting the release platform towards the woodland edge or towards the field. 50 meter releases were performed at two different locations.

Distance	Angle	*n* edge	*n* field	X^2	df	*P*
15	34	16	3	8.895	1	0.003
20	30	14	1	11.27	1	0.001
30	24	16	0			<0.001
35	21	12	3	5.400	1	0.020
40	19	15	3	8.000	1	0.005
50	16	8	5	0.692	1	0.405
50	15	5	8	0.692	1	0.405