3.3. INVESTIGATION OF THE LARGE-SCALE, SPATIO-TEMPORAL DYNAMICS OF PREDATORY EPIGEAL INVERTEBRATE EMERGENCE IN ARABLE FARMLAND.

Pitfall traps have many well known biases but the most important is that they measure a combination of activity and density, the catch being dependent on insects moving and falling into the traps (Adis, 1979). As a consequence, they only catch those species that can fall and be retained by the traps while the insect's activity is determined to some extent by the density of vegetation surrounding the traps. Some of the most numerous beneficial insects that occur within arable fields also overwinter as larvae within the soil, emerging in the spring/summer. Some of these carabid beetle species were shown to disperse little (<55m over 30 days) within arable fields (Thomas et al., 1998), therefore, to verify to what extent the distribution patterns recorded by pitfall trapping were reflecting actual density, their density on emergence was measured. In addition, during the first two years of the spatio-temporal study (section 3.2) the invertebrates were most numerous in those fields containing peas. As soil cultivation was conducted in the spring this may have affected invertebrate overwintering survival. Emergence trapping is the best method of measuring cultivation effects on invertebrates (Holland & Reynolds, 2003).

3.3.1. Materials and methods

Emergence boxes consisted of a 1m^2 x 0.2m high wooden box covered with an insect proof mesh. The boxes' sides were buried 5cm deep into the soil. Within each box, a 10 cm high guidance plate was placed diagonally, at the end of which was placed a pitfall trap (6 cm diam., partly filled with 50% ethylene glycol and detergent). One emergence box was placed within 3m of the pitfall trap sampling location in early April 2002 prior to the start of emergence. Two hundred emergence boxes were established in two fields (L2, winter wheat and S2, winter barley) along alternate rows. The pitfall traps within each box were opened on 3 May and emptied on 21 May, 30 May, 10 June, 17 June, 4 July and 11 July 2002. Most invertebrates collected were identified to species.

The spatial pattern of emergence was determined using the red/blue SADIE analysis for four beetle species that overwinter within fields (the carabids *Nebria brevicollis*, *Pterostichus madidus*, *P. melanarius* & the staphylinid *Philonthus cognatus*) and for the total number of carabid beetles. This was conducted for each field separately. Their spatial pattern was then compared to that obtained from the pitfall trapping using the SADIE association test and regression for each date when the two sampling methods were conducted simultaneously (weeks beginning 17 June and 11 July). The total numbers of the above species and total Carabidae that were collected were also compared to soil moisture levels measured in the autumn of 2001 (see section 3.2.2.6) using the SADIE association test.

3.3.2. Results

The number of invertebrates known to overwinter within the soil and captured within the boxes was 157 and 86 m^{-2} for the small and large field respectively (Table 3.25). This demonstrates the importance of arable soils as an overwintering habitat for beneficial invertebrates. The taxa were comprised of the larger Carabidae and Staphylinidae, e.g. *Pterostichus* spp., *Poecillus cupreus* and *Philonthus cognatus*. The time of emergence varied between species but peaked for Carabidae in mid-June (Fig. 3.14). Data for the many other species were collected but are not presented here.

Table 3.25. Total emergence (m^{-2}) over 69 days for field overwintering taxa.

Taxa	S2-winter barley	L2-winter wheat
Amara spp.	14.5	6.4
Calathus fuscipes	4.6	7.6
Harpalus affinis	1.4	1.2
Harpalus rufipes	1.6	4.1
Loricera pillicornis	6.6	2.2
Nebria brevicollis	7.9	8.2
Notiophilus biguttatus	2.0	1.3
Poecillus cupreus	10.6	3.1
Pterostichus madidus	26.8	41.9
Pterostichus melanarius	29.0	1.2
Trechus quadristiatus	1.4	1.8
Carabidae	**106.4**	**79.2**
Philonthus cognatus	43.6	5.9
Philonthus spp.	6.6	0.7
Staphylinidae	**50.1**	**6.6**
Total	**156.5**	**85.9**

All four species, total Carabidae in June, and all but *P. cognatus* in July within field S2 showed strong spatial and numerical correlations between abundance in pitfall traps and emergence trap catches (Table 3.26). Strong spatial and numerical correlations were also found in June and July for field L2, except for those species that were captured in too few numbers, although the regressions were often significant. The regression equations were relatively consistent between dates and fields. The strong correlations between the two sampling methodologies confirmed that the pitfall traps were providing evidence of emergence patterns and an indication of actual density.

Figure 3.14. Emergence period and density of four species of predatory beetle and total Carabidae in June 2002.
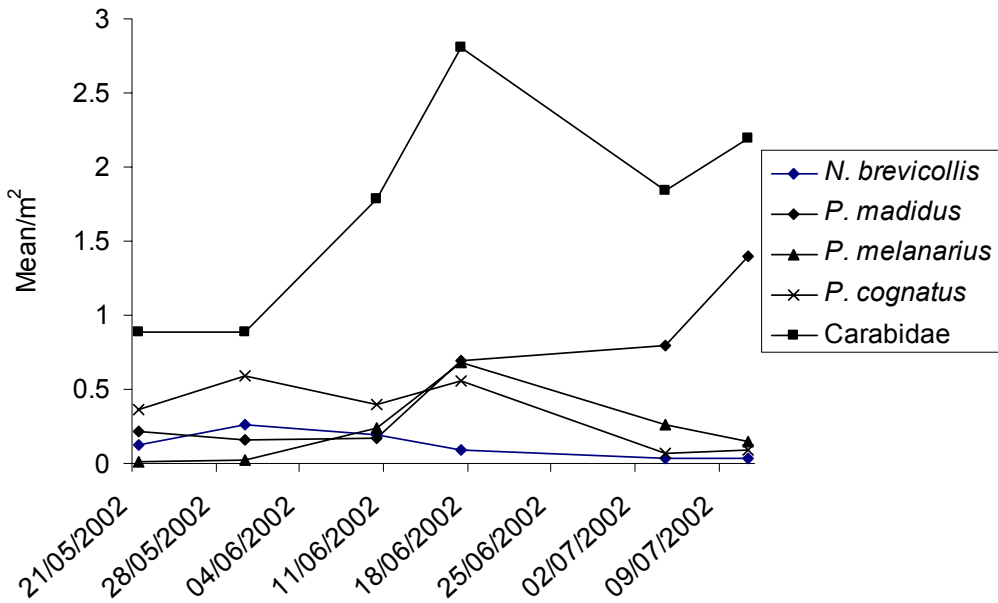
In S2 was there was a strong association between soil moisture and numbers of the four species tested and of total Carabidae, with emergence being highest in the wet areas (Values of -760 to -800) of the field (Fig. 3.15). In contrast, in L2 there was strong dissociation, although the soil wetness was higher in this field and it was the wettest areas that had the lowest emergence. The emergence of *Pterostichus madidus*, *Philonthus cognatus* and total Carabidae (Fig. 3.15) was highest in those areas of the field that had a moisture level of -750 to -800, as found in S2.

Figure 3.15. Pattern for total carabid emergence within fields a) S2 and b) L2 in 2002.

(filled squares indicate $v_i > 1.5$, empty squares indicate $v_j < -1.5$)

a)   b)
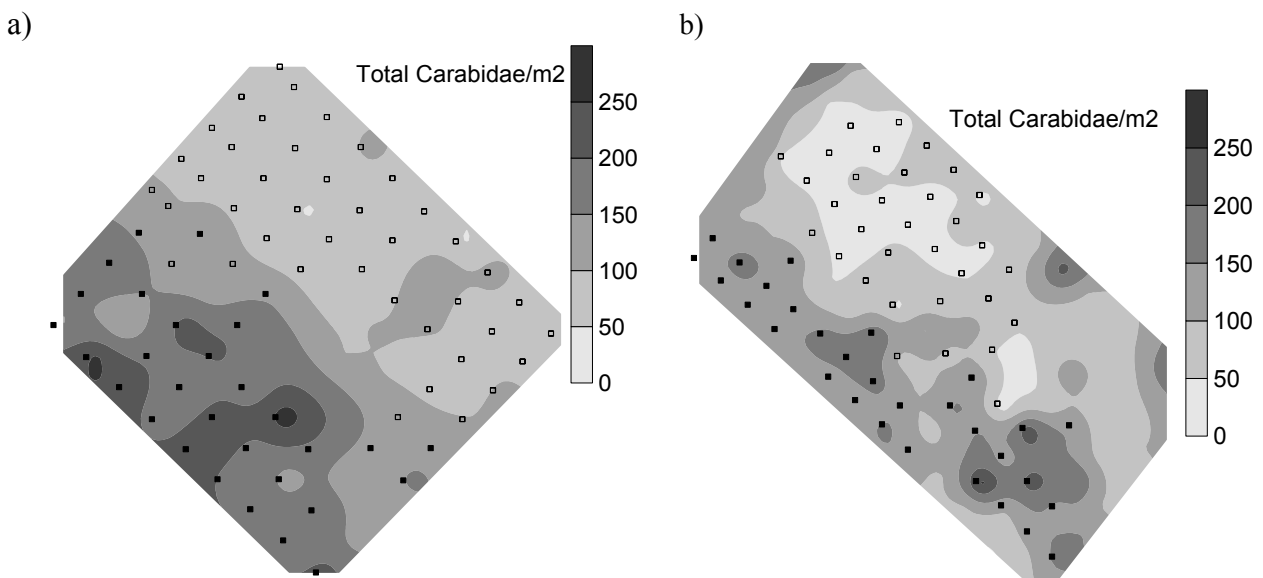
Table 3.26. Spatial association indices and regression values comparing beetles collected using emergence traps compared to pitfall traps for sampling conducted in June and July 2002.
(***=P_D<0.001 or >0.999, **= P_D<0.01 or >0.99, **= P_D<0.05 or >0.975)

Field S2	X	P_D	F ratio	p	Regression	R^2
Nebria brevicollis						
June	0.05	NS	3.9	0.05	y=0.15x +0.12	0.03
July	-1.0	NS	11	<0.001	y=0.33x+0.04	0.09
P. madidus						
June	0.55	***	32	<0.001	y=0.51x+0.28	0.22
July	0.55	***	142	<0.001	y=0.89x+0.26	0.34
P. melanarius						
June	0.82	***	132	<0.001	y=0.53x-0.004	0.54
July	0.77	***	58	<0.001	y=0.57x+0.03	0.34
Philonthus cognatus						
June	0.48	***	153	<0.001	y=1.0x+0.43	0.58
July	0.04	NS	0.6	0.4	NS	
Carabidae						
June	0.46	***	375	<0.001	y=0.08x+0.09	0.77
July	0.54	***	304	<0.001	y=0.96+0.17	0.73
Field L2						
Nebria brevicollis						
June	Insufficient capture		7.6	0.007	NS	
July	Insufficient capture		13	<0.001	y=0.45x+0.07	0.11
P. madidus						
June	0.68	***	31	<0.001	y=0.61x+0.74	0.22
July	0.59	***	24	<0.001	y=0.71x+0.85	0.17
P. melanarius						
June	Insufficient capture		1.1	0.3	NS	
July	Insufficient capture		16	<0.001	y=0.36x+0.6	0.13
Philonthus cognatus						
June	0.28	**	13	<0.001	y=0.4x+0.53	0.11
July	0.37	***	19	<0.001	y=0.51x+0.32	0.14
Carabidae						
June	0.25	**	0.1	0.7	NS	
July	0.33	***	1.4	0.2	NS	

3.3.3 Conclusions

1. Arable soils support high numbers of beneficial invertebrates through the winter.
2. The time of peak emergence varied between species but was highest for Carabidae in June.
3. Strong correlations were found between the spatial pattern of emergence and numbers emerging in the pitfall compared to emergence traps. The pitfall traps were therefore providing an indication of not just activity but also density.
4. The spatial pattern of emergence was related to soil moisture in the previous winter. An optimum soil moisture level that maximised emergence was found for some species and the Carabidae.

3.4. THE SPATIAL DYNAMICS AND MOVEMENT OF CARABID BEETLES BETWEEN AND WITHIN ARABLE FIELDS. (Published in *International Journal of Ecology and Environmental Sciences.* Special issue: *Habitat Manipulation and Arthropod Pest Management*)

Understanding dispersal power is essential for a number of reasons. Dispersal is a key mechanism for the exchange of genetic material between local populations. Barriers to dispersal can thus restrict opportunities for gene flow (Frankham, 1995) and may influence fitness (Reed & Frankham, 2003). They may also confine a population to a small area and consequently increase the risk of stochastic extinction of a local population. Species' dispersal ability and landscape permeability also determine the linkage between local populations within a metapopulation structure. This is especially relevant in agricultural landscapes where, for example, the application of a pesticide may result in the severe depletion or extinction of a local population. Evidence from simulation models has demonstrated that population persistence depends to a large extent on the permeability of the field boundaries and the frequency of exposure to pesticides (Sherratt & Jepson, 1993). The speed with which a species can respond to changes in its environment and food supply is also a function of dispersal ability (Wallin, 1986). Those that can respond the quickest are more likely to survive the sudden changes that can occur in such ephemeral habitats as cropped fields. The capacity for population expansion across a landscape, for example by an introduced species, is also dependent on dispersal power and landscape permeability.

During the first two years of this project, mark-release-recapture experiments were conducted at the farm scale to determine to what extent hedgerows and crop rotations influenced the distribution and movement of *Pterostichus* species carabid beetles. These species were chosen because *Pterostichus* species and especially *P. melanarius* are common and widespread in cultivated fields throughout Europe, North America and Japan (Luff, 2002), while *P. madidus* is common throughout Europe. Both species are considered to be important for biological control since they are known to consume a range of crop pests including cereal aphids and slugs (Sunderland, 2002). *P. melanarius* has also been shown to exhibit a spatial and temporal linkage to cereal aphid distributions (Winder et al., 2001).

3.4.1. Methodology for Mark-Recapture Studies

The same 66 ha study area described in section 3.2.1.1. was used along with the grid of pitfall traps. To determine the extent of movement by carabid beetles within the study area, mark-release-recapture studies were conducted in 2000 and 2001. In 2000, the study area was subdivided into 14 blocks of approximately 5 ha each (Fig. 3.16). Beetles were captured using dry pitfall traps left open for two days prior to marking on 15 and 16 June 2000. The two most numerous carabid species, *Pterostichus madidus* and *P. melanarius*, were marked and released at the point of capture. These two species overwinter as larvae in the soil and emerge in the spring as adults. A small proportion of the population may survive between years as adults by seeking refuge in the field boundaries during the winter. Immediately after emergence the males seek out females and may

therefore disperse over greater distances. However, once the females are ready to oviposit they may become more active. Permanent marks were made using a drill to engrave codes on their elytra according to the block in which they were captured, following the method developed by Thomas (1995). The beetles were then released within 2 m of their capture location. The presence of marked beetles and their location in the grid were recorded when the all the contents of the pitfall traps used for examining the beetle's distribution were identified.

Figure 3.16. Location of 14 blocks used for the mark-recapture study in 2000.
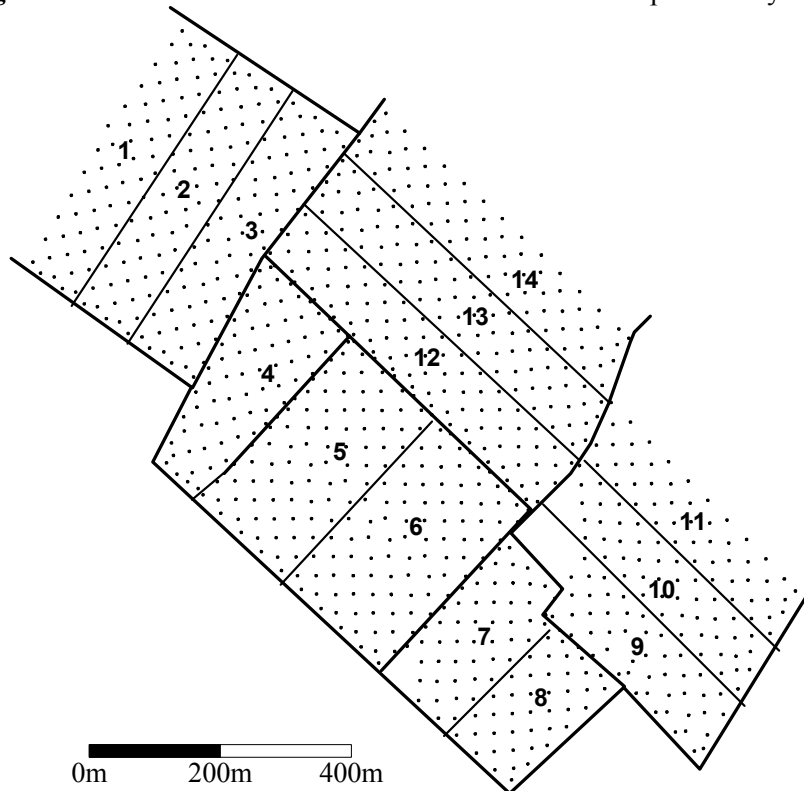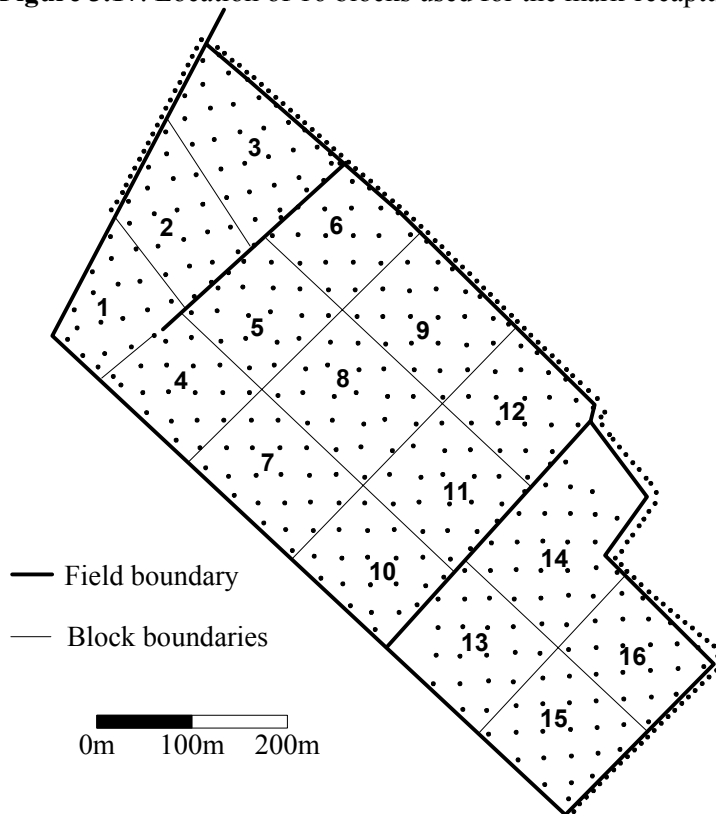

To examine the distribution of beetles across the study site in 2001 the same grid of pitfall traps described above was re-established. Traps were filled with a 50% solution of ethylene glycol and detergent and then opened for three periods (4-11 June; 9-16 July; and 5-12 September).

In 2001, the mark-release-recapture experiment was conducted in the three smallest fields to enable a more intensive study of within-field movement. This area was subdivided into 16 blocks of approximately 1.5 ha each (Fig. 3.17). Beetles of the three most numerous carabid species caught that year, *Pterostichus madidus*, *Nebria brevicollis* and *Poecilus cupreus*, were marked and released as above. Beetles were captured, marked and released on five two-day periods (10-11 May, 24-25 May, 13-14 June, 27-28 June, 2-3 August). Beetles were recaptured in dry pitfall traps between 13-16 August, and in wet traps as described above. In addition, 135 pitfall trap sites, 40 m apart, were established in a line around the outer boundary of the three fields to catch

beetles leaving the fields and so provide an estimate of emigration (Fig. 3.17). At each of these trapping locations, a pair of dry pitfall traps was set 1 m apart and joined by a linear barrier (1 x 0.20 m) to increase the capture rate. These were opened during six periods (23-25 May, 11-13 June, 26-28 June, 10-12 July, 27-30 July, 8-10 August).

Figure 3.17. Location of 16 blocks used for the mark-recapture study in 2001.

3.4.2. Data Analysis

The distribution of insects was analysed using SADIE analysis as described in section 3.2.1.5. To examine whether the stimulus for dispersal was density-dependent, regression analysis was used to examine the number of each species moving out of a particular block (m) in relation to the number captured (c) (both transformed log n +1). The regression was performed both ways (log (m+1) x log (c+1) and log (c+1) x log (m+1)) and a t-test was used to determine whether the slope differed significantly from 1. Density-dependent movement was assumed if both regressions were significant.

Beetles were not individually coded but their capture position was known. Therefore, to obtain an approximate indication of the distance moved by each marked beetle the distance between their capture position and the centroid of the block in which they were marked was calculated within Mapinfo 5.5 using the spherical distance procedure (Mapinfo Corporation, New York, USA). For each species, a t-test was used to determine whether the distance moved differed between the sexes.

In 2001, abundance estimates were calculated using Chapman's small sample adjustment to the Peterson index (Seber, 1982). Each successive pair of dates was treated as a single mark and recapture sequence. The confidence intervals were calculated assuming a Normal distribution for those instances that had recaptures >50 individuals; if <50 then recaptures were assumed to have a Poisson distribution and hence have asymmetric confidence intervals.

3.4.3. Results of Beetle Movement Studies

In 2000, a total of 1853 *P. melanarius*, and 1630 *P. madidus* were marked, of which the proportion recaptured was 11.4 and 7.4% respectively. In general, proportionally more of the recaptured *P. madidus* were found to have moved to a different block than remained in the block where they were originally marked and released. However, there were exceptions when all were recaptured inside the block in which they were marked (Table 3.27).

Table 3.27. Number and percentage of marked *P. madidus* that remained in the same or moved to a different block or field in 2000.

| Marking Field/Block		Recapture Field/Block															Total	% same	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14			Block	Field
L1	1					1											1	0	0
	2				2			2									4	0	
	3																0	--	
S1	4		1		13	6	6	12	4			3					45	29	29
S2.	5					4											4	100	91
	6						6						1				7	86	
S3	7							11									11	100	82
	8						3		3								6	50	
L1	9				1	2	1	2	3						1		10	0	2
	10				2		2	3	2					1	1		11	0	
	11				3	3	5	3	2			1			3		20	5	
L2	12												1				1	100	100
	13																0	--	
	14													1			1	0	
Total		0	1	0	21	16	23	33	14	0	0	4	2	2	5		121	32	33
		L1			S1	S2		S3		L3			L2						

Figure 3.18. Movement of marked *P. madidus* males and females between blocks in 2000. A central release point within each block was assumed.
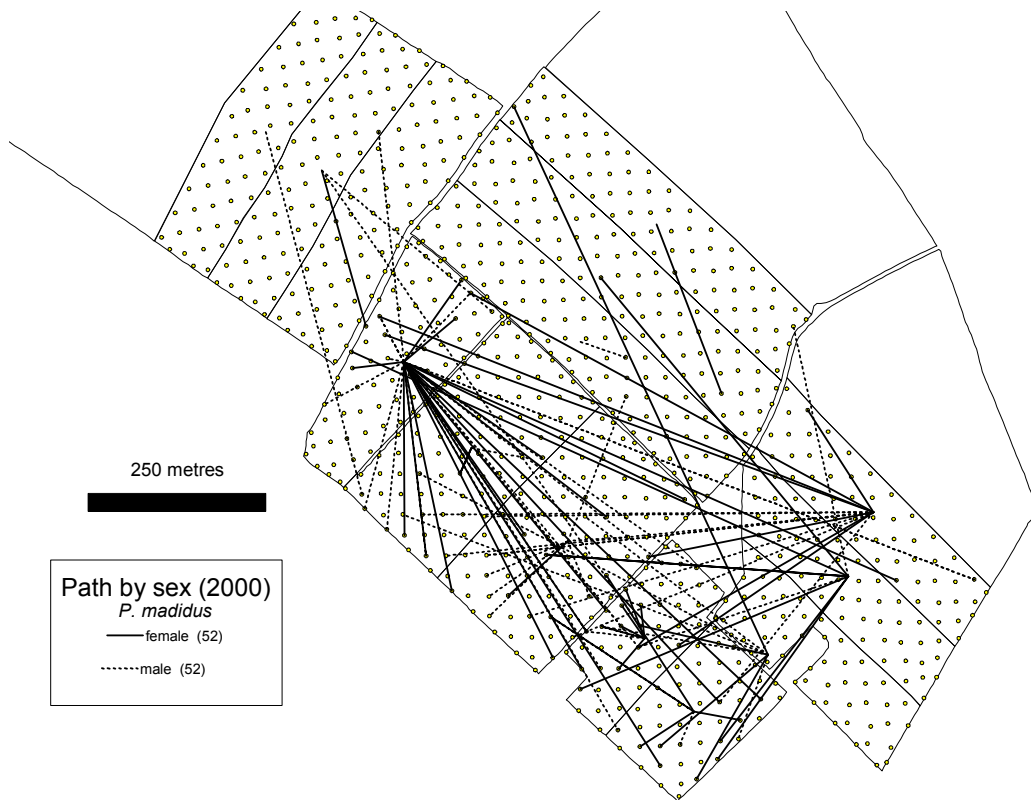
P. melanarius appeared to be more static, with a smaller percentage of marked individuals than *P. madidus* being recaptured in a block other than the one in which they were released, although again there were exceptions (Fig. 3.19). The overall proportion of *P. melanarius* that moved to another block and were recaptured was 20% compared to 67% for *P. madidus* (Tables 3.27 & 3.28). Overall a higher proportion of *P. madidus* moved between fields than remained in the field where they were originally released (Table 3.27). However, most movement occurred from those fields where activity-density was lowest and least where it was highest (Fig. 3.18). In contrast, in the fields where *P. melanarius* were most abundant, the majority remained within the same field (Table 3.28). However, the majority of recaptured *P. madidus* (94%) and all *P. melanarius* that were marked in the pea fields were also recaptured in pea fields. Of the 43 *P. madidus* that moved between fields and were recaptured, 74% crossed only one hedgerow, 21% crossed two and only 7% passed through three hedgerows. Of the 23 *P. melanarius* recorded moving between fields 78% crossed one hedgerow and the remainder crossed two hedgerows.

Fig. 3.19. Movement of marked *P. melanarius* males and females between blocks in 2000. A central release point within each block was assumed.
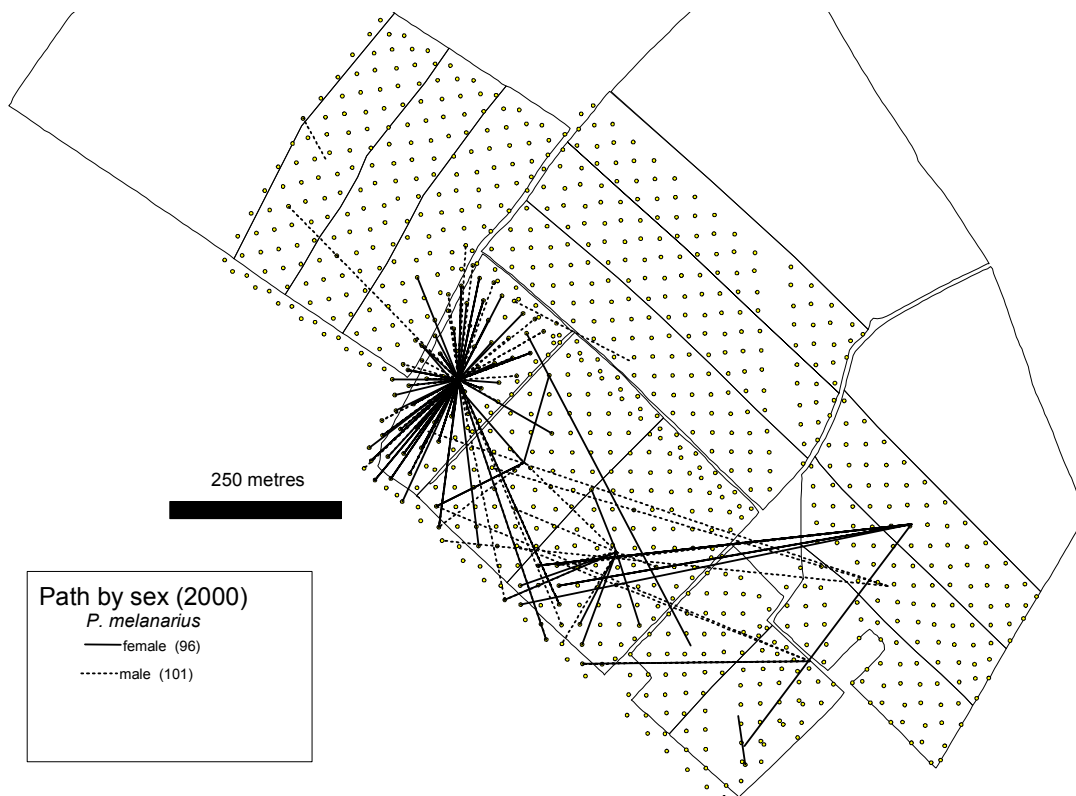
The average displacement distance of *P. madidus* was 12 m day^{-1} but values as high as 43 m day^{-1} occurred (Table 3.29). There was no significant difference between the sexes (t-Test) in the distance moved. Overall 36% moved less than 5 m day^{-1}, with the proportion moving greater distances gradually declining (Fig. 3.20). The speed of *P. melanarius* was only half that of *P. madidus*. 49% moved less than 5 m day^{-1} and only 4% moved more than 20 m day^{-1}, with a maximum of 29 m day^{-1} (Table 3.29). Again, there was no significant difference between the sexes. The maximum distance moved by a *P. melanarius* was lower (725 m over 25 days) than that recorded for *P. madidus* (859 over 20 days) and 83% of *P. melanarius* moved less than 200 m. These estimates may, however, underestimate the true dispersal distances because some beetles may have moved outside the pitfalled area and consequently they could not be recaptured. In addition, the differences between species may be artefacts of the different distributions of the release points, influencing the potential to detect long-distance movement.

Table 3.28. Number and percentage of marked *P. melanarius* that remained in the same or moved to a different block or field in 2000.

Marking Field/Block		Recapture Field/Block 1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total	% same Block	Field
L1	1	1														1	100	100
	2															0	--	
	3															0	--	
S1	4	1		5	148	7	7									168	88	88
S2	5				1	5										6	83	94
	6					2	10									12	83	
S3	7				1											1	0	50
	8								1							1	100	
L3	9					2	3								1	6	0	0
	10				1	2									1	4	0	
	11					2	8	1								11	0	
L2	12				1											1	0	0
	13															0	--	
	14															0	--	
Total		2	0	5	26	20	28	0	2	0	0	0	0	0	2	211	78	79
		L1			S1	S2		S3		L3			L2					

Table 3.29. Distances moved (m d^{-1}) by *P. madidus* and *P. melanarius*. (SE=standard error, N=number of beetles)

	P. madidus			*P. melanarius*		
2000	All	Males	Females	All	Males	Females
Mean	12	12	12	5.9	5.5	5.6
SE	0.8	1.3	1.3	0.4	0.5	0.5
Median	10	10	11	4.1	3.7	4.1
Minimum	0.6	0.6	1	0.4	0.4	0.6
Maximum	43	43	38	29	29	26
N	121	52	52	211	101	96
t value	0.28			0.18		
2001						
Mean	4	3.1	2.9			
SE	0.5	0.4	0.7			
Median	2.4	2.3	2.6			
Minimum	0.1	0.4	1			
Maximum	43	16	5			
N	134	66	5			
t value	-0.22					

Figure 3.20. Frequency distribution for distance moved by *P. madidus* and *P. melanarius* in 2000 and 2001. Frequencies were weighted by trap density for each distance class.
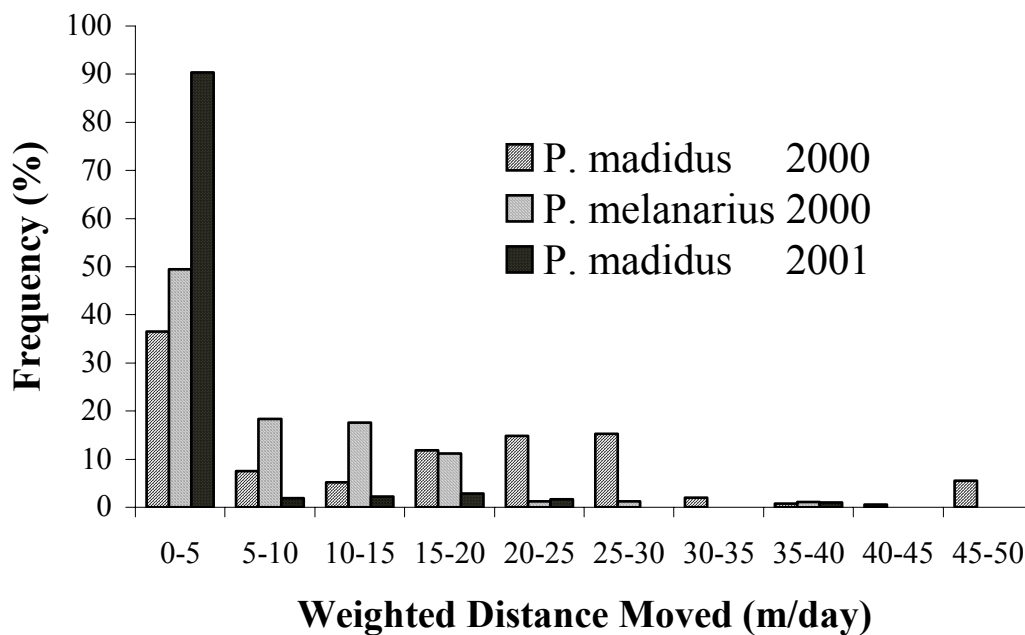
In 2001, the most frequently captured species was *P. madidus* and a total of 3813 were marked, of which only 3.6% were recaptured. Of the 1567 *N. brevicollis* that were marked 1.1% were recaptured while only one of the 303 marked *P. cupreus* was recaptured. Given the very low recapture rate for these two species, no further data are presented on them. As found in the previous year, a greater proportion of *P. madidus* (66%) had moved between blocks and been recaptured compared to those that stayed where they were marked (Table 3.30). Of the 24 *P. madidus* that moved between fields and were recaptured (Table 3.30), 92% crossed only one hedgerow and 8% crossed two boundaries (Fig. 3.21). Only five female beetles were recaptured of the 72 beetles that were sexed.

In 2001, the average daily displacement distance of *P. madidus* was a third of that found in 2000. 90% of beetles moved <5 m day^{-1} (Fig. 3.20). The maximum distance moved was the same as that found in 2000, but a higher proportion of beetles moved shorter distances, with 99% moving less than 25 m (Fig. 3.20). There was no significant difference between the distances moved by males and females (Table 3.29). These displacement distances may again be an underestimate of the true value because they reflect the scale of the sampling grid.

No marked beetles were recaptured in the line of pitfall traps surrounding the three fields.
No significant density-dependent movement was detected for either species in either year.

Table 3.30. Number and percentage of marked *P. madidus* that remained in the same or moved to a different block or field in 2001.

Marking Field/Block		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total	% same Block	Field
S1	1		1	3														4	0	68
	2	1	1	2				1	2			1						8	13	
	3		2	3	1		1											7	43	
S2	4				3		2	1					1					7	43	84
	5					1	1	1	1									4	25	
	6			1		1	4	1	2	1		1						11	36	
	7			1	2		1	2										6	33	
	8						1	1	1	1	1	3	1		1		1	11	9	
	9					2	1		2	2	1			1				9	22	
	10									1	2	1	1			1	1	7	29	
	11			1	1	3			1		1							7	0	
	12			1					1			3	1			1	1	8	13	
S2	13		1	1			1							3	1	1		8	38	80
	14				1			2	1	1					11	1		17	65	
	15								1					1	2	5	1	10	50	
	16													1		3	6	10	60	
Total		1	5	13	8	7	12	9	12	6	5	9	4	6	15	12	10	134	34	81
			S1						S2						S3					

Figure 3.21. Movement of marked *P. madidus* males and females between blocks in 2001. A central release point within each block was assumed.
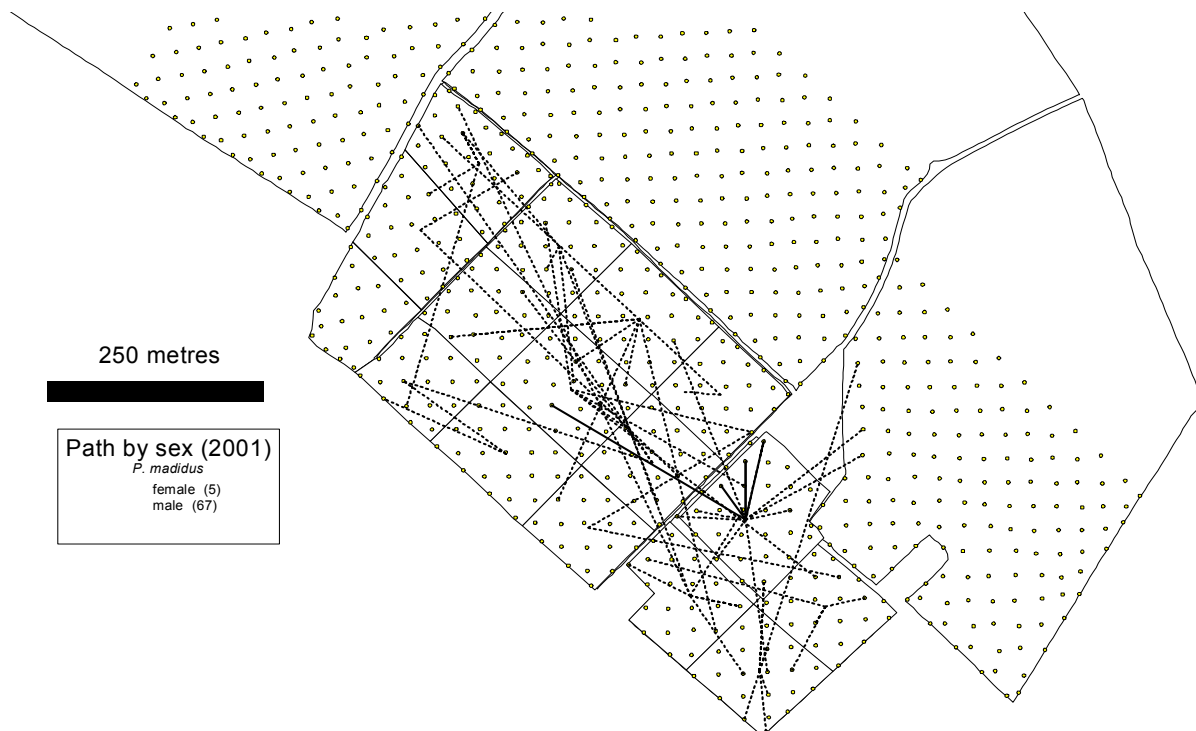
3.4.4. Conclusions

1. The two carabid species investigated differed in their mobility. *P. melanarius* was relatively immobile with most individuals remaining within the same areas where they emerged. A greater proportion of *P.madidus* moved within and between fields.

2. Both carabid species were shown to cross hedgerows.

3. The average distance moved by *P. madidus* varied between years indicating that movement may vary according to the conditions encountered.

4. No significant density-dependent movement was detected for either species in either year.