How limited is dispersal in the rare beetle, Cryptocephalus decemmaculatus *(Chrysomelidae, Cryptocephalinae)?*

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ORIGINAL PAPER

How limited is dispersal in the rare beetle, *Cryptocephalus decemmaculatus* (Chrysomelidae, Cryptocephalinae)?

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Abstract As suitable habitat becomes increasingly fragmented the ability of a species to reach new areas may often dictate whether populations persist or perish. An understanding of dispersal ability is a prerequisite for informed management decisions. This is particularly true for species that have become restricted to one or a small number of sites, as is the case for several species of *Cryptocephalus* beetle in the UK. Using mark–release–recapture, host-plant marking and direct observations we investigated population size, movement through suitable habitat and the flight behaviour of *Cryptocephalus decemmaculatus*. In the UK this species is known from only two sites and it is listed as a priority species on the UK Biodiversity Action Plan. At the time of the study, the one known English site for this species supported a population of $\sim$500 individuals. The adult beetles move through their habitat using suitable host-plants as 'stepping stones'. There appears to be no interchange of adults between sub-populations that are separated by small areas of unsuitable habitat (e.g. small tracts of woodland or areas devoid of scrub), a result reinforced by studies of genetic differentiation between sub-populations. The small population size of this beetle and its association with, mid-successional habitats makes it vulnerable to local extinction. Furthermore, its limited dispersal ability means that other habitat patches are unlikely ever to be colonised naturally.

Keywords Chrysomelidae · *Cryptocephalus* · Habitat fragmentation · Mark–release–recapture · Ecotones · Rare insects

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Introduction

Dispersal abilities of phytophagous insects range from less than 1 km to more than 20 km (Peterson and Denno 1998; St Pierre and Hendrix 2003). Ideal colonists respond rapidly to habitat change, quickly locating suitable new habitats and proliferating once there (MacArthur and Wilson 1967; Safriel and Ritte 1980). Theoretically, habitats that are unpredictable in space and time should play host to those species which are adept at colonisation (Southwood 1962), but the reverse has often been found (Thomas 1984, 1991; Warren 1987).

Human activity has fragmented the natural environment to such an extent that many insect species are no longer able to disperse freely through areas of suitable habitat. Indeed, long distance dispersal may be selected against in populations isolated by habitat fragmentation (Hanski and Gilpin 1991, 1997). Many insect species that persist as isolated populations are now of conservation concern since they are predisposed to local extinction even when the fragmentation of their habitat is minimal (Doak 2000; Samways 2007).

The consequences of poor dispersal ability are compounded by the extreme habitat specialisation of some insects. This is particularly the case for species that rely on dynamic, mid-successional habitats such as woody invasive scrub, which only remains optimal for a few years.

Limited information exists concerning the mobility and population dynamics of Chrysomelidae in general and *Cryptocephalus* species in particular. However, it has been shown that certain *Cryptocephalus* species in the UK exhibit considerable genetic differentiation between sub-populations that are separated by relatively small distances (<1 km) (Piper and Compton 2003).

This study of a wild population of *Cryptocephalus decemmaculatus* addressed the following questions. How mobile are the adult beetles and consequently, how isolated are any sub-populations? What is the size of the study population at the one known remaining English site for this species? The answers are used to suggest steps that can be taken to safeguard the remaining populations of this species and other insects with similar characteristics. Furthermore, this data may facilitate the identification of sites that are suitable for re-introductions.

Study species

Cryptocephalus decemmaculatus (Linnaeus, 1758) (Fig. 1) is listed as a priority species on the UK Biodiversity Action Plan (UKBG 1999), with only two UK sites currently known. The adult beetles are 4–5 mm long, fully winged and thermophilic. At the study site, the adult beetles are found on small *Salix cinerea* and *Betula pubescens* trees invading the sphagnum ‘lawn’ of a ‘Schwingmoor’ (see below) (Piper 2002a). The adults eat the foliage of both of these tree species, but the former is much preferred as a food-plant (Piper 2002b). Optimal host-trees for this beetle are typically small with a clear, south facing aspect and are sheltered from the wind.

In common with the other species in the genus, *C. decemmaculatus* females sit on their host-plant and encase their eggs in faeces as they are being laid (Erber 1988). The eggs are then ‘thrown’ from the host-plant onto the ground. The larvae carry this egg case with them, adding to it with their own faeces, forming a mobile retreat that they eventually pupate in. *Cryptocephalus* larvae typically feed on leaf litter (Steinhausen 1996).

Study site

Wybunbury Moss, a National Nature Reserve in Cheshire, supports the only known English population of *C. decemmaculatus*. The site is a ‘Schwingmoor’, one of only two in England, consisting of Alder-Carr woodland surrounding a central sphagnum ‘lawn’ (Fig. 2). The margins of this ‘lawn’ are invaded by *B. pubescens*, *S. cinerea* and *Pinus sylvestris*. Three sub-populations of *C. decemmaculatus* were identified at the site during regular surveys prior to this study (Piper 2002b). These sub-populations occupy three discrete areas (A, B and C in Fig. 2) separated by areas of unsuitable habitat (small tracts of woodland and areas devoid of scrub). The characteristics of these three areas are shown in Table 1.

Fig. 1 *Cryptocephalus decemmaculatus*—mating pair and solitary male

Materials and methods

Estimation of population sizes

Population sizes were estimated by mark–release–recapture in mid-June of 1999 and 2000 when most adults are encountered. Adult beetles in Areas A, B and C (Fig. 2) were captured, marked with a tiny spot of typing correction fluid on the pronotum and then released immediately.

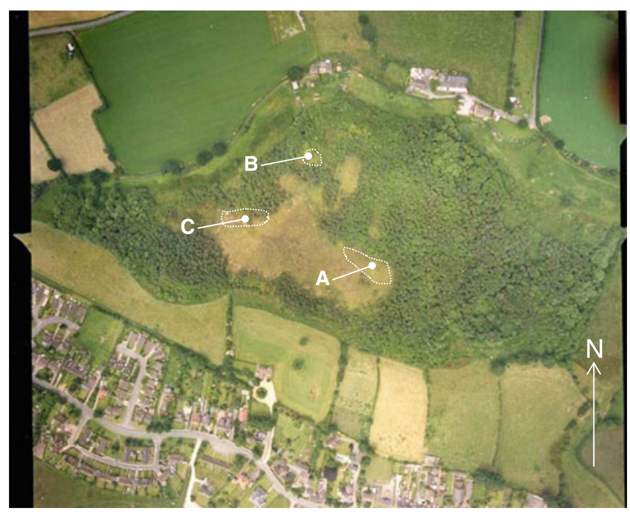


Fig. 2 Aerial photograph (1993) of Wybunbury Moss (450 m across) showing study areas. *A*, *B* and *C* = sub-populations of *Cryptocephalus decemmaculatus*

Table 1 Characteristics of sub-population Areas A, B and C

	Area A	Area B	Area C
Size (m^2)	5,100	1,000	1,500
No. of suitable *Salix cinerea* trees	153	70	60
Density of *Salix cinerea* trees (per m^2)	0.03	0.07	0.04

Recaptures were conducted 4 days later. The Lincoln index (Lincoln 1930) was used to estimate the population size of the adults, with Bailey's Correction (Bailey 1952) because of the small sample sizes.

Adult movements

This was conducted in mid-June of 2000, after the mark–release–recapture to estimate population size. All the *S. cinerea* and *B. pubescens* trees within Areas A, B and C (Fig. 2) were marked with a numbered waterproof tape tag. These trees were then mapped on X and Y co-ordinates by laying two 50 m measuring tapes at right angles to one another, forming axes. By plotting the position of each tree on the axes it was possible to produce maps of Areas A, B and C (Figs. 3, 4, 5).

Beetles in Areas A, B and C were collected at dusk when activity was minimal, and marked on the elytra with a small spot of typing-correction fluid using the code shown in Fig. 6. This marking code allowed the detection of any movement of individuals between the three sub-populations. Attempts were made to mark the beetles individually, but no technique was found to be sufficiently durable in the field on such a small beetle.

The beetles were retained over-night in large plastic storage boxes replete with sprigs of *S. cinerea*. Early the following morning, these boxes were placed beneath three host trees at Wybunbury Moss in Areas A, B and C (Figs. 3, 4, 5) and opened so the beetles could escape. After 4 days Areas A, B, C were carefully searched and the sex and location (tree number) of each marked beetle found was recorded. Recaptured beetles were retained until the whole study area had been searched. The weather over the 4-day release period was warm and dry.

Flight behaviour

To observe the flight behaviour of the beetles, nine males and 11 females were each observed for 30 min in the early afternoon of warm, sunny days when the activity of this species is at its peak. The distance of every observed flight was recorded using a measuring tape and the trajectory noted.

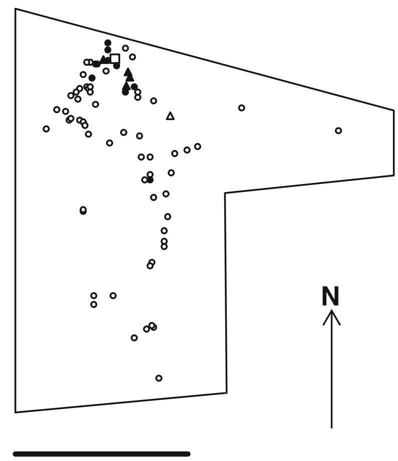


Fig. 4 Movements of released *Cryptocephalus decemmaculatus* adults in Area B of Wybunbury Moss (over a 4 day period in June 2000). *Open square* = release tree; *filled triangle* = *S. cinerea* tree with recaptures; *open triangle* = *Salix cinerea* tree with no recaptures; *filled circle* = *Betula pubescens* tree with recaptures; *open circle* = *Betula pubescens* tree with no recaptures; *scale bar* = 20 m. *Solid line boundary* = woodland border

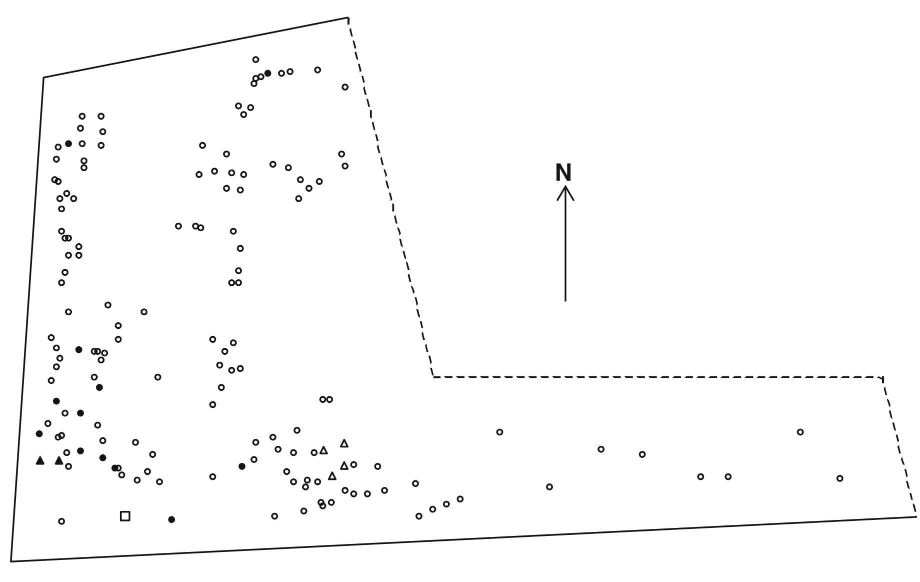


Fig. 3 Movements of released *Cryptocephalus decemmaculatus* adults in Area A of Wybunbury Moss (over a 4 day period in June 2000). *Open square* = release tree; *filled triangle* = *Salix cinerea* tree with recaptures; *open triangle* = *Salix cinerea* tree with no recaptures; *filled circle* = *Betula pubescens* tree with recaptures; *open circle* = *Betula pubescens* tree with no recaptures; *scale bar* = 20 m. *Solid line boundary* = woodland border; *dashed line boundary* = scrub-less habitat border

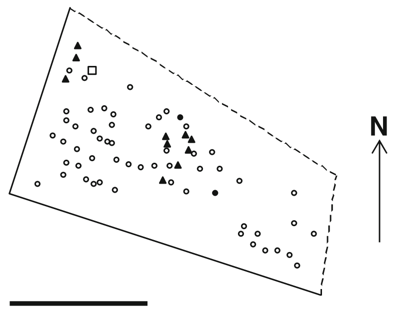


Fig. 5 Movements of released *C. decemmaculatus* adults in Area C of Wybunbury Moss (over a 4 day period in June 2000). *Open square* = release tree; *filled triangle* = *Salix cinerea* tree with recaptures; *filled circle* = *Betula pubescens* tree with recaptures; *open circle* = *Betula pubescens* tree with no recaptures; *scale bar* = 20 m. *Solid line boundary* = woodland border; *dashed line boundary* = scrub-less habitat border

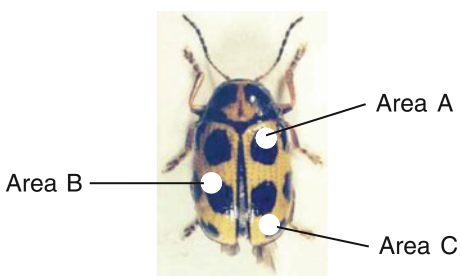


Fig. 6 Positions of typing correction fluid marks on the elytra of *Cryptocephalus decemmaculatus* adults corresponding to where they were captured

Results

Estimation of population size

To estimate population size 355 *C. decemmaculatus* beetles were marked at Wybunbury Moss (Table 2). The recapture rate in Area A was less than the other two sub-populations in both years (Table 2). Fewer females than males were recaptured (47.7 % in 1999; 43.3 % in 2000 for the site as a whole), although males were not significantly more likely to be recaptured than females [χ^2 (*df* 1) = 0.89, *P* = 0.66 (1999); χ^2 (*df* 1) = 0.59, *P* = 0.56 (2000)].

Table 3 *Cryptocephalus decemmaculatus* mark–release–recapture at Wybunbury Moss in 2000 to determine adult movements

	Individuals marked	Individuals recaptured (%)
Area A	76	28 (36.8 %)
Area B	118	59 (50 %)
Area C	78	42 (53.8 %)

Based on a corrected Lincoln Index, Area A at Wybunbury Moss had the largest estimated population size during both 1999 and 2000 (Table 2). The population estimates for the smaller areas were very similar in both years at around 100 (Table 1). The total English population of *C. decemmaculatus* was therefore estimated to be approximately 523 in 1999 and 408 in 2000 (Table 2).

Adult movements

Two-hundred and seventy-two beetles were marked and 115 recaptured in total to investigate the movements of adults (Table 3). The distances moved by both male and female beetles were typically very small (Fig. 7). More than half of the recaptured beetles had only moved 0–5 m over 4 days (Fig. 7). Indeed, two (6.7 %); 35 (59.3 %) and 15 (41.7 %) adults from Areas A, B and C, respectively, were recorded as still being on their original release trees 4 days after the release. No beetles were recorded as moving between Areas A, B and C, despite their close proximity. The longest recorded distance moved by an individual over 4 days was 41.7 m (a male in Area A).

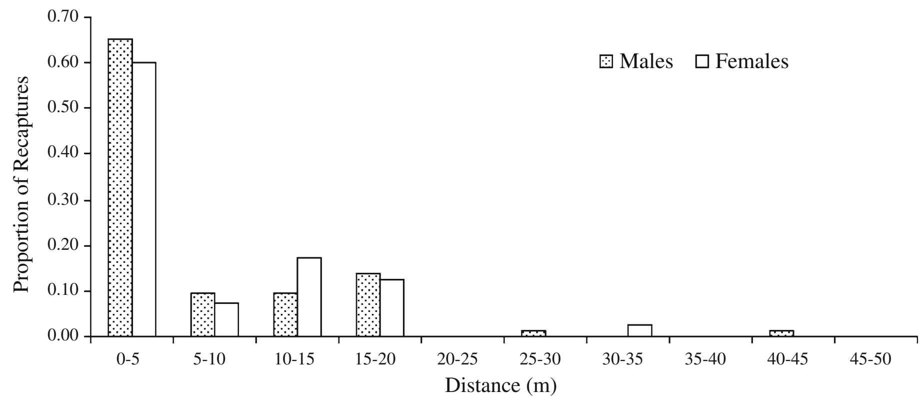
In Area A, the largest area, with the lowest density of *S. cinerea* host trees (Table 1), the mean recorded distance travelled was 3.1 m per day (SD = 2.2 m). Area C was smaller, but with trees at about the same density. Here the mean recorded diffusion was 1.9 m per day (SD = 2.1 m). Area B was smallest and had a higher density of suitable trees. Here the diffusion rate was considerably lower, averaging only 0.3 m per day (SD = 0.6 m).

No *S. cinerea* host-trees were located between 20 and 30 m from the release tree in any of the three areas (Figs. 3, 4, 5). The host-trees more than 30 m away from the release tree (Area A only) were not colonised by released beetles (Fig. 5).

Table 2 *Cryptocephalus decemmaculatus* mark–release–recapture at Wybunbury Moss in 1999 and 2000 to estimate population size

	Individuals marked (recapture rate)		Estimated population size	
	1999	2000	1999	2000
Area A	47 (17 %)	38 (18.4 %)	317 (±SE 83.06)	209 (±SE 63.02)
Area B	93 (44.1 %)	99 (42.4 %)	125 (±SE 9.45)	120 (±SE 7.51)
Area C	36 (33.3 %)	42 (35.7 %)	81 (±SE 15.17)	79 (±SE 13.04)

Fig. 7 Distances moved by released *Cryptocephalus decemmaculatus* males and females as a proportion of the total captures of each sex (Areas A, B and C combined)



Flight behaviour

A total of 63 flights were observed. These flights were all short, the longest being 6.7 m with an average flight distance of just 3.9 m (±SE 2.5 m). Movements were erratic and made use of suitable host trees as 'stepping-stones'. Adults observed around host-trees made short flights to different parts of the same tree. Adults take off steeply then fly rapidly towards the ground until they alight on another tree or a different part of the same tree.

Discussion

The only English population of *C. decemmaculatus* occupies an isolated wetland habitat set in a long-established agricultural landscape. The population was estimated to number about 500 in 1999 and 400 in 2000—extremely small for an insect. It seems that the colonization of new habitat patches by *C. decemmaculatus* is very slow, as no examples of dispersal between Areas A, B and C were detected. These three closely-situated sub-populations can be considered as forming a non-equilibrium metapopulation, where local populations are effectively isolated from one another (Harrison 1991).

Low rates of dispersal in *Cryptocephalus* beetles are further supported by genetic and other dispersal studies. Mitochondrial markers demonstrated considerable population structure at the micro-geographical scale in *C. decemmaculatus* and other rare UK *Cryptocephalus* species (Piper and Compton 2003). Considerable genetic differentiation existing between populations separated by <1 km was revealed (Piper and Compton 2003). *C. nitidulus* subpopulations on the North Downs in Surrey are isolated by relatively small areas of unsuitable habitat (Piper and Compton 2010). Similar local genetic differentiation has also been found in some other phytophagous beetle species (Chen et al. 2012; Jenkins et al. 2009; McCauley et al. 1988; McCauley 1991; Rank 1992). Ecological differences, such as subtle changes in host-plant preferences, are also present between populations separated by greater distances (Piper 2002b).

Cryptocephalus decemmaculatus as well as several other *Cryptocephalus* species depends on mid-successional, transitional habitats. Such habitats would have a short natural life span at any particular location, quickly changing to dense scrub and then woodland. Good dispersal ability would therefore appear to be a prerequisite for any species inhabiting this type of habitat, yet the converse seems to be the case.

The current dispersal abilities of species such as *C. decemmaculatus* may reflect an evolutionary response to long-term isolation, where even average dispersal abilities are selected against (Dempster et al. 1976; Dempster 1991). The movements of the beetles within their pockets of suitable habitat show them to be effective at locating host-trees over relatively small distances (within ~10 m), at least when there is warm, sunny weather during their brief adult life. In captivity, the mean longevity for females is 27 days (±SD 3.9 days) and 18 days (±SD 3.6 days) for males (Piper 2002a). Therefore, any inclement weather during their short adult life could severely limit flight activity.

Not all marked beetles were recaptured and there is always the possibility that some individuals left the site entirely to embark on longer range dispersal flights. However, the lack of potentially suitable habitat in the surrounding agricultural landscape presents no focal points for the beetles and subsequent survey for migrants. *Galerucella calamariensis* (Chrysomelidae) has been shown to be able to fly 850 m, but high mortalities are associated with flights of this distance; therefore, they occur rarely (Grevstad and Herzig 1997).

The evidence here suggests that *C. decemmaculatus* adults move through their habitat using suitable host plants as 'stepping stones'. Scrub-less areas and small tracts of woodland appear to be effective barriers to dispersal. This is further supported by evidence from translocations where *C.*

decemmaculatus beetles survived and bred in an area of suitable habitat where they had never previously been found (Piper 2002b). This area was separated from an existing sub-population by <100 m of mature woodland. This translocated population survived until the area was inadvertently cleared during routine habitat management at the end of 2001.

Other studies on Chrysomelidae have shown that many of the adults in a population will not disperse away from their natal site (Herzig 1995). In the case of *C. decemmaculatus*, females that disperse away from the natal site may oviposit above ground that is completely unsuitable for the larvae. An ovipositing female *C. decemmaculatus* makes no obvious selection of where her eggs will be dropped. Indeed, the habitat preferences of the adults and larvae are completely different. Adults require a complex ecotone of host-plants invading wetland with many discrete 'pockets' where temperatures may be significantly higher than around exposed trees (Piper 2002b). In contrast, the larvae spend around 11 months in amongst damp sphagnum moss and leaf litter. Consequently, the integrity of the population of this beetle at any one site may be dependent on an extremely limited number of trees that provide a chance juxtaposition of optimal conditions for the adults and larvae. Successive generations of beetle may develop beneath these trees and lay eggs from their branches.

With respect to other insects, dispersal studies of ermine moths (*Yponomeuta* spp.) have shown patterns of movement very similar to that exhibited by *C. decemmaculatus* (Brookes and Butlin 1994; Javoiš et al. 2005). *Yponomeuta padellus* was shown to have very limited dispersal with 91 % of adults released in one study moving less than 20 m (Brookes and Butlin 1994). The moths were also shown to move in a "stepwise" fashion using host bushes. Males in particular were less likely to disperse far in areas with a greater number of host plants as longer flights were often curtailed due to the presence of females (Brookes and Butlin 1994).

It is possible that the movement of *C. decemmaculatus* may be strongly influenced by the presence of conspecifics and volatile compounds that are given off by the primary host plant (*S. cinerea*). *Leptinotarsa decemlineata* (Chrysomelidae) adults are attracted by the volatile chemicals given off by their host-plants (Hare 1990). *G. calamariensis* has been shown to only be able to detect host patches if they are less than 50 m away (Grevstad and Herzig 1997). The presence of conspecifics already present on a patch strongly induces others to colonize (Grevstad and Herzig 1997). Below a threshold distance and depending on prevailing winds *C. deccemaculatus* beetles may be attracted to conspecifics and suitable host-plants. Further study should focus on defining the mechanisms that influence the way in which *C. decemmaculatus* adults move through their habitat.

The information in this paper on population size, the lack of movement between sub-populations and the way in which the beetles move through utilised habitat is valuable for the conservation of this species. The preservation and enhancement of this species at its last known English site can be assisted by: (1) altering the structure of the vegetation between the sub-populations by providing 'stepping stones' of bushes in suitable microclimatic conditions; (2) maintaining a complex scrub in the areas where the beetle is presently found, but controlling scrub maturation; (3) planting of host trees between sub-populations to provide artificially positioned host-trees to facilitate movement between sub-populations. The above proposals take into account the needs of the adults, but any management carried out should be undertaken with equal consideration for the requirements of larvae.

Since this study was conducted, Natural England who own and manage Wybunbury Moss have implemented the above recommendations within their ongoing management of the site. To assess the impact of this management on *C. decemmaculatus* a further mark–release–recapture estimate of population size was made in the summer of 2013. This recent estimate shows that the population of *C. decemmaculatus* at its one remaining English has increased to 943 (±SE 255) individuals (Piper 2013).

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