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Brouwers, N.C. , Newton, A.C. and Bailey, S. (2011) The dispersal ability of wood cricket (*Nemobius sylvestris*) (Orthoptera:Gryllidae) in a wooded landscape. European Journal of Entomology , 108 (1). pp. 117-125.

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1 **Full reference:**

2 **Brouwers, N.C.**, Newton, A.C., Bailey, S., 2011. The dispersal ability of wood cricket
3 (*Nemobius sylvestris*) (Orthoptera: Gryllidae) in a wooded landscape. **European**
4 **Journal of Entomology** 108, 117-125.

5

6 **Manuscript title:**

7

8 The dispersal ability of wood cricket (*Nemobius sylvestris*) (Orthoptera: Gryllidae) in a
9 wooded landscape

10

11 **Running head:**

12 Dispersal ability of wood cricket

13

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38

39 **Abstract**

40

41 Information on the dispersal ability of flightless insect species associated with
42 woodlands is severely lacking. Therefore, a study was conducted examining the
43 dispersal ability of wood cricket (*Nemobius sylvestris*) juveniles (nymphs) and adults in
44 a wooded landscape on the Isle of Wight, UK, to further our understanding of the
45 ecology and management of this and other flightless insects. A series of experiments
46 were conducted where nymphs and adults were released and observed at a range of
47 spatial-temporal scales within different habitat environments. The results of this
48 investigation indicated no difference in the dispersal ability of wood cricket nymphs and
49 adults. However, adult females moved less than adult males. Adult males were found
50 to spread twice as fast as females, and males were found capable of traversing up to
51 55 m away from woodland habitat through semi-natural and grazed grassland.
52 Additionally, rates of population spread of both wood cricket nymphs and adults (males
53 and females) were found to be accurately described by the inverse-power function,
54 predicting only few individuals dispersing over time. Together this indicates that overall
55 colonization success and rate of population spread, being female dependent, is likely to
56 be low for this species. Wood crickets were found to live in and able to move along
57 mature woodland edges directly bordering agricultural land. This indicates that
58 conservation initiatives focusing on creating woodland corridors and developing
59 woodland habitat networks have the potential to facilitate the spread and population
60 viability of wood crickets, if the woodland edges are given enough time to develop.
61 However, long-term monitoring is needed to evaluate the overall effectiveness of such
62 approaches.

63

64 **Keywords:** *Nemobius sylvestris*; dispersal ability; woodland; forest; population spread;
65 landscape; habitat network; insect;

66

67 **Introduction**

68

69 Dispersal is widely considered to be a key process influencing the survival of
70 populations of species within fragmented landscapes (Hanski & Gilpin, 1997; Kindvall,
71 1999; Turner et al., 2001; Fahrig, 2003; Diekötter et al., 2005; Ranius, 2006). However,
72 the dispersal ability (i.e. speed and distance over time) of many groups of species is
73 poorly known (Dolman & Fuller, 2003; Ranius, 2006). Investigations of specific
74 dispersal strategies using experiments undertaken at fine spatio-temporal scales can
75 provide valuable initial insights into the dispersal ability of species (Turchin, 1991;
76 Turchin, 1998; Samu et al., 2003; Brouwers & Newton, 2010b). However, dispersal
77 typically takes place over large scales (Levin, 1992) and therefore needs to be
78 examined across a range of spatio-temporal scales (Brouwers & Newton, 2010b).
79 Deriving reliable estimates of dispersal in natural environments represents an ongoing
80 challenge, but is highly important in terms of understanding population dynamics and
81 predicting species persistence within the landscape (Turchin, 1998; Trakhtenbrot et al.,
82 2005; Nathan, 2008).

83

84 Few studies have examined the dispersal ability of relatively immobile invertebrate
85 species that are ground-dwelling and move by walking (Diekötter et al., 2005; Diekötter
86 et al., 2010). Compared to flying invertebrates, such species move over finer scales,
87 and may therefore be considered more vulnerable to habitat fragmentation (Tscharrntke
88 et al., 2002; Diekötter et al., 2005). However, most dispersal studies of ground-dwelling
89 invertebrates have focused on species associated with open semi-natural grassland
90 habitats (e.g. Vermeulen, 1994; Baur et al., 2005; Öckinger & Smith, 2008), where
91 similar studies for woodland-associated species are rare in the literature (Brouwers &
92 Newton, 2009c).

93

94 Some studies have investigated dispersal of ground-dwelling species by fitting
95 regression curves to field data (e.g. Chapman et al., 2007), which is useful as an
96 indicator of the dispersal ability of a species and for making predictions of dispersal
97 range (i.e. distance) over time. A common approach to model and quantify dispersal is
98 to fit a curve to observational data obtained in the field (Turchin, 1998). Curves
99 commonly used to describe the spread of species, such as the fraction of a population
100 moving a certain distance, are often based on equations such as the negative-
101 exponential and inverse-power functions (Turchin, 1998). For some species,
102 observations made in the field were best described by the negative-exponential
103 function (Conrad et al., 1999; Baguette et al., 2000; Baguette, 2003; Kuras et al., 2003;
104 Ranius, 2006; Fric & Konvicka, 2007), whereas for others the inverse-power function
105 was found to provide a better fit (Hill et al., 1996; Baguette et al., 2000; Roslin, 2000; St
106 Pierre & Hendrix, 2003; Fric & Konvicka, 2007). The most important difference between
107 these two curves is the behaviour of the tail, where the power function typically predicts
108 a higher frequency of long-distance dispersal events than the exponential function
109 (Turchin, 1998). Determining this relationship for a species therefore provides a helpful
110 tool for conservation management.

111

112 In order to halt and reverse the effects of species habitat fragmentation, conservation
113 policy and practice is increasingly focusing on the creation of habitat networks (Hobbs,
114 2002). Networks are typically created through the development of vegetation links or
115 corridors to increase connectivity between individual habitat fragments (Bennett, 2003;
116 Crooks & Sanjayan, 2006). However, the degree of habitat connectivity within a given
117 landscape is highly dependent on the characteristics of the vegetation and the species
118 being considered (Baguette & Van Dyck, 2007). Particular vegetated features in the
119 landscape can function either as conduits (i.e. habitat) or barriers to different species
120 (Hobbs, 2002). The role of developing corridors as conduits in terms of facilitating
121 species dispersal still lacks a firm evidence base (Bennett, 2003; Crooks & Sanjayan,

122 2006; Bailey, 2007; Öckinger & Smith, 2008). For example, a recent review of the
123 functioning of hedgerows as possible corridors between woodlands found insufficient
124 empirical evidence to establish their role in facilitating species dispersal (Davies &
125 Pullin, 2007). Nonetheless, the development of habitat networks utilizing corridors has
126 been widely applied in practice (Hobbs, 2002). In the UK, for example, a large number
127 of initiatives have recently been implemented aiming to reconnect woodland to
128 increase habitat connectivity for woodland species (Humphrey et al., 2003; Humphrey
129 et al., 2005).

130

131 The aim of the study presented here was to investigate the dispersal ability and
132 evaluate the potential of wooded corridors and creating woodland habitat networks in
133 facilitating dispersal for ground-dwelling woodland insects. Research was conducted on
134 the Isle of Wight, UK, where such habitat networks are currently being developed. For
135 this study, two life-stages of a ground-dwelling flightless woodland insect, the wood
136 cricket (*Nemobius sylvestris*), were investigated. The wood cricket was selected for
137 study as it was found to be a good model species representing ground-dwelling insects
138 with a strong association with woodland habitat (Brouwers & Newton, 2009c; Brouwers
139 & Newton, 2010b). Furthermore, it is a local species of conservation concern (NBN
140 Gateway, 2010) that might be expected to benefit from the development of a woodland
141 habitat network, given its association with wooded edges (Richards, 1952; Bailey, 2007;
142 Brouwers et al., 2010).

143

144 The specific objectives of this study were: (1) to investigate the differences in dispersal
145 ability observed for wood cricket nymphs and adults (males and females) at a range of
146 spatio-temporal scales within a wooded landscape; (2) to model population spread (i.e.
147 derive the best-fit dispersal curve) for wood cricket nymphs, adult males and females;
148 and (3) to determine to what extent wood crickets disperse along edge habitat outside
149 woodland within an agricultural landscape. This study specifically adopted a range of

150 small to large spatio-temporal experiments, to allow comparison with observations and
151 earlier results for wood crickets found at small spatio-temporal scales (2-25 minutes,
152 15-16m²) (Brouwers & Newton, 2010b). Based on these earlier findings it was
153 hypothesized that: (a) wood cricket adults would show a higher dispersal ability than
154 wood cricket nymphs, as adults showed a more directed movement strategy than
155 nymphs (Brouwers & Newton, 2010b), (b) wood cricket males and females show
156 similar levels of dispersal ability, as no differences in movement strategy was found
157 between the sexes (Brouwers & Newton, 2010b), and (c) dispersal distances achieved
158 over a given time would be further along mature woodland habitat edges than along
159 hedge edges or along new woodland plantings, based on observations made in earlier
160 investigations of wood crickets showing a habitat preference for mature woodland
161 edges (Brouwers & Newton, 2009b, a).

162

163 **Material and methods**

164

165 *Study species*

166

167 Wood cricket (*Nemobius sylvestris*) (Orthoptera: Gryllidae) (Bosc, 1792) is a small (~ 1
168 cm) flightless cricket species that has a semi-voltine (i.e. two-year) life cycle in the UK.
169 After overwintering, eggs hatch in June/July and nymphs develop and grow throughout
170 the summer and autumn by means of moulting up to 5 times from the 1st to the 5th
171 instar stage. Moulting ceases completely in September and the nymphs overwinter at
172 sheltered locations within thick leaf litter layers. In the second year, nymphs continue to
173 develop (5th - 8th instar) from April onwards until they reach sexual maturity (i.e.
174 become adults) in July/August and reproduce through to September/October until they
175 die (Gabbutt, 1959; Brown, 1978). The species is generally associated with deciduous
176 oak (*Quercus* spp.) dominated woodlands and, being a thermophilic insect, is typically
177 found in wooded edge habitat along woodland tracks, footpaths, railway lines and

178 woodland peripheries, and in relatively sheltered open woodland areas such as
179 clearings (Richards, 1952; Morvan & Campan, 1976; Beugnon, 1980). Wood crickets
180 live on the ground and prefer a well-developed leaf litter layer, which serves as shelter,
181 food source and breeding ground (Richards, 1952; Brown, 1978; Proess & Baden,
182 2000). In natural populations wood crickets can be found in high densities at relatively
183 small spatial scales (up to 200 individuals per square meter) (Gabbutt, 1959). At the
184 landscape scale, the species was found to be associated primarily with relatively large
185 woodland patches that were situated in close proximity to each other (Brouwers &
186 Newton, 2009b). The main habitat requirements and preferences identified for this
187 species were presence of a thick leaf litter layer, an open canopy and low cover of
188 ground vegetation (Brouwers & Newton, 2009a; Brouwers & Newton, 2010b). Adult
189 wood crickets were found to move with a higher velocity and a more directed strategy
190 through leaf litter than juveniles (i.e. nymphs) (Brouwers & Newton, 2010b).
191 Furthermore, small watercourses were found not to act as a dispersal barrier, and their
192 orientation capacity was found to play a possible important role in their ability to
193 disperse within fragmented landscapes (Brouwers & Newton, 2010a). This information
194 was used to formulate the hypotheses and inform the design of the experiments that
195 were undertaken in this study.

196

197 *Study site*

198

199 The study was carried out in the Briddlesford area (50° 42' 41.00" N, 1° 13' 30.50" W)
200 situated on the Isle of Wight (UK) which is owned by 'The People's Trust for
201 Endangered Species' (PTES), a non-governmental conservation organization. Natural
202 populations of wood crickets are present across this area. The majority of woodlands in
203 this area are classified as 'ancient woodland' and are dominated by native deciduous
204 tree species, particularly pedunculate oak (*Quercus robur*), with undergrowth of hazel
205 (*Corylus avellana*). Since 2005, extensive new plantings of native tree species have

206 taken place in this area in order to increase connectivity between the individual
207 woodland fragments to create functional habitat networks.

208

209 *Materials*

210

211 In 2007, a series of experiments were conducted investigating the dispersal ability of
212 the wood cricket using nymphs (6-7th instar) and adult males and females. For the
213 experiments, both nymphs and adults were caught using a pooter. This is a device that
214 is used to collect insects by sucking them into a hold container. Before being released,
215 caught individuals were kept in a plastic container (21x33x20 cm) with ample supplies
216 of food (bread, various fungi, and oak leaf litter). To increase the visibility of individual
217 wood crickets that were released during the experiments, individuals were marked by
218 dusting them with non-toxic fluorescent pigment (UV Gear, Mark SG Enterprises,
219 Surrey, United Kingdom, www.uvgear.co.uk) (following Cronin, 2003). Marking was
220 achieved by placing individuals in a plastic container with a small amount of pigment,
221 and shaking the container gently until all specimens were marked sufficiently. To
222 investigate the influence of the marking pigment, a control study was performed
223 observing 20 marked and unmarked nymphs and adults within a plastic container
224 (21x33x20 cm) continuously for the first 2 hours and then at intervals of 24 hours for 5
225 days. This study revealed no changes in behaviour and no mortality for either group.

226

227 At all experimental site locations, vegetation measurements were carried out using a
228 50x50 cm quadrat, measuring (1) ground vegetation cover (in %) and height (in cm), (2)
229 leaf litter cover (in %) and depth (in cm), and (3) canopy closure (in %) using a convex
230 spherical densiometer (Forest Densiometers, Bartlesville, US). All experiments were
231 conducted under similar meteorological conditions where mean daytime temperature
232 did not drop below 15 °C.

233

234 *Enclosure experiment*

235

236 To measure population spread of wood crickets over time and distance, five circular
237 enclosures with different diameters were created within an oak-dominated forest stand.
238 The enclosures ranged in size from 2-7 m radius. For nymphs enclosures of 2, 3, 4 and
239 5 meter radius were used and, because of their observed higher movement velocity
240 (Brouwers & Newton, 2010b), an additional 7 meter radius enclosure was created for
241 adults. The enclosures were constructed from 50 cm high translucent sheet plastic
242 inserted 5 cm into the ground. The interior habitat of the individual enclosures was
243 homogenized by clearing the ground surface of most of its herbaceous vegetation,
244 resulting in a mean ground vegetation cover of 10% (range 5-20%), a mean vegetation
245 height of 10 cm (range 5-10 cm), and a mean litter cover of 99% (range 95-100%), 3
246 cm deep (range 2-3.5 cm). The mean overhead canopy closure for all sites was 90%
247 (range 85-96%). These particular habitat characteristics were found to be positively
248 linked with the presence of wood cricket populations (Brouwers & Newton, 2009a). The
249 initial design included pitfall traps at regular intervals along the inside of the enclosure
250 walls to derive an accurate rate of dispersal (Vermeulen, 1994). A pilot release of wood
251 crickets revealed a low level of mortality over time, and that, unlike ground beetles,
252 wood crickets were able to avoid being caught by pitfall traps. Therefore, the pitfall
253 traps were removed during the actual experiments. Although the pitfall design failed,
254 observations made over the first 48 hours after release, both in the pilot study and the
255 actual experiment, revealed that individuals reaching the circumference of the 3-7 m
256 enclosures remained at the same locations and numbers accumulated over this period
257 of time. Therefore, observations made during the surveys in the first 48 hours of the
258 experiment (further described below) were used to estimate the rate of dispersal and
259 derive differences in dispersal ability for this species.

260

261 At the centre of each enclosure, 50 wood cricket nymphs were released simultaneously
262 at noon on the 11th of June. A second release was conducted for adult wood crickets
263 on the 31st of July, in this case releasing 20 adult males (M) and 20 females (F). The
264 release was achieved by inverting a circular transparent plastic container (21x10 cm),
265 including the wood crickets and a small amount of leaf litter, in the centre of the
266 enclosures and releasing the specimens after 15 seconds. After the initial release,
267 continuous observations of the released population within the smallest enclosure (2 m
268 radius) took place for the duration of 1 hour. Following this period, all the enclosures
269 were surveyed five times for five successive hours by walking slowly outside the
270 enclosures examining the leaf litter inside the enclosure for presence of marked wood
271 crickets. To account for the difference in chance of observation, the surveys were
272 performed using a constant walking speed for all enclosures. During the following four
273 days, all enclosures were similarly surveyed at 24 h intervals. Within each enclosure,
274 the number, sex, location, distance between observed males and females, and
275 distance from the enclosure periphery was recorded for each individual observed. For
276 both experiments, the weather was predominantly dry with occasional showers and a
277 mean ground surface temperature of 15 °C.

278

279 *Analyses*

280

281 Because individuals were found to accumulate and remain at the circumference of the
282 3-7 m enclosures (see *Enclosure experiment* and Table 1), but not after, only data
283 collected in the first 48 hours after release were used in the analyses. To investigate
284 the differences in dispersal ability for wood cricket nymphs, adult males and females
285 (i.e. individuals observed moving the straight-line distance of the enclosure radius over
286 time); differences between the number of: (i) nymphs and adults, (ii) males and females,
287 and (iii) female vs. male-female pairs (being individuals less than 5 cm apart) were
288 tested with chi-square 'goodness of fit' tests. All individuals that travelled the radius

289 distance from the release point and were observed less than 10 cm away from the
290 enclosure peripheries were included in these analyses. Furthermore, pairs were
291 compared with single females, because of their assumed attraction to males. To
292 compare the differences between nymphs and adults, the observed numbers were
293 corrected for the difference in the total sample size used (nymphs ($n = 200$) and adults
294 ($n = 160$)). Additionally for nymphs and adults the rate of dispersal was calculated and
295 differences tested between nymphs and adults and males and females with an
296 independent samples t-test were.

297

298 To model the population spread of wood cricket nymphs, adult males and females, the
299 proportion of the released population observed at the periphery was calculated. The
300 numbers observed over the first 48 hours (i.e. 2 days) were used to calculate the
301 proportions of the populations moving in meters per day (m day^{-1}). For this calculation,
302 individuals of the released populations moving from the release point to the enclosure
303 periphery on the first day (for all enclosures), and the additional number reaching the
304 periphery on the second day (2-5 m enclosures for nymphs, 3-7 m for adults) were
305 used (see Table 1). For each enclosure, these proportions were plotted against the
306 straight-line distance from the point of release (i.e. the enclosure radius). [Simple linear](#)
307 [regression and the negative-exponential \(\$y = ae^{-kx}\$ \) and inverse-power regression](#)
308 [functions \(\$y = ax^{-n}\$ \) were used to fit these data for nymphs, all adults, males and](#)
309 [females. In these cases, y indicates the proportion of the population moving as a](#)
310 [function of: scaling constant \(a\); distance travelled in meters \(x\); and parameters](#)
311 [determining the slope of the regression \(k and n\). Best-fit of these functions was](#)
312 [demined by investigation of the residuals following Pallant \(2007\). All statistical](#)
313 analyses and curves were evaluated using output generated with SPSS (Version 14.0,
314 SPSS Inc., Chicago, Illinois, USA) following Tabachnick & Fidell (2001) and Pallant
315 (2007).

316

317 *Dispersal surveys in the landscape*

318

319 To determine to what extent wood crickets moved/dispersed along edge habitat outside
320 woodland within the agricultural landscape, **marked** wood cricket nymphs and
321 **unmarked** adults were released and monitored over time in three different habitats
322 represented by linear wooded features at six locations within the landscape (i.e. 2
323 replicates per wooded edge habitat). **Absence of the species at the monitoring sites**
324 **was established during two surveys conducted prior to performing this study. This**
325 **ensured that the observations that were made could only be that of released individuals.**
326 On the 26th of June 50 wood cricket nymphs and on the 3rd of August another 100 adult
327 wood crickets (sex ratio = 0.5) were released at each location. The six release sites
328 were located at the exact L-junctions of linear landscape features running away from a
329 main body of woodland, being (i) a 10 m-wide strip of mature woodland, (ii) a 3 m-wide
330 mature hedge, and (iii) a mature hedge with 3 m-wide strips of newly planted tree
331 saplings along each side. The 1x1 m release sites were prepared in a similar fashion
332 as the enclosures, representing favourable habitat conditions for wood crickets (see
333 above). The specific edge habitats represented: (1) mature woodland bordering grazed
334 grassland (WE), (2) mature hedges bordering grazed grassland (HE), and (3) ungrazed
335 semi-natural grassland with newly planted saplings bordering grazed grassland (JE).
336 Further habitat characteristics of these edges are given in the results. Additionally,
337 semi-natural and grazed grassland (vegetation height: 15-30 cm, and cover: 100%)
338 adjacent to occupied woodland edges was also surveyed. After release, the two edges
339 running away from each release site (situated in the corner of the L-junctions) were
340 surveyed for three consecutive days and re-surveyed four times, sixty days after the
341 initial release of the nymphs. The survey procedure involved walking slowly along or
342 through the different edge habitats in a systematic manner up to 80 meters from the
343 release sites. Individuals were found based on actual sightings **of marked and**
344 **unmarked specimens** or the sound of stridulating males, following the survey method of

345 Proess and Baden (2000). Five-minute listening periods were taken at 5-meter
346 intervals along the edge to complement the visual searches. Where specimens were
347 observed or heard, straight-line distances from the point of release and/or the occupied
348 woodland edge were measured. All surveys were of 30-40 minutes duration and were
349 undertaken under dry weather conditions with a mean daytime temperature of 15 °C or
350 higher. To indicate to what extent wood crickets were able to move/disperse along
351 edge habitat present within the agricultural landscape, the observed dispersal
352 distances were compared between the different edge habitats using Mann-Whitney *U*
353 tests in SPSS.

354

355 **Results**

356

357 *Enclosure experiment*

358

359 Compared to nymphs, adult wood crickets appeared to move in a more directed (i.e.
360 linear) manner, moving mainly by walking. In the first five hours, adults were observed
361 to spread out gradually from the point of release. After the first 24 hours following
362 release, males were heard stridulating within the enclosures and over time (0-96 hours)
363 males and females were increasingly observed in pairs. Contrary to the nymphs, after
364 96 hours the adults were absent from the release site.

365

366 *# Table 1 approx here #*

367

368 In general, the number of nymphs and adults observed at the periphery decreased with
369 an increase in enclosure size (Table 1). Furthermore, the number of nymphs and adults
370 observed at the periphery of each enclosure increased in the first 48 hours and then
371 levelled off (Table 1), because individuals started to move back into the interior of the
372 enclosures after 48 hours. For the adults, all first arrivals at each individual enclosure

373 periphery were males, and on every survey day, the total number of males that was
374 observed was higher than the number of females (Table 1). Furthermore, except for
375 one female, only males were observed at the periphery of the 7 m enclosure, together
376 indicating a lower dispersal ability/tendency for females than males.

377

378 *Nymphs vs. Adults*

379

380 The total number of nymphs observed at the 2-5 m enclosure peripheries was found to
381 be no different than the number of adults after 24h (Chi-square: Nymphs = 16 vs.
382 Adults = 23, $\chi^2 = 1.256$, $df = 1$, $P = 0.262$) and after 48h (Chi-square: Nymphs = 26 vs.
383 Adults = 31, $\chi^2 = 0.439$, $df = 1$, $P = 0.508$). This indicates that both life stages show a
384 similar dispersal ability/tendency, therefore rejecting hypothesis (a).

385

386 *Males vs. Females*

387

388 Male wood crickets were observed twice as often at the periphery of the 3-7 m
389 enclosures than females both after 24h (Chi-square: Male = 15 vs. Female = 4, $\chi^2 =$
390 6.368 , $df = 1$, $P = 0.012$) and 48h (Chi-square: Male = 27 vs. Female = 13, $\chi^2 = 4.900$,
391 $df = 1$, $P = 0.027$). This indicates a higher ability and/or tendency for dispersal by males,
392 therefore rejecting the second hypothesis (b). Additionally, the number of male and
393 female pairs within the enclosures increased over time. Overall and over time (i.e. after
394 72h), the number of pairs was significantly higher than the number of single females
395 observed (Table 2).

396

397 *# Table 2 approx here #*

398

399 *Rate of dispersal*

400

401 A mean straight-line dispersal rate in m day^{-1} was calculated for individuals of the
402 released populations moving from the release point to the enclosure periphery on the
403 first day, and the additional number reaching the periphery on the second day after
404 release. The mean straight-line dispersal rate for nymphs was 2.57 m day^{-1} (range:
405 $1.67\text{-}3.13$, $n = 52$), which was observed for 26% of individuals from the released
406 populations within the enclosures, indicating that 74% of individuals dispersed with
407 lower rates or not at all. For 25% of individuals in the adult population, the mean
408 dispersal rate observed was 2.91 m day^{-1} (range: $2.07\text{-}3.84$, $n = 40$). This higher
409 dispersal rate for adults was however not statistically different from the rate observed
410 for nymphs (Independent samples t-test: $t = 1.343$, $df = 90$, $P = 0.183$). Males
411 dispersed with a mean rate of 3.15 m day^{-1} (range: $2.08\text{-}4.00$, $n = 27$) and females with
412 a mean rate of 2.42 m day^{-1} (range: $2.06\text{-}3.25$, $n = 13$), which was observed for 34%
413 and 16% of individuals within the released populations, respectively. This indicates
414 higher dispersal rates for males, however this was not found to be statistically different
415 from the rate observed for females (Independent samples t-test: $t = 1.758$, $df = 38$, $P =$
416 0.087). Overall, these results indicate that the majority of individuals (75%) within wood
417 cricket populations on average disperse less than 3 m day^{-1} .

418

419 *Modelling population spread*

420 (Brouwers et al., 2010)

421 For nymphs and adults, the proportion of the total population observed at the enclosure
422 periphery per day was plotted against distance (Fig. 1). The negative-exponential curve
423 and the inverse-power curve were found to fit these data best. Based on the R^2 values,
424 both curves fitted these data well with R^2 values ranging between 0.78 and 0.97 for the
425 negative-exponential curve, and slightly higher values (0.80-0.99) for the inverse-power
426 curve (F-test, $P < 0.05$, Fig. 1). However, where only few data points were used,
427 investigation of the residuals are essential to determine the true fit of these curves
428 (Pallant, 2007). The residuals that were shown in the output plot for the negative-

429 exponential curve were unevenly distributed around the central line, which is reason to
430 reject this relationship (Tabachnick & Fidell, 2001; Pallant, 2007). The even distribution
431 of the residuals for the inverse-power curve indicated the best overall fit for these data.
432 Overall, the inverse-power curves for both nymphs and adults all show a rapid decline
433 in the number of wood crickets moving with distance (see Fig. 1). *Estimates derived*
434 *from the inverse-power equations (see Fig. 1) indicate that potentially only 3.71% of*
435 *nymphs, 0.75% of adults, 1.08% males and 0.11% females within a population are*
436 *dispersing up to 25 meters, indicating a likely low level of dispersal for this species.*

437

438 *# Figure 1(a-d) approx here #*

439

440 *Dispersal surveys in the landscape*

441

442 *# Table 3 approx here #*

443

444 Wood crickets were found to move furthest along mature woodland edges (Mann-
445 Whitney U : WE vs. HE, $U = 22$, $Z = -4.510$, $P < 0.01$ and WE vs. JE, $U = 28$, $Z = -4.504$,
446 $P < 0.01$,

447 Table 3), confirming hypothesis (c). Over time, wood crickets were observed to move
448 more than two or three times as far along mature woodland edges than along hedge
449 edges and new woodland plantings respectively (

450 Table 3). Distances recorded along the hedge edges and new woodland plantings were
451 not significantly different (Mann-Whitney U : HE vs. JE, $U = 167$, $Z = -1.335$, $P = 0.182$).

452 The difference between the edge habitats was also reflected in the habitat
453 characteristics. The dispersal distance decreased with a decrease in litter cover (LC),
454 litter depth (LD) and canopy cover (CC) (

455 Table 3), indicating a relationship with these habitat characteristics also found in an
456 earlier study on wood cricket presence (Brouwers & Newton, 2009a). Additionally,

457 wood cricket males ($n = 17$) were also found in semi-natural and grazed grassland 2.5-
458 55.0 m away from occupied woodland edges.

459

460 **Discussion**

461

462 In this investigation, we acquired novel information on the dispersal ability of wood
463 crickets at a range of spatio-temporal scales. [Studies using different spatio-temporal](#)
464 [scales of investigation have been undertaken for mobile insects \(e.g. Baguette, 2003;](#)
465 [Purse et al., 2003; Keyghobadi et al., 2005\), but generally are still lacking \(Turchin,](#)
466 [1998\), in particularly for ground-dwelling woodland related insect species \(Brouwers &](#)
467 [Newton, 2010b\).](#) Our study highlights the importance of adopting a multi-scales
468 approach. Furthermore, to fully understand the dispersal ability of a species it was
469 found important to consider both juvenile and adult life-stages (Diekötter et al., 2005).
470 In this study, nymphs showed a similar dispersal rate as adults, contrary to earlier
471 findings on the more directed movement strategy of adults that suggested a higher rate
472 of dispersal compared to nymphs (Brouwers & Newton, 2010b). This is likely to be a
473 consequence of differences in the spatio-temporal scale that was used for the
474 experiments. This result is highly important in terms of inferring their population spread.
475 Using only small spatio-temporal scales to investigate the dispersal ability of a species
476 can therefore be misleading, and for wood crickets, dispersal is therefore most likely to
477 take place both during their juvenile and adult stages. Our results are similar to those
478 obtained for other orthopteran species, such as the dark bush cricket (*Pholidoptera*
479 *griseoptera*) investigated in Switzerland (Diekötter et al., 2005). At large spatio-
480 temporal scales, Diekötter *et al.* (2005) found no differences in dispersal ability
481 between juveniles and adults of this species. This non-flying cricket species shows an
482 overlap with the preferred habitats of wood crickets (Diekötter et al., 2005; Brouwers &
483 Newton, 2009a), suggesting that all individual life-stages are important when assessing
484 dispersal of this type of non-flying cricket species.

485

486 Another scaling issue was revealed in the comparison of the sexes. In a previous study
487 using experiments performed at a small spatio-temporal scale (i.e. $< 8 \text{ m}^2$, ~ 20 minute
488 observations), no differences were found in the movement strategy between adult
489 males and females, suggesting a similar dispersal rate for both sexes (Brouwers &
490 Newton, 2010b). However, the current study revealed that, when using larger spatio-
491 temporal scales for observation, adult males were found to move further and more
492 quickly than females. This indicates that the scale of investigation influenced the
493 findings for this species, and highlights the importance of investigating dispersal at a
494 range of scales. Differences in dispersal ability between sexes have been observed
495 previously for grasshoppers (Maes et al., 2006); however, for cricket species similar in
496 their habitat preferences to wood crickets this was not observed (Diekötter et al., 2005).
497 Wood cricket males [are likely to attract](#) females with their stridulation, as has been
498 found in several other cricket species (Marshall & Haes, 1988; Simmons & Ritchie,
499 1996; Scheuber et al., 2003). In the current study, the increasing number of wood
500 cricket pairs that were observed over time is a likely indication of the influence of this
501 factor. Altogether, this might indicate that adult wood cricket males act as the primary
502 dispersers potentially attracting females with their stridulation. However, this type of
503 species-specific trait needs to be investigated more closely to derive its actual influence
504 on dispersal success (Holyoak et al., 2008).

505

506 Only a small fraction ($\sim 25\%$) of wood cricket nymphs and adults averaged a daily
507 straight-line dispersal rate of 2.9 m day^{-1} , with the majority of the populations moving
508 with lower velocity. For the bush cricket (*Pholidoptera griseoptera*), Diekötter *et al.*
509 (2005) found that nymphs and adults of this species were equally sedentary, but overall
510 the species showed higher dispersal rates compared to wood crickets. In this case the
511 daily rate was calculated over the first 24 h using distances observed for all the
512 individuals in the released population, recording mean rates of $1.7\text{-}3.8 \text{ m day}^{-1}$ for

513 juveniles and $3.0\text{-}6.3\text{ m day}^{-1}$ for adults (Diekötter et al., 2005). For field crickets
514 (*Gryllus campestris* L.) living in herb-rich meadows, rates were obtained for all males,
515 which moved a mean distance of 2.8 m day^{-1} (Ritz & Kohler, 2007). Considered
516 together these results suggest that, compared to other cricket species for which data
517 are available, dispersal within wood cricket populations is limited, and the species can
518 be considered as relatively sedentary.

519

520 Population spread of both adults and nymphs was most accurately described by the
521 inverse-power function. These results are supported by findings in a study conducted
522 on adult wood crickets in France (Morvan et al., 1978). After we performed further
523 analyses on mark-resight data collected in their study (Morvan et al., 1978), population
524 spread was also found most accurately described by the inverse-power function. The
525 dataset collected by Morvan *et al.* (1978) was gathered in similar habitat to that of our
526 study. These combined results suggest that the inverse-power function is appropriate
527 to describe the spread for both wood cricket nymphs and adults. The use of the
528 inverse-power equation for describing population spread or dispersal in cricket species
529 that move by walking is supported by results from other studies. For instance, the
530 frequency distribution of the number of two-coloured bush crickets (*Metrioptera bicolor*)
531 dispersing through their preferred dry grassland habitat environment within a matrix of
532 pine forests and arable land (Kindvall, 1999), correlated closely with the inverse-power
533 relationship. This indicates that the inverse-power equation seems an appropriate tool
534 to describe the spread or dispersal of non-flying cricket species in this type of
535 investigation.

536

537 The overall observed limited dispersal distances and population spread achieved by
538 the species through their preferred habitat (i.e. open canopy woodland with leaf litter
539 and sparse ground vegetation) are supported by earlier observations of wood cricket
540 nymphs and adults moving through this type of habitat (Gabbutt, 1959; Morvan &

541 Campan, 1976; Morvan et al., 1977, 1978). However, the current study also showed
542 that some individual males were able to disperse up to 55 m away from favourable
543 habitat. This is consistent with a previous mark-recapture experiment within continuous
544 open woodland habitat, where adult wood crickets were shown to be able to disperse
545 up to 60 m over a period of 30 days (Morvan et al., 1978). These observations together
546 suggest that at least some wood crickets (i.e. males) are able to disperse relatively
547 long distances, with an apparent threshold distance of around 50 m per year (Brouwers
548 & Newton, 2010a). However, since females show about half the level of dispersal
549 ability compared to males, overall population spread, being female dependent, is
550 therefore likely to be no more than 25 m per year.

551

552 In terms of colonization success of new habitat, this study revealed that over time wood
553 crickets moved most readily along mature wooded edges and less along hedges and
554 immature new plantings within the landscape. Dispersal can however only be
555 successful if suitable edge habitat is available for the species to establish a viable
556 population, as represented along woodland edges. Establishing a woodland habitat
557 network by creating wooded corridors between woodlands might therefore increase
558 dispersal incidence and prove beneficial for the persistence of wood crickets within the
559 wider landscape over time. The positive effect of maintaining linear features within an
560 agricultural matrix in terms of colonization success has been shown in detailed studies
561 on Roesel's bush-cricket (*Metrioptera roeseli*) (Berggren et al., 2001; Berggren et al.,
562 2002). Results suggested that these features helped in facilitating dispersal and the
563 persistence of this cricket species within the wider landscape (Berggren et al., 2001;
564 Berggren et al., 2002), as also found for Orthoptera occurring in the Bialowieza Forest
565 (Theuerkauf & Rouys, 2006). For wood crickets, corridor functioning is likely to be
566 highly dependent on its maturity and factors such as tree and ground vegetation cover,
567 leaf litter presence and the geographical orientation of the corridor edges (Brouwers &
568 Newton, 2009a). Therefore the design and maturity of the wooded corridor will

569 determine if the species is inclined and able to disperse along and through these
570 features, as suggested in other studies (Bennett, 2003; Bailey, 2007). Initiatives
571 focusing on long-term management planning and careful designation of locations for
572 woodland habitat networks will further be essential. Given time, the ongoing investment
573 of creating wooded corridors between woodland fragments therefore has the potential
574 to facilitate colonization success and population viability of wood crickets and similar
575 species within the wider landscape.

576

577 **Acknowledgements**

578

579 We like to thank the Forestry Commission and the Scottish Forestry Trust for funding
580 this research. Furthermore, we like to thank the People's Trust for Endangered Species
581 (PTES) for providing us with the opportunity to work in their woodlands on the Isle of
582 Wight. We also like to thank Allan Watt (Centre for Ecology and Hydrology), Keith Kirby
583 (Natural England), Kevin Watts (Forest Research) and three anonymous reviewers for
584 their input and comments on this manuscript.

585

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757
758

759

760 **Table 1**

761 The number of wood cricket nymphs and adults observed at the enclosure peripheries for the
 762 separate enclosures over four consecutive days. Each enclosure contained a population of 50
 763 nymphs or 20 adult male and 20 female wood crickets.

Time	24 h			48 h			72 h			96 h		
Radius	N	M	F	N	M	F	N	M	F	N	M	F
2	14	12	7	17	9	6	12	10	7	10	18	9
3	6	5	3	15	12	6	9	8	9	12	10	7
4	6	7	1	12	9	5	9	8	4	7	8	3
5	6	2		8	2	1	5	3		8	3	2
7		1			4	1		4			2	
Total	32	27	11	52	36	19	35	33	20	37	41	21
T Adults	38			55			53			62		

764

765 Radius = radius of the enclosures in meters. N = Nymph, M = Adult Male, F = Adult Female, T

766 Adults = Total number of adults

767

768

769 **Table 2**770 Chi-square 'goodness of fit tests' for differences between the number of wood cricket female (*n*771 = 100) and male (*n* = 100) pairs (F + M) and single females (F) observed at the enclosure

772 periphery over time, for the 2-7 m enclosures together.

Time	F + M	F	χ^2	df	<i>P</i>
24h	6	5	0.091	1	0.763
48h	11	8	0.474	1	0.491
72h	15	5	5.000	1	0.025
96h	16	5	5.762	1	0.016
Total	48	23	22.31	1	0.000

773

774

775 **Table 3**

776 Straight-line dispersal distances (m) recorded for wood crickets along different habitat edges

777 over 60 days.

Edge	Median	Range	<i>n</i>	VH	VC	LC	LD	CC
WE	18.7	3.8-29.5	17	22-47	26-36	64-80	1.8-2.2	82-99
HE	3.0	1.2-12.0	20	12-24	34-100	24-38	1.0-1.5	63-72
JE	4.1	1.1-8.5	22	24-54	62-65	3-15	0.4-0.8	32-38

778

779 Edge: mature woodland bordering grazed grassland (WE), mature hedge bordering grazed

780 grassland (HE), ungrazed semi-natural grassland with newly planted saplings bordering grazed

781 grassland (JE). Median: median straight-line distance for wood crickets. Range: range of

782 straight-line distances recorded. Range of vegetation characteristics present along the edges

783 that were surveyed: VH = mean vegetation height (cm), VC = total vegetation cover (%), LC =

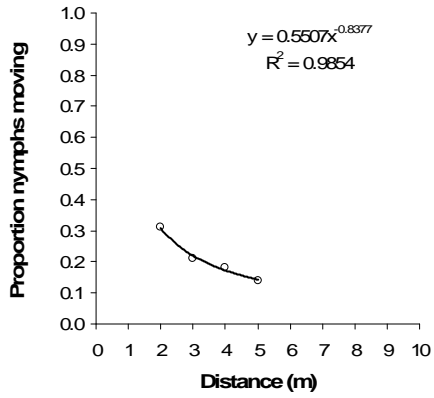
784 total litter cover (%), LD = litter depth (cm), CC = canopy closure (%).

785

786

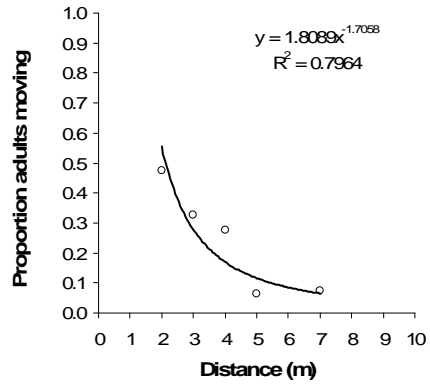
787 **Fig. 1.** The proportion of wood crickets moving per day fitted against straight-line distance from
788 the release point. (a) nymphs ($n = 50$ for each distance/enclosure), (b) all adults ($n = 40$), (c)
789 males ($n = 20$), and (d) females ($n = 20$). Circles indicate the proportion of the population
790 observed that reached the periphery (i.e. dispersed) within each enclosure (i.e. distance) over
791 24 hours. Inverse-power function is fitted to the data. y = proportion of the population moving, x
792 = distance (m).

793

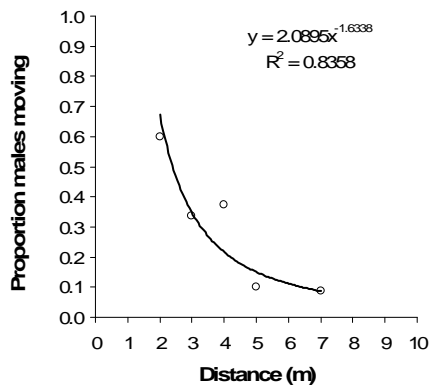


794

(a)

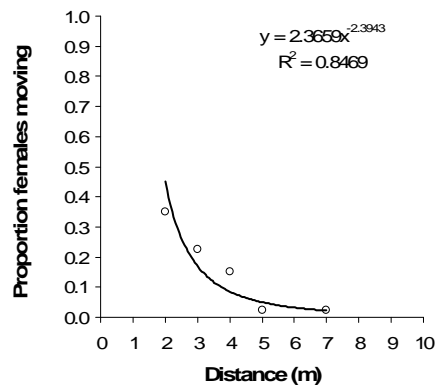


(b)



795

(c)



(d)

796 Fig. 1. see attached files Fig 1 (a-d).jpg

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