

**PITFALL TRAP SAMPLING OF
CARABID BEETLES AND SPURIOUS
EDGE EFFECTS**

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Abstract

This study examined variation in pitfall trap captures across a woodland/grassland transect, using enclosed, equal populations of 2 common woodland carabid species: *Nebria brevicollis* and *Abax parallelepipedus*, and 1 common generalist species: *Pterostichus madidus*. The first 2 species showed no significant variation in numbers caught across the transect repeats, best fitting the null model. However, overall average capture numbers for *A. parallelepipedus* showed a significant best fit unimodal model despite no significant difference in capture numbers between the woodland, edge or grassland habitats. For the third species, *P. madidus*, there were significantly more captures in woodland than grassland and best fitted a linear model.

The study also showed that *P. madidus* was caught significantly less frequently than the other 2 species in woodland, grassland and edge habitats. Using capture rates as an indication of movement rates this could mean *P. madidus* moves more slowly than the other 2 species. The significant difference in capture rates between woodland and grassland for *P. madidus* indicates that this species moves slower in the grassland despite being found naturally in both habitats.

To investigate if habitat structure influenced capture numbers and rates a follow up experiment swapped sections of grassland and woodland habitats. However the results showed the null model fitted best and a control experiment to test for disturbance showed that habitat disturbance had affected the results and so made them inconclusive.

If other generalist carabid species demonstrate higher capture numbers and rates in a particular habitat this could bias pitfall trap data on abundance and biodiversity. This could be particularly significant for edge effect studies where spurious edge effects could be generated. Also where carabids are used as bioindicators it could also mean abundance is underestimated in certain habitats for some species which could influence habitat or biodiversity management recommendations.

1. Introduction

1.1 Fragmentation and Edge Effects

Habitat fragmentation is considered a major cause of species decline worldwide, and has become a significant issue for conservationists endeavouring to maintain biodiversity (Davies & Margules, 1998). Present day habitat fragmentation is widespread due to human activity, which has increased the occurrence of edges and as a consequence edge effects have become increasingly important (Fahrig, 2003). Edges are described as the boundary between two different habitat types (Reis *et al*, 2004) and can be abrupt or a zone of transition where communities can merge into one another (Yahner, 1988). Edge effects have been recognised since 1933 when Aldo Leopold first used the term and can have positive or negative impacts on the abundance and diversity of species in relation to the distance from the edge (Reis *et al*, 2004). Whilst edge effects have been shown on larger spatial scales (Ewers & Didham, 2008, Laurance, 2000) it is generally accepted that 50m into to each habitat is sufficient to show edge effects (Murcia, 1995; Matlock, 1994). Edges can affect microclimatic and environmental gradients such as air temperature or soil moisture content (Didham *et al*, 1998). In the past edges were thought to be of benefit to wildlife and the creation of edges was positively encouraged for habitat management (Yoakum & Dasmann, 1971). However it has become increasingly accepted that many characteristics of edges are undesirable in terms of wildlife conservation (Harris,1988) and can have particularly negative impacts on forest fragments (Murcia, 1995).

1.2 Carabid Beetles and Pitfall Trapping

Beetles in the family Carabidae are speciose, varied and abundant in many parts of the world (Lovei & Sunderland, 1996). They are sensitive to environmental change (Niemela, 2000) and it has been shown that habitat fragmentation can affect carabid beetle assemblages (Niemela, 2001). This, together with a relatively well understood natural history, makes carabids useful as bioindicators of environmental change (Avgin & Luff, 2010, Rainio & Niemela, 2003, Scott & Anderson, 2003; Stork, 1990).

Most studies involving carabids use pitfall trapping as an easily standardisable and cost effective method of capturing ground beetles (Spence & Niemela, 1994). Pitfall trapping has often been used to study the impact of fragmentation and edge effects on the diversity and

abundance of ground beetles (Gaublomme *et al*, 2008; Magura, 2002; Phillips *et al*, 2006). However there is no general trend found in carabid diversity and abundance in relation to edges. Some studies have shown significantly higher carabid diversity at the edge and in the grassland than in the forest (Molnar *et al*, 2001; Magura, 2002). Others have shown no significant increase in diversity at the edge (Taboada *et al*, 2004; Heliola *et al*, 2001) and others show species richness was higher in the forests than the grasslands (Kotze & Samways, 2001). Studies of carabids can make recommendations for general conservation and habitat management (Kotze & Samways, 2001; Mullen, 2008; Pearce & Venier, 2005) and therefore it is important that the conclusions drawn are accurate and reliable.

However there have been suggestions that pitfall traps can be unreliable for estimating diversity due to the variation in surface activity between species affecting the likelihood of capture (Desender and Maelfait, 1989). Other studies have indicated that pitfall trapping can overestimate the abundance of carabidae possibly linked with the vegetation complexity and diversity of the habitat (Lang, 2000).

Greenslade (1964) also suggested that density of vegetation could impede carabid movements and affect catch rates and it has been shown that carabid catch rates can be reduced in taller vegetation. Jopp & Reuter (2005) state that vegetation density, leaf litter or gravel constitutes local spatial resistance which is an important influence on the movements of invertebrates. A study by Wiens & Milne (1989) on Tenebrionid beetles in the grassland of the Sevilleta National Wildlife Refuge in New Mexico concluded that landscape heterogeneity affected beetle movement. They observed that beetles moved quickly across bare ground and more slowly amongst dense grassland. Crist *et al* (1992) also found that the movement of these beetles was affected by the permeability of vegetation according to plant structure in a semi-arid grassland in Colorado. Wallin & Ekbohm (1988) studied the movements of *P. melanarius* and *P. niger* in both cereal fields and woodland. They found both species moved further and faster in the field than the woodland although they naturally occurred in both habitats.

If movement rate affects pitfall catches and vegetation type affects movement this is particularly relevant to edge effects studies which involve two very different habitats. Where lower numbers of carabids are caught in one habitat over another this could indicate that there is a lower population in that habitat or it could indicate that less individuals are caught due to the influence of vegetation structure on movement. If the latter is true this could affect edge effect studies, biasing data and generating spurious edge effects.

1.3 Research Objectives

While habitat structure and movement rates have been thought to play a part in the pitfall trapping this can be difficult to quantify in natural habitats due to unknown populations. This also makes comparisons between species and habitats particularly difficult.

This study aims to investigate the effect of vegetation on the pitfall trapping of carabid beetles across a forest/grassland transect. By using controlled populations of carabids across the edge transect any variation in catch numbers should be immediately apparent. Whilst many environmental variables can influence catch rates, this study aims to focus particularly on habitat structure.

The null hypotheses under investigation are:

- 1) There is no significant variation in catches of controlled equal populations of carabids across a woodland/grassland transect using pitfall trap methods.
- 2) Habitat structure does not influence the number of captures of carabid beetles across an edge transect.

It is expected that hypothesis 1 will be disproved as it is predicted that the different vegetation types will affect carabid movement and subsequently the number of captures of the controlled populations. This will then allow for further investigation into whether the habitat structure is a fundamental cause rather than other environmental factors. This could be important for future carabid studies where pitfall trapping is used to explore edge effects and species abundance or diversity, especially where carabids are used as bioindicators in a more general context.

2. Methods

2.1 Species Selection and Capture

The study took place at Silwood Park (51°24'30"N, 0°38'19"W), in Berkshire and used 3 carabid species common to the area: *Nebria brevicollis*, *Abax parallelepipedus* and *Pterostichus madidus* which were identified according to Luff's key (2007). Individuals of the three species were live captured using pitfall traps from woodland and grassland areas away from the experimental sites. The pitfall traps used were plastic cups of 70mm diameter and 80mm depth with a small amount of soil in the bottom of the cups to allow the beetles to hide and avoid predation. The traps were emptied several times a week. The captured beetles were kept outside in their natural habitat in a 1m by 1m square aluminium enclosure, until needed for the experiment. This enclosure is dug into the ground with 30cm high sides to avoid escape and covered in chicken wire to prevent predation and is identical to those used in the enclosed transect experiment (See Experimental Design).

Nebria brevicollis was the most commonly found carabid in Silwood Park and is common throughout the UK and most of Europe. It is a generalist species (Gaublomme et al, 2008), and although it is found predominantly in woodland it can be found in a wide range of habitats apart from very wet or saline areas (Kavanaugh & LaBonte, 2008). In Silwood Park this species was caught only in woodland and edge habitats with no captures in grassland areas.

According to Niemela (2001) *Abax parallelepipedus* is a woodland specialist and does not enter grassland. However a study by Magura (2000) found this species to be numerous in forest, grassland and edge habitats. In Silwood Park occasional captures were made in grassland but the majority of individuals were captured in woodland.

Studies by Greenslade (1964) showed *Pterostichus madidus* occurs in both woodland and grassland habitats although it has also been described as a forest generalist (Gaublomme et al, 2008). This study captured individuals in both grassland and woodland habitats and although there was a bias towards the woodland habitat enough were captured in the grassland to warrant this species being considered a generalist species.

Unfortunately no specialist grassland species was captured in sufficient numbers for use in this experiment.

2.2 Experimental Sites

3 woodland/grassland edges at Silwood Park were chosen to conduct the experiment, the sites were chosen for their suitable edges and also for their distance from other experiments which could affect the study.

Site 1 - Merten's Acres Wood into Pond Field

The woodland here is on a gentle slope and dominated by *Quercus robur* with some *Acer pseudoplatanus*. There are occasional patches of *Urtica dioica* but the ground is mostly bare covered with a layer of leaf litter. The grassland is flat with moist soil and the most varied grasses of the 3 sites including *Holcus mollis*, *Holcus lanatus* and *Agrostis capillaris*. *Cirsium palustre* is also abundant and less frequently *Rubus fruticosus* and *Urtica dioica* are present. At this site there is a grassy footpath which runs between the -10m and -20m points in the grassland.

Site 2 – Elm Slope into Gunnes's Hill Field

Again the woodland is predominantly *Quercus robur* and the ground is mostly bare with a layer of leaf litter. The grassland appears to be under much greater pressure from rabbit grazing and is subsequently cropped much shorter than the grassland at Site 1. *Rumex acetosella* is abundant. Moss is also abundant at this site.

Site 3 – Gunnes's Thicket into Church Field

The woodland in Gunnes's thicket is close to Silwood Lake, the area is flat and the soil is moist. *Quercus robur* again dominates however while there are areas of bare ground with only leaf litter coverage there are also large patches of *Urtica dioica* and areas of *Juncus effusus*. The grassland of Church Field has very sandy soil and slopes gently upwards from the edge. There is considerable rabbit activity evidenced by burrows and disturbed ground. Moss is abundant at this site, together with *Luzula campestris* and *Rumex acetosella*.

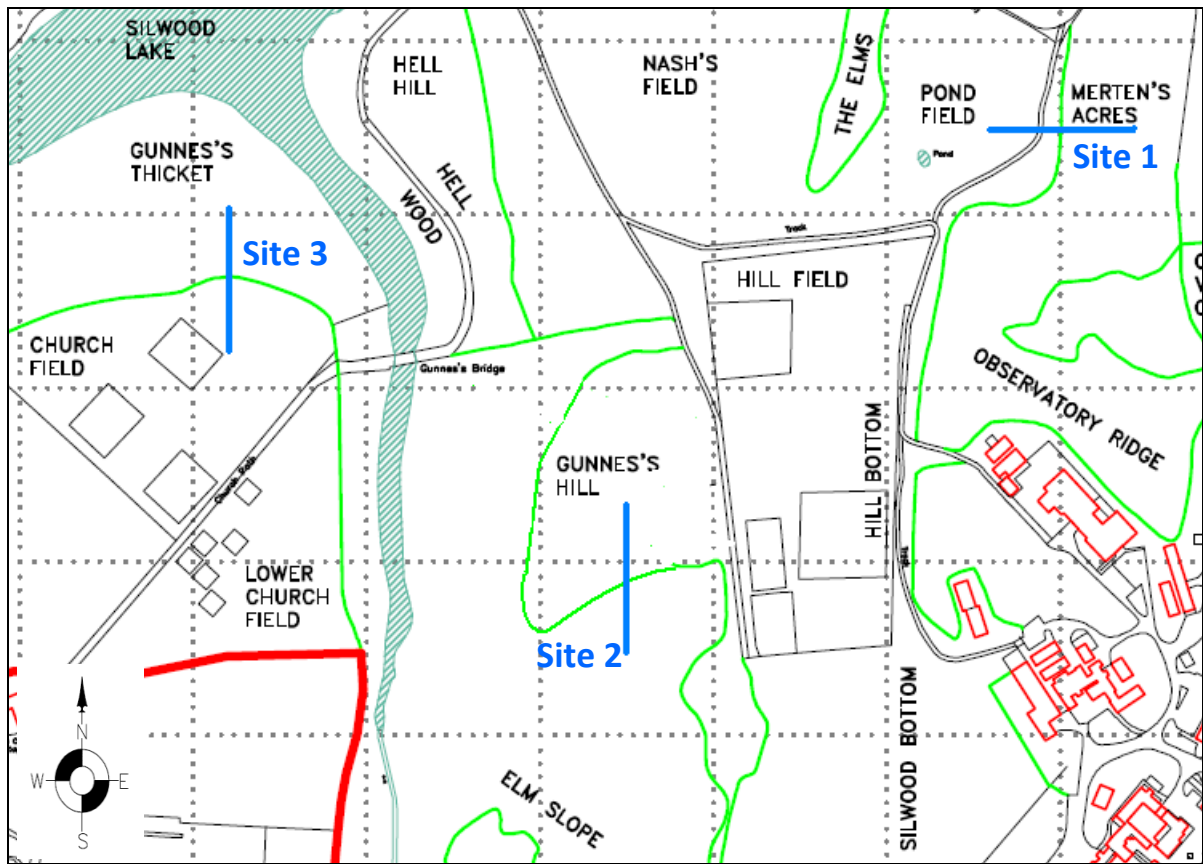


Figure 1: Map showing the 3 experimental sites at Silwood Park, Berkshire.

2.3 Experimental Design

A normal unenclosed transect was established across the edge at each site to record the numbers of live captures of carabids of the three species of interest and their natural distribution across the transects. A pitfall trap was placed at the edge and then every 10m, 40m into the woodland and 40m into the grassland. Plastic cups measuring 70mm in diameter and 80mm in depth were used as traps, buried flush with the surface of the ground. These pitfall traps were covered with clear plastic discs held up with wire legs to protect the beetles from predation and precipitation. Distances were labelled at the edge as 0m and then positive distances extend into the woodland (10m, 20m, 30m, 40m) and negative distances into the grassland (-10m, -20m, -30m, -40m). This transect was used Carabid numbers were collected over a 13 week period from 29th April to 29th July 2010 but this was standardised for sampling intensity due to problems of trap disturbance by jackdaws and deer which meant that 69 trapping days were recorded.

A second transect was then established at each site to run the enclosed transect experiment, positioned approximately 4m away parallel to the open transect. On this transect each pitfall trap was positioned at the centre of a 1m x 1m aluminium square enclosure with walls 30cms high. These enclosures were partially dug into the ground to ensure the area was completely enclosed. Once in place the 1m² area was thoroughly searched for the presence of any carabids, which were then removed from the enclosure.

The pitfall traps were covered by the clear plastic discs with wire legs to protect from precipitation and each enclosure was covered in chicken wire to minimise the risk of predation of the enclosed beetles.

Carabids of the required species were then removed from the holding enclosure and placed in an empty plastic container. Then 8 carabids were randomly chosen and placed at equally spaced intervals around the edge within each enclosure.

The carabids were then left for 2 weeks or until 7 of the 8 individuals were caught, whichever was soonest. Once the experiment time had transpired the enclosed arenas were then thoroughly searched to ensure all beetles not captured were accounted for. The traps were then cleaned to avoid the risk that contamination by previous captured carabids may attract carabids in the next experiment and bias results. (Luff, 1986) The experiment was then repeated with each species on each transect.

As *Nebria brevicollis* and *Abax parallelepipedus* always had at least 7 individuals caught within a week it was possible to run the experiment with them twice in each transect. However as *Pterostichus madidus* was caught less frequently it was only possible to run the experiment once in each transect for this species.

Habitat Swap Experiment

After completion and analysis of the results of the first experiment it was obvious that *Pterostichus madidus* showed a significant difference in catch rates across the transect. Therefore the next part of the experiment was to investigate if differences in habitat structure were the cause of this variation. In order to investigate this each 1m by 1m section of grassland habitat was moved into the woodland and vice versa. The experiment was conducted on the 3 enclosures from 20m to 40m in the woodland and from -20m to -40m in the grassland. The new position for each was chosen at random by pulling positions out of a hat.

The grassland habitat was dug up by hand and moved in a complete section where possible to cause the minimum disturbance to the habitat structure. However most sections had to be cut in half in order to be dug up and moved due to difficulties with roots.

It was not possible to move the woodland habitat as a complete section due to the loose soil. Therefore the top leaf litter layer was removed first and then the soil was moved to the new position and the leaf litter replaced on top.

Pitfall traps were then placed at the centre again and 8 randomly chosen *Pterostichus madidus* individuals were added to the enclosures at equal distances around the edge. They were then left for 2 weeks or until 7 carabids had been caught. This experiment was conducted on each of the 3 transects.

Habitat Disturbance Experiment

In order to test for effects of the disturbance of digging up the squares, additional enclosures were established parallel to the habitat swap transect, approximately 4m away. The 1m by 1m area was then dug up in the same way but replaced in the same position and the experiment run in the same way with 8 randomly chosen *Pterostichus madidus*. If there is no affect from the disturbance the results should follow similar trends to that produced in the original enclosed transect experiment.

2.4 Data Analysis

To analyse the data for significance between distance, habitat and number of carabids caught generalised linear models (GLMs) were used in R version 2.9.0. (R Development Core Team). Poisson errors were used when possible, as appropriate for count data and quasipoisson was used where residual deviance was greater than residual degrees of freedom leading to overdispersion.

The number of captures across the 3 enclosed transects was examined using a statistical method to analyse data for the existence of edge effects as detailed by Ewers & Didham (2006). This method analyses the data in the compatible version 2.5.1 of R (R Development Core Team) using a general logistic model to fit the best of 5 models: null, linear, exponential, logistic and unimodal. This method also examines the extent and magnitude of any edge effects which can normally be interpreted from the logistic curves shown in figure 2 (Reis et al, 2004), but edge effects can also be examined from unimodal models (Ewers &

Didham, 2006). Linear models can also show variation across an edge transect although it is more difficult to interpret the extent or magnitude of edge effects from this result.

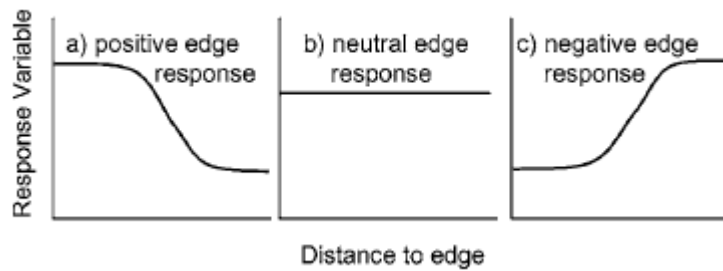


Figure 2: Expected edge effects shown graphically as logistic curves (Figure taken from Reis *et al*, 2004).

The best fit model was decided by comparing Akaike Information Criterion values. AIC weights were also calculated to indicate the probability of the models being the best fit model.

In order to examine the habitat specialisation of the 3 species an indicator value was calculated. These are percentage values which denote if the species is a good indicator of the habitat and were calculated using within species abundance and occurrence comparisons as per the method detailed by Dufrene & Legendre (1997). A value of over 25% indicates a good indicator species for that habitat, (Legendre & Legendre, 1998). Indicator values for both the open and enclosed transects were calculated for comparison.

Mixed effects models were used to investigate the relative importance of the categorical explanatory variables affecting the variance in capture rates. A variance component analysis was conducted using linear mixed effects model, with habitat as a fixed effect, fitted with restricted maximum likelihood (REML). The standard deviations of the model summary are squared to get the variances which are then expressed as percentages of the total to show which components of the overall variance are the most important. Where necessary models with different fixed effects and the maximum likelihood method (ML) were compared using anova to confirm the best model.

Capture rates using individuals caught per day were calculated for enclosed and unenclosed transects to give an indication of the movement rates of the species. For the purposes of comparison of habitats 3 points on the transects are grouped: woodland: 40m, 30m and 20m, edge: 10m, 0m & -10m and grassland: -20m, -30m and -40m.

Results

3.1 Capture Rates

Average capture rates (individuals caught per day) in the enclosed transects are shown for each species and habitat in Figure 3. The figure shows that whilst there was considerable variation in catch rates the median rate was relatively similar in all habitats for *N. brevicollis* and *A. parallelepipedus*. *N. brevicollis* and *A. parallelepipedus* showed capture rates between 0.6 and 0.8 individuals per day across all habitats and were not significantly different ($z=0.280$, $df=106$, $P=0.779$).

P. madidus demonstrated capture rates of less than 0.4 in all habitats with a rate of only 0.14 in grassland as shown in Figure 2c. *P. madidus* was caught significantly less frequently than *A. parallelepipedus* ($t=-5.13$, $df=79$, $P<0.001$) and *N. brevicollis* ($t=-6.058$, $df=79$, $P<0.001$), which could be because this species moves more slowly than the others. The capture rate for *P. madidus* were significantly different between the grassland and woodland ($t=4.78$, $df=16$, $P<0.001$) and there was also a less significant difference between grassland and edge capture rates ($t=-2.21$, $df=16$, $P=0.042$). There was no significant difference between catch rates in woodland and edge habitats for *P. madidus* ($t=1.865$, $df=16$, $P=0.81$).

Variance component analysis using mixed effects models on the enclosed transect capture rate for *P. madidus* which showed that site was not important and that distance as a repeat within habitat was the most important component accounting for over 84% ($sd=0.11$) of the variation.

Figure 4 shows the catch rates for the species in the open transect. It is clear to see that *N. brevicollis* and *A. parallelepipedus* are woodland species with *N. brevicollis* being caught more frequently in that habitat than *A. parallelepipedus*. The open catch rates are not directly comparable to the enclosed transects due to the unknown difference in population abundances between species. However *P. madidus* shows a higher number of individuals caught per day in the woodland and very little difference between the grassland and edge transects.

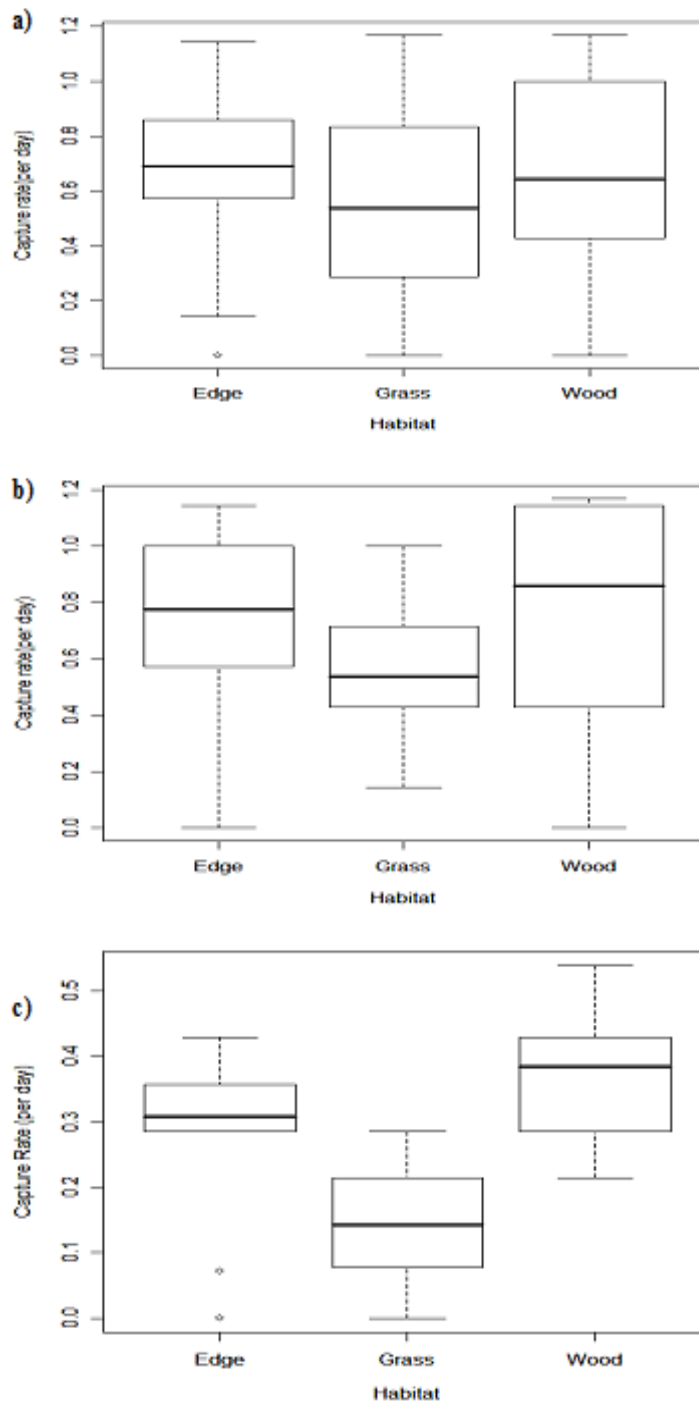


Figure 3: Enclosed transect capture rates, individuals caught per day for **a)** *N. brevicollis*, **b)** *A. parallelepipedus* **c)** *P. madidus*. The median value is denoted by the darker line.

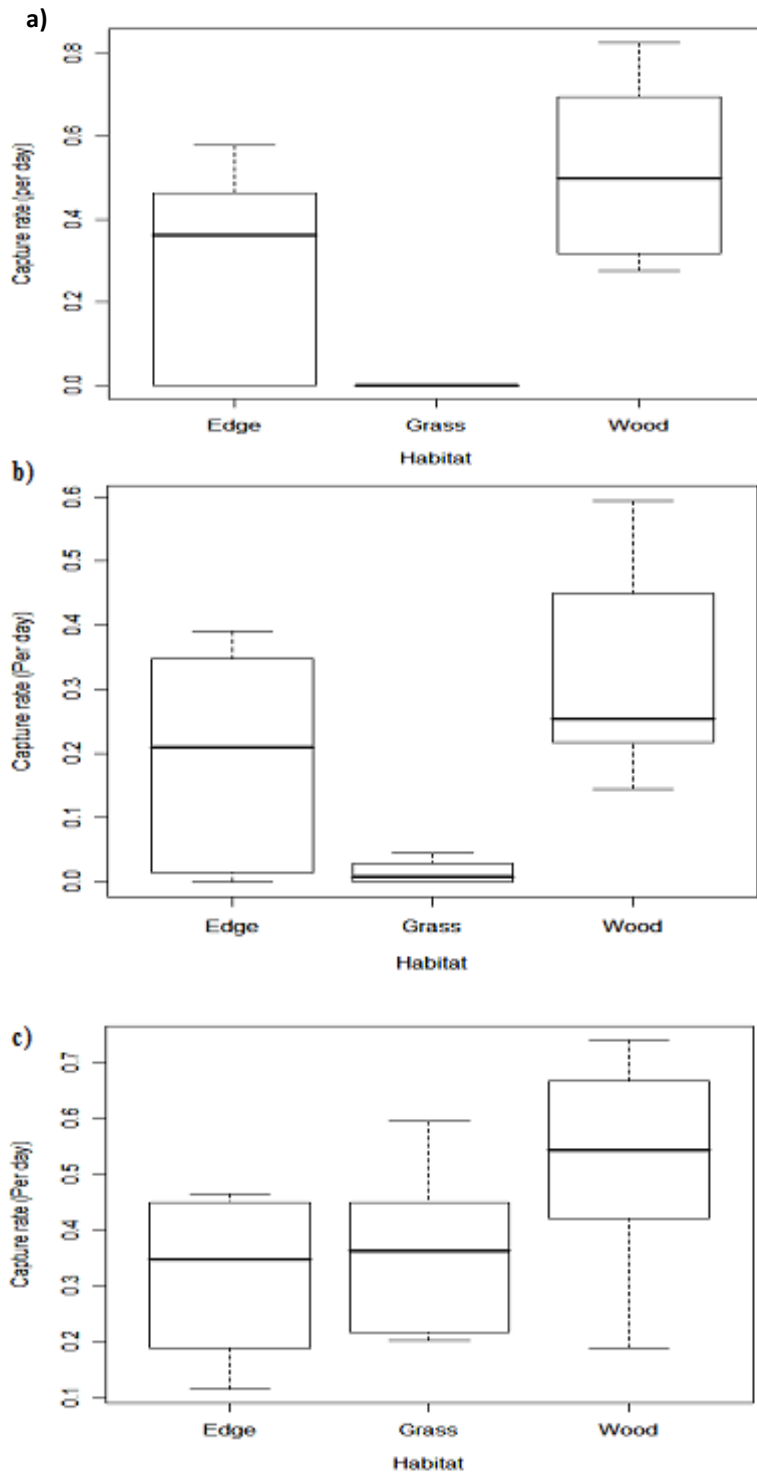


Figure 4: Open transects capture rates individuals caught per day for a) *N. brevicollis*, b) *A. parallelepipedus* c) *P. madidus*. The median value is denoted by the darker line.

3.2 Open transects

The averages of the open transects for sites 1 and 3 were used to show the general abundance and distribution of the 3 species of interest as shown in Figure 4. Only data from sites 1 and 3 was used in analysing the unenclosed transect as site 2 was disturbed too often by animals and birds to be comparable.

A. parallelepipedus and *N. brevicollis* showed a significant trend in number caught with distance ($t=2.98$, $df=7$, $P=0.021$; $t=3.59$, $df=7$, $P=0.009$). *P. madidus* was captured in grassland more than the other 2 species but also showed a significant variation with distance ($t=4.465$, $df=7$, $P=0.03$).

The data was examined for the best fit models for each species using the method designed by Ewers & Didham (2006) and the results are summarised in Table 1 below. Both *N. brevicollis* and *A. parallelepipedus* showed the best fit model is logistic, which is the typical model showing edge effects, with a negative response from forest to grassland with abundance decreasing near the edge. (Reis *et al*, 2004). The P values were highly significant as would be expected as these species are woodland species. The middle of the edge was very similar in both species at approximately -2.4m.

Table 1: AIC and P values for the different models for the average abundances of the 3 species across the unenclosed transects at site1 & site 3.

Species	Null AIC	Linear AIC	Logistic AIC	Best Model	F.value	P.value
<i>N. brevicollis</i>	80.756	66.123	58.758	Logistic	150.087	0
<i>A. parallelepipedus</i>	72.036	63.989	60.568	Logistic	41.755	0.008
<i>P. madidus</i>	72.567	63.783	-	Linear	8.132	0.025

A linear model was the best fit for the averaged capture numbers for *P. madidus*, with a significant P value of 0.025. *P. madidus*, as a generalist species, is found in both grassland and woodland habitat although significantly more individuals were captured in woodland than grassland ($t=3.14$, $df=4$, $P=0.035$). There was no significant difference between numbers caught in the woodland and the edge ($t=2.199$, $df=4$, $P=0.093$) or between the edge and the grassland ($t=-0.259$, $df=4$, $P=0.809$).

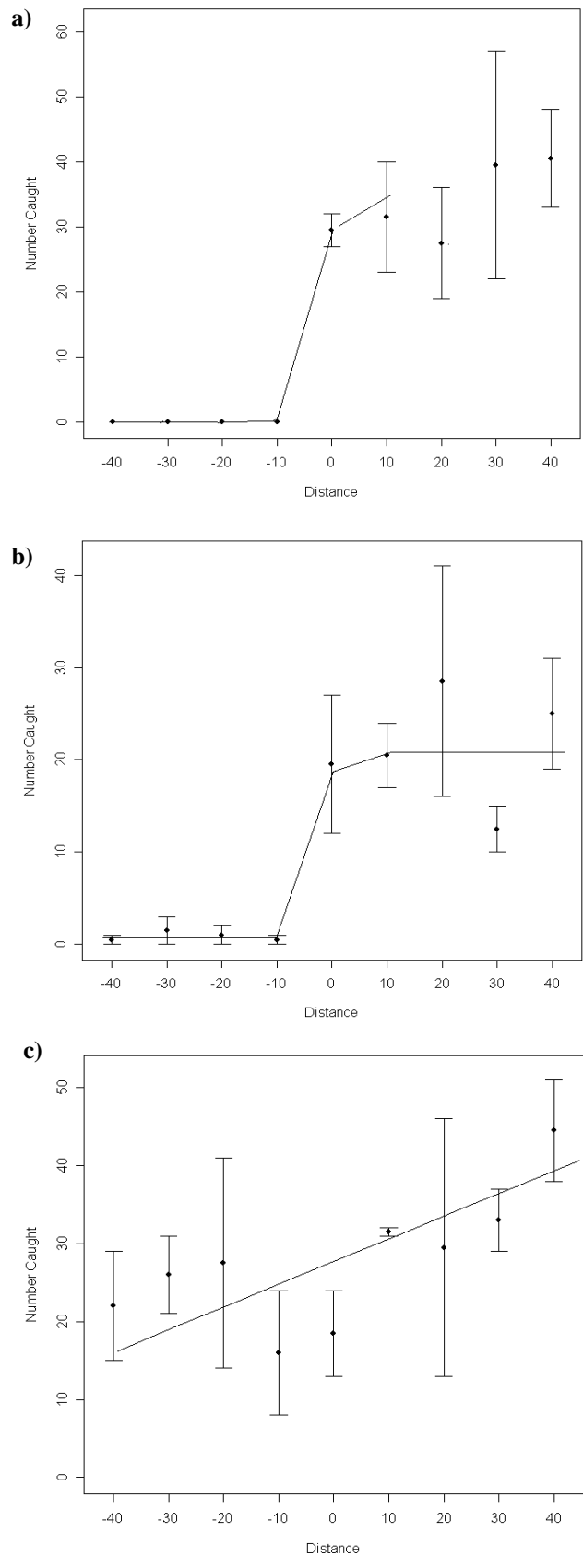


Figure 5: The average abundance across the open transects for **a) *N. Brevicollis*** **b) *A. parallelepipedus*** and **c) *P. madidus***. Positive distances are woodland and negative distance are grassland.

3.3 Enclosed Transect Experiment

The average number of individuals caught (from the controlled population of 8) across all sites and transects or the enclosed transect experiment are shown in Figure 5. Initial analysis of the data showed that distance was not significant for *A. parallelepipedus* ($t=1.164$, $df=53$, $P=0.25$) or *N. brevicollis* ($t=1.318$, $df=53$, $P=0.193$). However distance significantly affected numbers caught for *P. madidus* ($t=3.87$, $df=36$, $<P=0.001$).

The numbers caught in the enclosed transects from all 3 sites was also analysed using the same statistical procedure as the unenclosed transects (Ewers & Didham, 2006) and the IC values and best fit models are shown in tables 2 and 3.

The null model was the most common best fit model for both species indicating there is no significant variation in numbers caught across the transect and no edge effect is shown. Where AIC values are similar it is important to examine the difference in AIC values between the models. According to convention, a difference of less than 2 in the AIC values show that there is still a considerable level of support for the model with the higher value (Burnham & Anderson, 2002). The AIC weights shown in brackets give the probability that the model is the best model based on the AIC values.

Table 2: Best fit model results for *N. brevicollis* enclosed transect captures. Response refers to species, transect number and first or second repeat. NB Ave is the average of all transects and repeats. Percentage values in brackets are the AIC weights showing the probability of the model being the best fit.

Response	Null AIC	Linear AIC	Logistic AIC	Best Model	F.value	P.value
NB1a	42.557 (58%)	43.186 (42%)	-	Null	-	-
NB1b	40.242 (35%)	39.669 (46%)	41.438 (19%)	Linear	5.22	0.056
NB2a	36.827 (58%)	37.477 (42%)	-	Null	-	-
NB2b	39.827	-	-	Null	-	-
NB3a	42.398 (42%)	41.741 (58%)	-	Linear	3.54	0.102
NB3b	44.224 (59%)	44.962 (41%)	-	Null	-	-
NBAve	32.245 (60%)	33.056 (40%)	-	Null	-	-

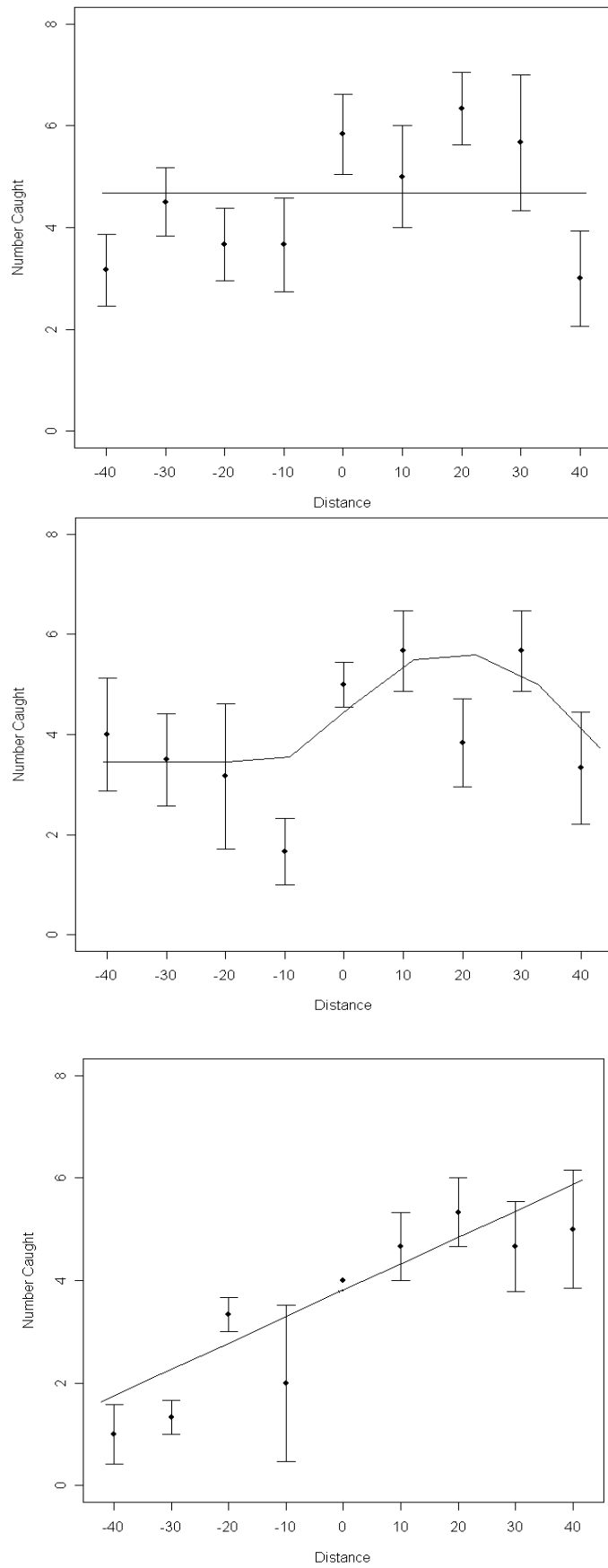


Figure 6: Average number caught across all transects and repeats along the grassland/edge/woodland transects, with best fit model line shown for a) *N. brevicollis* b) *A. parallelepipedus* and c) *P. madidus*.

Table 3: Best fit model results for *Abax parallelepipedus* enclosed transect captures. Response refers to species, transect number and first or second repeat. APave is the average of all transects and repeats. Percentage values in brackets are the AIC weights showing the probability of the model being the best fit.

Response	Null AIC	Linear AIC	Exponential AIC	Unimodal AIC	Best Model	F.value	P.value
AP1a	44.607 (10%)	41.226 (51%)	41.738 (39%)	-	Linear	5.73	0.048
AP1b	45.704 (68%)	47.224 (32%)	-	-	Null	-	-
AP2a	41.385 (55%)	41.806 (45%)	-	-	Null	-	-
AP2b	49.426 (73%)	51.397 (27%)	-	-	Null	-	-
AP3a	40.242 (32%)	38.707 (68%)	-	-	Linear	4.51	0.071
AP3b	46.910 (66%)	48.268 (34%)	-	-	Null	-	-
APave	33.137 (17%)	34.149 (29%)	-	31.889 (54%)	Unimodal	6.58	0.037

Table 2 shows 2 experimental repeats for *N. brevicollis* showed the linear model as the best fit model. However the AIC weights showed the null model still had a high probability of being the best model (35% for NB1b and 42% for NB3a). The average of all the transects and repeats also showed the null model was the best fit although it should be noted that with an AIC weight of 40% there was still considerable support for the linear model.

Table 3 shows that for *A. parallelepipedus* there were also 2 experimental repeats which showed the linear best fit model. AP3a showed a high probability of the null model being the best fit with an AIC weight of 32%. However there was less support for the repeat AP1a with only 10% probability of the null model being the best. The average of all the transects showed a unimodal model as the best fit for the average of all the data. Although the individual repeats showed most support for the null model the average unimodal model showed an edge effect with a midpoint of 16.84m and preference to woodland captures. This could be expected as this is a woodland species and may be expected to move slower and therefore be caught less in the unfamiliar grassland. However further analysis showed there was no significant difference between the average number of captures in the woodland and grassland ($t=0.830$, $df=34$, $P=0.412$), the woodland and edge habitats ($t=0.830$, $df=34$,

P=0.834) or the grass and edge habitats (t=-0.646, df=34, P=0.523). Therefore overall the null model was considered the best fit model overall for *A. parallelepipedus*.

As the null model appears to be the best fit overall for both species, a post hoc power analysis was undertaken to investigate the power of the sample size used in the experiments. The sample size for both the species shown above was 54 which is enough to uncover an effect size of 2.7 which is a medium effect size, based on power of 0.8 and a significance level of 0.05 (Cohen, 1988).

Pterostichus madidus

Table 4 shows significant results for *P. madidus* for transects PM1 and PM2 with best fitting logistic and linear models respectively. PM1 showed an edge effect midpoint of 19.5m in the grassland, extending just over 2m. Transect PM3 also showed a linear best fit model but this did not have a significant P value. The Akaike weights for the null models showed smaller probabilities than the logistic or linear models of being the best fit in all 3 transects.

The average of the 3 transects showed very little difference in AIC values between the linear (AIC weight 62%) and logistic models (AIC weight 38%). With considerable support for the linear and logistic models for this species it is clear that an edge effect could be interpreted from these results.

Table 4: Best fit model results for *Pterostichus madidus* enclosed transect captures. Response refers to species, transect number and first or second repeat. PMAve is the average of all transects and repeats. Percentage values in brackets are the AIC weights showing the probability of the model being the best fit.

Response	Null AIC	Linear AIC	Logistic AIC	Best Model	Preference	F.value	P.value
PM1	36.213 (10%)	28.937 (37%)	28.243 (53%)	Logistic	Woodland	26.06	0.001
PM2	44.267 (26%)	33.310 (42%)	35.901 (32%)	Linear	Woodland	22.53	0.002
PM3	40.037 (19%)	38.012 (53%)	39.328 (28%)	Linear	Woodland	3.95	0.087
PMAve	37.512 (<0.001%)	24.267 (62%)	25.237 (38%)	Linear	Woodland	14.32	0.007

P. madidus was significantly more likely to be captured in the woodland than the grassland in the enclosed transects ($z=3.419$, $df=16$, $<P=0.001$). A mixed effects model with habitat as a fixed effect showed that distance within habitat was by far the most important component of overall variance with 99% of the total variance, site was insignificant. More individuals were also caught at the edge than in the grassland ($t=-2.194$, $df=16$, $P=0.043$). However there is no significant difference between numbers caught in the woodland and numbers caught at the edge ($z=1.474$, $df=16$, $P=0.14$).

3.4 Indicator values

The indicator values calculated are shown in Table 4. A value of over 25% indicates a good indicator species for that habitat (Legendre & Legendre, 1998). In the case of *N. brevicollis* and *A. parallelepipedus* the open transects show a strong degree of habitat specialisation towards the woodland habitats and with *A. parallelepipedus* also showing as a good indicator of edge habitat. However the enclosed transects eradicate this specialisation showing each of the species as a good indicator species across all 3 habitats.

P. madidus has open transect indicator values showing it is a good indicator species for woodland and edge habitats but only just exceeds the 25% limit for grassland. The enclosed transect shows it is a poor indicator species for grassland. However due to this species being caught less in the grassland it is likely that the indicator values for this habitat in the open transect is underestimated.

Table 5: Indicator values for enclosed and open habitats for each species.

Species	Treatment	Woodland	Edge	Grassland
<i>P. madidus</i>	Open	48	26.96	25.05
	Enclosed	44.33	31.52	16.75
<i>N. brevicollis</i>	Open	46.33	12.67	0
	Enclosed	35.3	30.43	24.25
<i>A. parallelepipedus</i>	Open	52.4	32.94	3.57
	Enclosed	31.16	34.42	30

3.5 Habitat swap and disturbance experiments

The capture numbers of *P. madidus* from the habitat swap and disturbance experiments were analysed for the best fit model. The habitat swap experiment results are displayed in Table 6. It shows that the null model was the best fit for all 3 transects and the overall average. This

was unexpected as it was predicted that *P. madidus* would still show a tendency for more captures in the woodland habitat even though it was now positioned in the grassland.

Table 6: Best fit model results for *Pterostichus madidus* captures in the habitat swap experiment. Response refers to species, transect number and first or second repeat. PMAve is the average of all transects and repeats. Percentage values in brackets are the AIC weights showing the probability of the model being the best fit.

Response	Null AIC	Linear AIC	Logistic AIC	Unimodal AIC	Best Model	Preference	F.value	P.value
PM12	20.321	22.242	-	-	Null	Generalist	-	-
PM22	26.657	28.317	-	-	Null	Generalist	-	-
PM32	20.321	22.002	24.594	23.624	Null	Generalist	-	-
PMAve2	37.504	39.445	-	-	Null	Generalist	-	-

Table 7 shows the results for the disturbed habitat experiment where the vegetation was removed and replaced in the same position. This was expected to show the same pattern as the original enclosed transect experiment, however the number of catches in the grassland was significantly different in the disturbed habitat experiment compared with the original enclosed transect experiment ($z=3.419$, $df=16$, $P=<0.001\%$). Transects PM1 and PM3 both show null models as the best fit. Transect PM2 and the average of all transects showed linear best fit models with a preference to being captured in the grassland. These results are different to the woodland preference shown in the original enclosed transect experiment and suggests that habitat disturbance has affected the outcome of the experiment and therefore the results of the swapped habitat experiment are unreliable.

Table 7: Best fit models for disturbed habitat experiment. Response refers to species, site and experiment number.

Response	Null AIC	Linear AIC	Exponential AIC	Best Model	Preference	F.value	P.value
PM13	27.890	29.428	31.239	Null	Generalist	-	-
PM23	31.225	26.378	-	Linear	Grassland	8.521	0.043
PM33	28.496	29.260	-	Null	Generalist	-	-
PMAve3	22.877	13.711	-	Linear	Grassland	4.509	0.101

4. Discussion

Using controlled populations in the field, this study has allowed comparisons of capture numbers across a grassland/woodland edge transect, between 3 common carabid species, as well as differences in frequency of capture between species.

The null hypothesis, that there is no significant variation in the catches of controlled, equal populations, across a grassland/woodland transect is supported by the capture numbers of *N. brevicollis*. The average number of captures for *A. parallelepipedus* showed that a false edge effect could be generated, despite individual repeats showing the null hypothesis. The null hypothesis seemed to be the most supported model with no significant difference in numbers caught between habitats. More repeats of the experiment would be necessary to obtain more data to enable small effects to be detected which would give more confidence in the results with this species. In this study 54 data points were obtained from 3 transects and 2 repeats on each transect for both *A. parallelepipedus* and *N. brevicollis*, but this number of data points only allowed enough power to detect medium sized effects; In order to detect a small effect size it would be necessary to have a sample size of 393 (Cohen, 1988) which would not have been feasible in this study.

This null hypothesis was disproved in the case of *P. madidus* which showed significant variation in capture numbers across the transect and was caught significantly more in woodland and edge habitats than grassland habitats. This showed a linear model best fit with support for the logistic model which could show that a spurious edge effect can be generated. Therefore the number of captures in the grassland in the open transects is likely to underestimate abundance due to the species propensity for less captures in this habitat. According to the number of captures from the enclosed transects *P. madidus* is 2.65 times more likely to be caught in the woodland than the grassland and 1.41 times more likely than at the edge than at the edge. If the open transect figures are adjusted to allow for this bias then the best fit model for the open transect would be null rather than the original best fit linear model. The difference between numbers caught in grassland and woodland would no longer be significantly different ($t=-2.467$, $df=4$, $P=0.069$) demonstrating how abundance data collected by pitfall trap sampling could be inaccurate.

A meta-analysis conducted by Brouwers & Newton (2009) on 11 carabid species, including *N. brevicollis* and *A. parallelepipedus*, suggests that woodland species move much more slowly than generalist species (only an average of 2.1m day⁻¹ compared with 11 m day⁻¹ in generalists). As movement and activity can affect pitfall trap captures (Desender & Malfaet, 1989), a higher movement rate in generalist species would predict that *P. madidus* would be more active and likely to be caught more frequently than the other 2 woodland species which has not been the case in this study. Here, capture rates (number of individuals captured per day) were used as an indication of movement and *P. madidus* was caught significantly less often than the other 2 species. This could indicate that broad trends for species grouped as generalists or woodland specialists may be inaccurate for some species.

The Brouwers & Newton (2009) meta-analysis also showed a wide range of movement rates from 5 – 18.4m day⁻¹ for generalist species with no attempt to analyse possible differences in environmental variables which could cause this variation. The results of the enclosed transect experiment suggest that generalist species could be more sensitive than woodland species to environmental variables such as habitat structure which affects their activity and could also possibly explain such a range of movement rates shown from meta-analysis.

The effect of habitat structure and density on capture rates has often been acknowledged (Phillips & Cobb, 2005; Spence & Niemela, 2004); unfortunately the follow up experiments in this study were unable to establish the importance of habitat structure and density in relation to capture rates across woodland/grassland transects, due to problems with conducting the experiment. Therefore the second null hypothesis, habitat structure does not influence the number of captures of carabid beetles across an edge transect, remains inconclusive. Vegetation density at all 3 sites in this study was greater in the grassland than in the woodland where the ground was mostly leaf litter with little other vegetation. Although this did not significantly affect the captures of the woodland species between habitats, it could be an explanation for the significant difference in number of captures between habitats for *P. madidus*, where distance within habitat was an important component in variance analysis.

Edge effect studies such as Phillips & Cobb (2006) have found a correlation between carabid abundance and vegetation cover using pitfall trapping methods. They looked at salvaged and unsalvaged forests and found a decrease in carabid abundance with increased percentage vegetation density. They particularly highlight *Pterostichus adstrictus*, a common generalist

species (Lindroth, 1969) as an example of decreased abundance with increased vegetation cover. However the *P. madidus* results show that this is not necessarily an indication of decreased abundance but merely lower movement rates and decreased captures.

Capture rates have been shown to be higher in larger bodied carabids than small bodied (Halsall & Wratten, 1988; Spence & Niemela, 1994). Brouwers & Newton (2009) also showed a positive correlation between movement and body size. The 3 species used in the enclosed transect experiment are medium to large sized carabids: *N. brevicollis* 11–14mm, *P. madidus* 14–18 mm and *A. parallelepipedus* 17-22mm (Luff, 2007). This would also incorrectly predict that *P. madidus* would be caught more frequently than the smaller species *N. brevicollis*.

It was noted during work with the carabids in this study that *P. madidus* often buries itself in soil where possible which was only occasionally noted in *A. parallelepipedus* and not seen in *N. brevicollis*. It is possible that these behavioural differences could have some impact on the movement rates and therefore the likelihood of capture.

It would be desirable to adjust carabid abundance data to account for species sensitivity to environmental variables affecting movement and capture numbers. Although this is a complex undertaking it has been attempted by Esch et al (2008). Using laboratory experiments with 11 forest carabid species they found positive correlations with the probability of pitfall trap capture and temperature and body size. These findings were then used to calculate correction factors for the effects, which when applied to field data from pitfall trap samples, increased the correlation with known or estimated field abundance. The enclosed transect experiment shows that some species may demonstrate more sensitivity than others to environmental variables and the development of correction factors may allow for more accurate abundance estimations in future studies. However it would be necessary to conduct these experiments on a wide variety of species to look for trends in woodland, grassland and generalist species and then it may still be necessary to judge this on a species by species basis.

4.1 Implications

The results of this study are particularly important for studies of edge effects where pitfall trapping is used to sample abundances and assemblages across 2 habitats separated by an edge. A spurious edge effect could be generated from data where generalist species demonstrate a bias for capture in one habitat over another.

Studies which have found higher carabid abundances in forests than grasslands (Kotze & Samways, 2001) could also have biased data if some species are caught less often in the grassland. Although some studies have found greater biodiversity in grasslands than woodlands (Molnar *et al*, 2001; Magura, 2002), grassland habitats are often perceived as less valuable than forest despite also being under anthropogenic pressures from fragmentation and farming (Kotze, 2001). If other carabid species are caught less in grasslands as with *P. madidus* it could mean that diversity or abundance in grasslands could be underestimated.

Forests are often thought to be a vulnerable habitat to the negative effects of edges (Murcia, 1995). Although the enclosed transect data for *A. parallelepipedus* generally showed the null model, the average of all repeats showed a false unimodal edge effect. This was not considered to be supported by the probability of the best model fit or the results of the individual transect repeats. However it could indicate that there are small effects which were not detected in this study. It is therefore possible that further research with more sample power could show other species are caught less in forest than grassland. This could also mean some abundances or biodiversity in forests could also be underestimated.

The limitations of pitfall trapping have been previously been widely discussed and acknowledged. This study supports previous suggestions that carabid abundances and assemblages estimated from pitfall traps must be interpreted with due respect to the biology of the species and the limitations of pitfall trapping (Spence & Niemela, 1994). This is especially important where abundance and biodiversity of carabids are used as bioindicators for more general biodiversity which could influence policy or habitat management (Morecroft *et al*, 2009).

4.2 Limitations

The major limitation of this study was the lack of success conducting the habitat swap and control habitat disturbance experiments which failed to show habitat structure affecting the number of *P. madidus* individuals caught. Previous studies had indicated that carabids are sensitive to vegetation disturbance (Shibuya et al, 2008) and the control disturbance experiment in this study showed that the disturbance of digging and moving the habitat affected the results. It was necessary to move the habitat by hand in more than one section due to equipment restrictions which could be the reason for the disruption. The habitat swap experiments could be more successful if the habitat sections could be removed and moved in one section, possibly through the use of a turf strimmer or earth moving equipment, to cause minimum disturbance to the structure. The habitat was also disturbed during a particularly hot and sunny period which meant the grassland vegetation quickly wilted once moved and therefore did not provide exactly the same habitat structure. Disturbing habitat during cooler spells could help with the survival of the vegetation to make the habitat more comparable.

Other environmental variables can effect carabid responses such as moisture (Koivula, 2002) and warm microclimate which has been shown to correlate with more pitfall catches (Honek, 1988, Botes et al, 2007). Distance from edge can effect such environmental variables (Didham *et al*, 1998) and future studies using the same enclosed transect technique could benefit from measuring surface temperature and soil moisture to enable these variables to be considered in analysis. These were not measured in this study due to equipment and time limitations.

Before the experiments were conducted the carabids were retained outside in enclosures the same as those used in the enclosed transect experiment. They were fed on natural food such as caterpillars and small slugs. However, due to the numbers of beetles captured it was impossible ensure all individuals were fed equally. Previous studies have demonstrated an increase in the activity of starved carabid beetles over satiated individuals (Forneau & Loreau, 2001; Lenski, 1984). Although no beetles used in this experiment were starved it is recognised that some may have been less satiated than others. This could affect the movement rates of individuals and therefore the likelihood of capture, although the affect in this experiment should be limited due to the beetles being chosen at random. Beetles could be retained in a laboratory environment to ensure equal food allocation but the unnatural environment could also affect their natural behaviour on release.

Despite some small differences in vegetation, the three sites in this study had no significant affect on the variation in catches across transects. However the scale of the study limited the siting of all transects to within Silwood Park in Berkshire. Further research in other areas and habitats would be useful to see if the results are indicative of more general habitat types.

As previously mentioned the 3 species used in this study are medium to large sized carabids. The experiments would be difficult to conduct with smaller carabids due to difficulties ensuring the area is clear of naturally occurring individuals before the experiment can begin and also finding the uncaught carabids after the experiment ends.

4.3 Further research

Repeats of the enclosed transect experiment with other species would indicate whether *P. madidus* is an exception or if other species demonstrate a similar preference for capture in one habitat over another. It would be particularly useful to focus future research on other generalist species and also grassland specialists. A potential grassland species in the Silwood area is *Poecilus cupreus*; this species was not abundant at the time of commencing live captures of carabids in early April but appeared to be caught more frequently later and was caught exclusively in the grassland.

Although capture rates in grassland and woodland were significantly different in this study for *P. madidus* the rate of individuals caught per day can only be considered an indication of their actual movement rate. A more accurate method of examining movement would be the use of radio tracking which has previously been used by Charrier *et al* (1996) in a study on the movement rates of *A. parallelepipedus*. That study compared 4 different woody habitats and found that mean distances per unit of time decreased as vegetation cover decreased. Radar tracking was also used by Wallin and Ekbohm (1988) to compare movement rates and showed some species moved faster than others. Radio tracking of *P. madidus* in both woodland and grassland would allow a comparison of actual movement rates in the two habitats.

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APPENDIX

1A Experiment 1

Table 8: Enclosed transect capture numbers for *P. madidus*

Distance	Transect Number		
	1	2	3
40	5	7	3
30	6	5	3
20	4	6	6
10	6	4	4
0	4	4	4
-10	5	0	1
-20	3	3	4
-30	2	1	1
-40	2	1	0

Table 9: Enclosed transect capture numbers for *N. brevicollis*

Distance	Transect	Caught	Distance	Transect	Caught
40	1a	6	40	1b	3
40	2a	5	40	2b	1
40	3a	3	40	3b	0
30	1a	8	30	1b	8
30	2a	8	30	2b	2
30	3a	7	30	3b	1
20	1a	3	20	1b	6
20	2a	8	20	2b	7
20	3a	7	20	3b	7
10	1a	7	10	1b	5
10	2a	8	10	2b	5
10	3a	4	10	3b	1
0	1a	7	0	1b	7
0	2a	8	0	2b	4
0	3a	6	0	3b	3
-10	1a	6	-10	1b	4
-10	2a	5	-10	2b	5
-10	3a	2	-10	3b	0
-20	1a	2	-20	1b	4
-20	2a	7	-20	2b	3
-20	3a	3	-20	3b	3
-30	1a	7	-30	1b	4
-30	2a	4	-30	2b	2
-30	3a	5	-30	3b	5
-40	1a	3	-40	1b	2
-40	2a	6	-40	2b	3
-40	3a	1	-40	3b	4

Table 10: Enclosed transect capture numbers for *A. parallelepipedus*

Distance	Caught	Transect	Distance	Caught	Transect
40	7	1a	40	3	1b
40	3	2a	40	6	2b
40	1	3a	40	0	3b
30	4	1a	30	3	1b
30	7	2a	30	8	2b
30	5	3a	30	7	3b
20	5	1a	20	4	1b
20	5	2a	20	0	2b
20	3	3a	20	6	3b
10	5	1a	10	7	1b
10	6	2a	10	7	2b
10	2	3a	10	7	3b
0	4	1a	0	4	1b
0	6	2a	0	6	2b
0	4	3a	0	6	3b
-10	0	1a	-10	1	1b
-10	3	2a	-10	0	2b
-10	2	3a	-10	4	3b
-20	0	1a	-20	8	1b
-20	1	2a	-20	3	2b
-20	7	3a	-20	0	3b
-30	1	1a	-30	2	1b
-30	2	2a	-30	7	2b
-30	5	3a	-30	4	3b
-40	4	1a	-40	0	1b
-40	5	2a	-40	8	2b
-40	5	3a	-40	2	3b

Table 11: Catch rates for *A. parallelepipedus*

Distance	Transect	Rate	Habitat	Distance	Transect	Rate	Habitat
40	AP1a	1	Wood	40	AP1b	0.428571	Wood
40	AP2a	0.714286	Wood	40	AP2b	0.166667	Wood
40	AP3a	0.166667	Wood	40	AP3b	0	Wood
30	AP1a	0.571429	Wood	30	AP1b	0.428571	Wood
30	AP2a	1.142857	Wood	30	AP2b	0.333333	Wood
30	AP3a	0.833333	Wood	30	AP3b	1	Wood
20	AP1a	0.714286	Wood	20	AP1b	0.571429	Wood
20	AP2a	1.142857	Wood	20	AP2b	1.166667	Wood
20	AP3a	0.5	Wood	20	AP3b	0.857143	Wood
10	AP1a	0.714286	Edge	10	AP1b	1	Edge
10	AP2a	1.142857	Edge	10	AP2b	0.833333	Edge
10	AP3a	0.333333	Edge	10	AP3b	1	Edge
0	AP1a	0.571429	Edge	0	AP1b	0.571429	Edge
0	AP2a	1.142857	Edge	0	AP2b	0.666667	Edge
0	AP3a	0.666667	Edge	0	AP3b	0.857143	Edge
-10	AP1a	0	Edge	-10	AP1b	0.142857	Edge
-10	AP2a	0.714286	Edge	-10	AP2b	0.833333	Edge
-10	AP3a	0.333333	Edge	-10	AP3b	0.571429	Edge

Table 12: Catch rates for *N. brevicollis*

Distance	Transect	Rate	Habitat	Distance	Transect	Rate	Habitat
40	NB1a	0.857143	Wood	40	NB1b	0.428571	Wood
40	NB2a	0.714286	Wood	40	NB2b	0.166667	Wood
40	NB3a	0.428571	Wood	40	NB3b	0	Wood
30	NB1a	1.142857	Wood	30	NB1b	1.142857	Wood
30	NB2a	1.142857	Wood	30	NB2b	0.333333	Wood
30	NB3a	1	Wood	30	NB3b	0.142857	Wood
20	NB1a	0.428571	Wood	20	NB1b	0.857143	Wood
20	NB2a	1.142857	Wood	20	NB2b	1.166667	Wood
20	NB3a	1	Wood	20	NB3b	1	Wood
10	NB1a	1	Edge	10	NB1b	0.714286	Edge
10	NB2a	1.142857	Edge	10	NB2b	0.833333	Edge
10	NB3a	0.571429	Edge	10	NB3b	0.142857	Edge
0	NB1a	1	Edge	0	NB1b	1	Edge
0	NB2a	1.142857	Edge	0	NB2b	0.666667	Edge
0	NB3a	0.857143	Edge	0	NB3b	0.428571	Edge
-10	NB1a	0.857143	Edge	-10	NB1b	0.571429	Edge
-10	NB2a	0.714286	Edge	-10	NB2b	0.833333	Edge
-10	NB3a	0.285714	Edge	-10	NB3b	0	Edge
-20	NB1a	0.285714	Grass	-20	NB1b	0.571429	Grass
-20	NB2a	1	Grass	-20	NB2b	0.5	Grass
-20	NB3a	0.428571	Grass	-20	NB3b	0.428571	Grass
-30	NB1a	1	Grass	-30	NB1b	0.571429	Grass
-30	NB2a	0.571429	Grass	-30	NB2b	0.333333	Grass
-30	NB3a	0.714286	Grass	-30	NB3b	0.714286	Grass
-40	NB1a	0.428571	Grass	-40	NB1b	0.285714	Grass
-40	NB2a	0.857143	Grass	-40	NB2b	0.5	Grass
-40	NB3a	0.142857	Grass	-40	NB3b	0.571429	Grass

Table 13: Catch rates for *P. madidus*

Distance	Transect	Rate	Habitat
40	PM1	0.357143	Wood
40	PM2	0.538462	Wood
40	PM3	0.214286	Wood
30	PM1	0.428571	Wood
30	PM2	0.384615	Wood
30	PM3	0.214286	Wood
20	PM1	0.285714	Wood
20	PM2	0.461538	Wood
20	PM3	0.428571	Wood
10	PM1	0.428571	Edge
10	PM2	0.307692	Edge

10	PM3	0.285714	Edge
0	PM1	0.285714	Edge
0	PM2	0.307692	Edge
0	PM3	0.285714	Edge
-10	PM1	0.357143	Edge
-10	PM2	0	Edge
-10	PM3	0.071429	Edge
-20	PM1	0.214286	Grass
-20	PM2	0.230769	Grass
-20	PM3	0.285714	Grass
-30	PM1	0.142857	Grass
-30	PM2	0.076923	Grass
-30	PM3	0.071429	Grass
-40	PM1	0.142857	Grass
-40	PM2	0.076923	Grass
-40	PM3	0	Grass