Ann. Zool. Fennici 33: 185–195 ISSN 0003-455X
Helsinki 14 June 1996

Use of Carabids as environmental indicators in grasslands and cereals

Martin L. Luff

Luff, M. L., Department of Agricultural & Environmental Science, University of Newcastle upon Tyne, NE1 7RU, UK

Received 7 September 1995, accepted 24 January 1996

Recent work on Carabidae of grasslands and cereals in northern Europe is summarised. In cereals, the biology and role of individual carabids in pest management has been studied in some detail. Grassland studies have concentrated more on classifying the assemblages present, and relating the fauna to environmental conditions and vegetation management. This information is used in the ecological evaluation of grassland habitats. Recent works emphasize landscape features and pattern in the agricultural environment. Examples are given of the author's studies on: pitfall trapping for assessing carabid assemblages; management effects on grassland carabids; multivariate analyses of carabids in UK cereals. A prime need is for further work on individual carabid biologies and population dynamics.

1. Introduction

Grasslands (in the widest sense) and cereal fields were grouped together by Thiele (1977) as 'open country', when he listed and ranked the typical carabid species of these habitats; this list was updated in the review of carabids in agriculture by Luff (1987) and for Eastern European crop fields by Lövei and Sarospataki (1990). The possible importance of carabids as pest control agents has been evident since the classical works of Balduf (1935) and Forbes (1883) in north America. In northern Europe, there has been much emphasis on their role as predators on aphids in cereals (e.g. Sunderland & Vickerman 1980, Chiverton 1986, Lys & Nentwig 1991), and the biology of some of the dominant species has been studied (e.g. Wallin *et al*. 1992, Bilde & Toft 1994). The carabids of cereals have also been compared with those of other crops, both in terms of their diversity patterns (Booij 1994) and species composition (Hance & Gregoire-Wibo 1987). More recently, however, the actual importance of carabids in pest suppression has been questioned, compared with that of some aphid-specific predators (Winder *et al*. 1994), and the use of carabids in cereals has tended to be seen more in the wider context of their value as indicators of the diversity and 'naturalness' of the agricultural environment.

As the biological studies have shown the importance of field margins for carabids (e.g. Desender *et al*. 1981, Sotherton 1985) recent workers have also considered the overall landscape within which the beetle populations exist, and the role of landscape features in enabling their persistence and dispersal (e.g. Den Boer 1977, Burel 1992, Cardwell *et al.* 1994, Kiss *et al.* 1994, Lys *et al.* 1994, Frampton *et al.* 1995, Mauremooto *et al.* 1995). Rough field margins and hedgerows both increase the overall carabid diversity; the use of artificial 'grass strips' in fields to mimic field boundaries has also been tested (Thomas *et al.* 1991, Lys & Nentwig 1992), and enables overwintering of species that would not otherwise survive within the field itself.

Although cereal fields are only a form of artificial grassland, they differ from most grasslands in two important features: (i) there is drastic soil disturbance during annual cultivations; (ii) there are substantial seasonal changes in soil surface microclimate and availability of prey as the crop grows. Even on a small scale, these differences distinguish the carabid assemblages of grassland and arable land (Luff 1990, Cárcamo *et al.* 1995). Within grasslands, there is a transition from the fauna of intensively managed agricultural pastures to the 'natural' ground beetle assemblages of semi-natural un-managed grassland and moorland. The carabid assemblages of this range of habitats in northern England can be classified according to site management, soil water and bulk density, and altitude (Luff *et al.* 1992). The responses of individual species to these factors has also been modelled (Rushton *et al.* 1991). Although the role of carabids as pest control agents in grasslands has been considered (e.g. Asteraki 1993), the wider range of habitat types included within the term 'grassland' has led to attempts to use carabid assemblages to characterize these habitats, often as an aid to evaluate their conservation value (e.g. Rushton *et al.* 1990, Maelfait & Desender 1990). The biology of many species in managed grasslands has been studied in Belgium, where such work in all agricultural habitats has been reviewed by Alderweireldt and Desender (1994).

The conclusions of this brief review of recent studies on Carabidae of grasslands and cereals are that, in cereals, although there is much data on the fauna of particular fields and crops, there is no overall classification of the carabid fauna according to their physical, environmental or geographical factors. The details of the biology of many species have been studied; they may often feed on pest insects, but quantitative data on their actual impact in pest management still remains somewhat scarce. In terms of their 'use', one can only hope that the types of landscape management advocated in recent work will increase the diversity and abundance of carabids, and increase their potential if not necessarily their actual value to agriculture.

In grasslands, possibly due to the wider range of habitats covered, such classifications of the carabid fauna do exist, although doubtless they should continue to be refined. There is, as yet, little evidence of any pest management benefit of grassland carabids; their 'use' in grassland habitats has been more in habitat evaluation and assessing conservation value. The aims of this paper are to highlight some recent work in these areas with which the author has been involved, to indicate further gaps in our knowledge of the carabid biology and ecology of grassland and cereal fields, and to encourage further critical consideration of some of the methodology commonly used in such work. The topics covered are somewhat disparate, but it is hoped that the, often preliminary, data presented will stimulate further and more detailed studies.

2. Pitfall trapping efficiency

A majority of studies on ground beetles of open habitats rely on this technique (reviewed by Adis 1979) for assessing the species present, although it is only one of a range of available methods for estimating carabid (and other invertebrate) densities (see Sunderland *et al.* 1996). Many authors (cited in the Introduction) proceed to use pitfall catches either as a relative measure of population densities, or in order to calculate assemblage characteristics such as diversity. The use of a seasonal pitfall catch as population size may be applicable to a given species in a particular habitat (Baars 1979, but see also Ericson 1979, Chiverton 1984), but comparison of pitfall catches between species is confounded by the differing rates of movement, activity periods and trappability of each species. Halsall and Wratten (1988) have shown that the trappability of many species is in fact very low, and that many individuals of some species can hang by their tarsi on the lip of the trap, and then climb out. In order to obviate this, a test was carried out on a modified trap, and preliminary results on carabid catches are presented here.

2.1. Method

Two sets of ten plastic pitfall traps, 8.5 × 10 cm (diam. × depth) , were installed at 5 m intervals in, respectively, a weedy cereal plot and a rough grassy bank near Newcastle upon Tyne, UK. Traps were part- filled with commercial anti-freeze as a preservative. Five traps in each set (selected randomly) were covered with curved funnels made by heat-deforming the lid of a 9 cm diameter plastic petri dish, and cutting off the pointed end of the resulting cone. The intention was to remove any definite 'lip' at the edge of the trap, so that beetles could not hang on to the trap edge. A secondary benefit was to make it more difficult for captured beetles to escape from the trap.

The traps were emptied weekly for a four week period from 9 May to 6 June, and the funnels were alternated between individual traps in each week.

2.2. Results

In both habitats, the funnel-covered traps caught both more species and individuals/week (Fig. 1) than the un-modified ones. The difference in numbers of individuals caught was greater than in the numbers of species, especially in the more open cereal field. By the fourth week the rate of species accretion had slowed in all but the covered arable traps, suggesting that increasing the trapping efficiency may increase the overall estimate of species richness. More detailed data on the catches of individual carabid species, and the catches of other invertebrate taxa, will be published elsewhere.

3. Assessing carabid diversity

Dritschilo and Erwin (1982) concluded that diversity indices were not useful when using carabids in impact assessments; although agricultural management affected both species richness and the total numbers caught, the overall effect on diversity statistics was minimal. Despite this, diversity calculations continue to be used to demonstrate changes in carabid assemblages, such as between crops and field margins (Kiss *et al.* 1993). Some pragmatic thoughts on diversity statistics, pitfall catches and Carabidae are presented here.

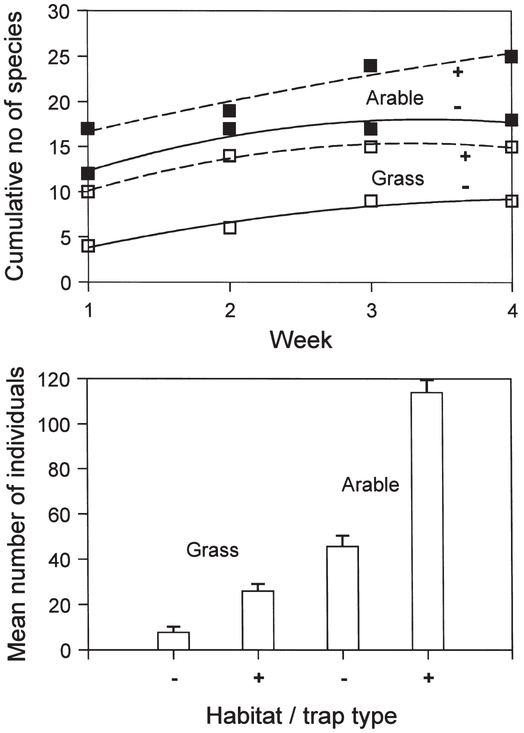

Fig. 1. Cumulative numbers of carabid species caught over four weeks, and mean numbers of individuals caught per week (+*S.E.*), using pitfall traps with (+) and without (–) curved funnel covers, in grass and arable habitats.

3.1. Method

If indices of diversity are to be useful for assessing carabid assemblages, they must respond to changes in the carabid fauna that result from environmental changes. Diversity indices, whatever their theoretical model, essentially incorporate the relationships between three parameters: the number of species present (species richness), the number of organisms present (total population size) and the distribution of these organisms between the species (evenness). Data from May to October catches of carabids from 69 sets of nine (un-covered) pitfall traps in grasslands and moorland (details in Luff *et al.* 1992) were examined to see the relationships between these statistics, and to what extent they varied between grassland habitat groups previously identified using TWINSPAN analyses. The measures used were numbers of species, individuals (transformed to natural logs because of the skew distribution of catches), 'diversity' (Williams' alpha) and evenness. The latter was calculated by plotting, for each site, the log catch of each species in decreasing order of rank (Southwood *et al.* 1979), and calculating, by linear regression, the absolute value of

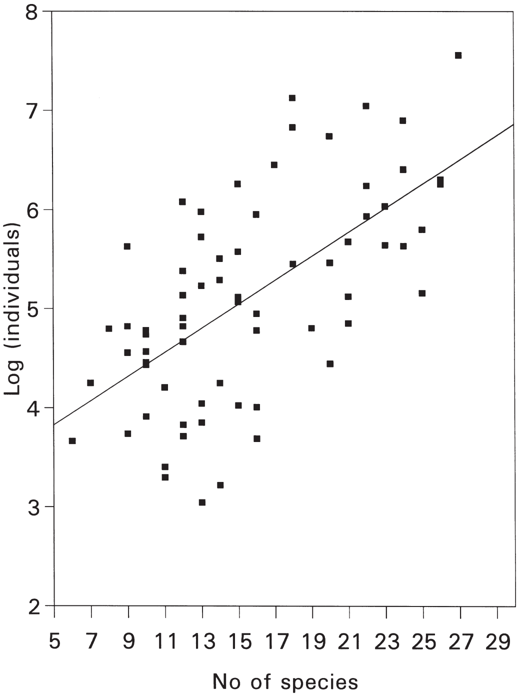

Fig. 2. Natural logarithm of numbers of carabids caught in 69 grassland sites, plotted against numbers of species found, with fitted regression line.

the slope of the relationship. This (negative) slope will be zero if all species have equal catch, and its value becomes increasingly negative as the evenness decreases.

3.2. Results

Table 1 gives the mean values of the numbers of species, log individuals, alpha and evenness slope for each of the ten grassland groups previously recognised, together with the *F* and *P* values for one-way analyses of variance between habitat groups.

Only the log-transformed numbers caught differed significantly between habitat groups, being greatest in group 7 (intensively managed lowland pastures) and lowest in group 10 (managed upland pastures), suggesting purely an effect of altitude on beetle activity. In fact, despite the non-significant effect of group on species richness, these groups had almost the same ranking in this parameter. A plot of log-catch against species richness (Fig. 2) shows an apparently bivariate normal distribution, with a significant positive correlation ($r_{67} = 0.627$, $P < 0.001$).

The scatter about the trend line in Fig 2 suggests that an alternative means of assessing the 'diversity' of each site, in terms of the relative numbers of species and individuals, would be to use the distance of each point (i.e. site) in the scatter plot from the trend line. Points most above the line have more individuals caught per species than might be expected, and vice versa. This was quantified by calculating the standardised residuals of each site from the fitted linear regression of log-catch on number of species. These residuals were then analysed by ANOVA as for the original data in Table 1: there was a significant effect of habitat group ($F_{9,59} = 3.97, P < 0.001$) with the extremes again being groups 7 (residual + 1.0072) and 10 (residual – 0.9966). This measure of relative numbers of individuals and species caught was therefore a better way of assessing between habitat type differences in the diversity of the carabid assemblages, than were conventional statistics such as alpha and the calculation of evenness. It is, in effect, an analysis of co-variance, with log (number of individuals caught) as a co-variable. Surprisingly however, a similar analysis, using the more usual convention of species richness (y) plotted against log (catch) (x) did not yield significant habitat group differences.

As this measure combines both species richness and evenness, it could also be compared with indices such as Simpson of , or with the calculation of expected species richness using rarefaction: Both parameters (slope and itercept) of the species rank/log (catch) could also be tested. Such comparisons, using a larger data set, will be the subject of a later paper.

Table 1. Species richness, diversity (Williams' 'alpha') and 'evenness' of carabids of 10 grassland habitat groups, together with calculated $F_{9,59}$ and P-values from one-way analyses of variance between habitat groups.

Group	Species	log(indivs)	'diversity'	'evenness'
1	17.2	4.87	6.06	0.179
2	11.5	4.03	4.87	0.189
3	16.8	4.79	5.36	0.183
4	16.8	5.57	4.65	0.246
5	13.5	4.93	3.52	0.304
6	21.0	5.76	4.98	0.194
7	15.5	5.91	3.23	0.307
8	14.8	5.24	3.96	0.280
9	14.7	4.63	5.26	0.212
10	10.2	3.65	4.81	0.249
F-statistic	1.60	4.03	1.13	1.87
P-value	0.13	< 0.001	0.35	0.07

4. Effects of grassland management on carabid assemblages

Indices of assemblage structure, considered in the previous section, take no account of differences in actual species composition between grasslands. Several studies (see Introduction) have considered grassland management effects on ground beetles at both the species and assemblage levels. The aim of this section is to present outline results from two 'case studies' with which the author has been involved, in order to pose questions about the way in which such assemblage data can be considered. The first example arises from the installation of a gas pipeline under coastal dune grassland in northern England, the second concerns the effects of changing management of upland pasture in Wales. In both cases only brief and preliminary details are given at this stage.

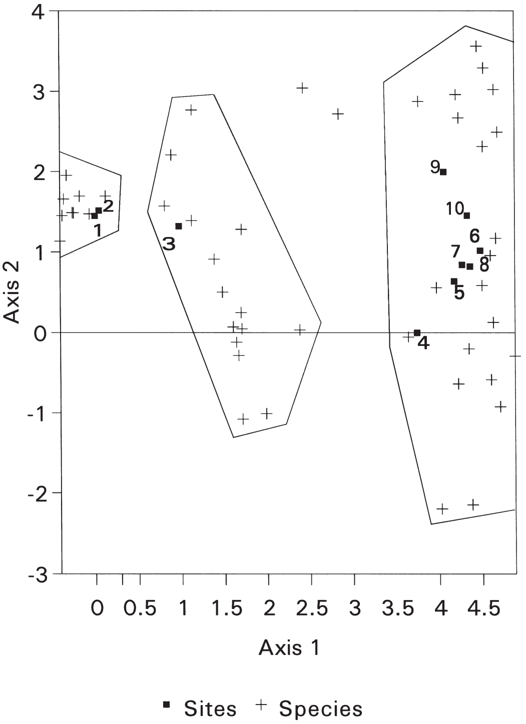

Fig. 3. First two axes of DECORANA ordination of actual pitfall catches from 10 sets of traps in coastal grassland at Coatham, Yorkshire. Sets of traps are numbered (odd numbers = after disturbance, even numbers = un-disturbed). Species have been grouped visually into three groups (excepting two outliers).

4.1. Lowland disturbance

4.1.1. Site and method

At Coatham Common, north Yorkshire, a natural gas pipeline was installed in 1990 under an area of coastal grassland, salt marsh and dunes. In 1995, pitfall traps have been used to compare the carabid assemblages on the disturbed and un-modified habitats at various distances from the actual shore line. At each of 5 pairs of sites, 10 traps were operated from May–July 1995, part-filled with ethylene glycol and emptied monthly. Sites 1 and 2 were furthest (ca 500m) from the coast, in wet dune slack, sites 9 and 10 were on the fore dunes just above the beach; all odd-numbered sites were in the disturbed area, even-numbered ones were in corresponding un-disturbed grassland. The carabid fauna of each site was ordinated using DECORANA, in order to assess visually the relationships between the assemblages present; species richness and evenness (see previous section) were also compared using analyses of variance. Correspondence analysis was used in these analyses for its ability to plot species and site scores in the same multidimensional space, and detrending was used because the considerable turnover in species occurrence across the sites was otherwise likely to result in the second axis scores becoming a function of those of the first axis (see Ter Braak 1988).

4.1.2. Results

An ordination of the actual pitfall catches (Fig. 3) shows that sites 1–3 were very distinct from the remainder; they had substantial numbers of 'wet' species such as *Pterostichus nigrita*, *Stenolophus mixtus*, *Bembidion clarki*, *Dyschirius luedersi*, *D. globosus*, and *Elaphrus cupreus*. Site 3 also had substantial numbers of *Asaphidion flavipes* and *Nebria salina*. Site 4 was quite unlike 3, and still somewhat separated from the remaining more coastal sites, with large catches of common, inland dry grassland species such as *Badister bipustulatus*, *Amara aenea*, *A. communis*, *A. tibialis* and *Metabletus foveatus*. The last two of these species were also present in the more coastal sites 5–8, but in smaller numbers; they were overshadowed by large catches of the specialist coastal species *Amara spreta*, as well as *A. lucida*, *Calathus erratus*, *C. mollis,* and *C. ambiguus*. The most littoral sites, 9 and 10 were again somewhat separate in the ordination, and were characterised by larger catches of *Demetrias atricapillus*, *Broscus cephalotes*, and *Dromius linearis*. Axis 1 of the ordination appears to represent a moisture gradient, with the dryer sites at the right separating on axis 2, with the more coastal assemblages further up this axis. The species ordination (Fig. 3) thus divides the beetles into three more or less distinct groups, namely 'wet', 'dry inland' and 'dry coastal', based on the known habitat preferences of the species.

This analysis was carried out on actual pitfall catches, as the totals caught only varied by a factor of 3.5 from 132 beetles (site 9) to 472 (site 8). In previous work we have often standardised catches to percentages of the site total, so that the analysis shows up changes in species composition, rather than in actual numbers caught, or have used presence absence data alone. It could also be argued, however, that from the point of studying individual species, the proportion of the total catch of each species over all sites, rather than of each site over all species, should be analysed. Comparable analyses were therefore done on this premise, as well as on a combined percentage of contribution both to the site, and to the species total.

Table 2 shows that the percentage of variation explained by these alternative analyses was never more than by pitfall catch alone, and sometimes was considerably reduced. However, the data incorporating percentages of the species totals had inherently more variation, so that the actual amount of variation explained was greater than by using either pitfall catch, or percentage of the site totals. Ordination diagrams (not shown here) enabled rather similar conclusions to be drawn to those from the analysis of actual catch above, except in the case of presence/absence data, where the occurrence of most species over many sites, (but in greatly varying numbers) obscured the differences in their relative catch between sites, so that no conclusions were evident.

In no case were the effects of the pipeline disturbance consistently shown in the ordination plots. The only differences that could be detected between the undisturbed and disturbed sites were in their species richness (means: disturbed 22.6, undisturbed 19.0, $F_{1,8} = 5.27, P < 0.1$) and, more markedly in their evenness (means: disturbed – 0.152, undisturbed – 0.204, $F_{1,8} = 8.54, P < 0.02$). Thus the disturbed sites had more carabid species; their greater evenness was due to a longer 'tail' of species caught singly or in small numbers.

3.2. Upland management

3.2.1. Site and method

At Pwllpeiran E.H.F. in Wales, experiments involving mosaics of improved and semi-natural rough grazing are being run by the Agricultural Development and Advisory service (A.D.A.S.). Two sites, Parc-y-Llyn and Llechwedd Brith are subjected to two contrasting intensities of management: conventional management and fertilising is being compared with no further nitrogen and reduced grazing. Both sites of these experiments were sampled using pitfall traps in 1990, 1991, 1992 and 1993. The ground beetles pitfall catches were ordinated using DECORANA, and ground beetles axis scores from each treatment, year and site were compared statistically using analyses of variance.

3.2.2. Results

Ordination (Fig. 4) and analysis of the carabid assemblages showed highly significant differences between the axis 2 scores for each year ($F_{3,48} = 7.34$, $P < 0.001$) and significant differences between the two sites ($F_{1,48} = 7.34$, $P < 0.001$) and the treatments ($F_{1,48} = 5.51, P < 0.05$). Variation in axis 1, the main source of variation in the data was, however, only marginally related to the year ($F_{3,48} = 2.46, 0.05 < P < 0.1$) and not at all to treatment or the paddock. The striking

Table 2. Summary statistics from DECORANA analyses of carabids caught in coastal grasslands, according to the type of data analysed.

Data type	Cumulative % variance of species data				Total variation	Variation explained
	Axis: 1	Axis: 2	Axis: 3	Axis: 4		
catch	48.3	56.8	58.9	59.5	1.854	1.103
% of site total	45.0	55.3	58.4	59.1	1.929	1.140
% of species total	21.5	30.4	33.7	33.9	3.756	1.273
combined %	26.3	42.8	47.8	50.0	3.627	1.813
presence/absence	32.2	41.1	43.3	43.4	1.417	0.615

feature about Fig. 4 is the way in which the results for 1992 differ from the remaining years; it is evident that year to year variation in the carabid assemblage was greater than the (still significant) differences between sites and management regimes. Yet none of these factors was related to the major trend of variation in the data, as evidenced by axis 1 of the ordination. Not only is year to year variation clearly important (but often neglected in environmental assessment work), but the major factors responsible for variation in these ground beetle assemblages of upland grasslands remained unknown.

5. Multivariate analyses of cereals carabids

The above example of the use of carabids as indicators of environmental impact stresses the possible importance of year to year variations, and was at a larger scale than the coastal data presented in Section 4.1. Within cereals, Sanderson (1994) showed that variation in invertebrate assemblages within a single, whole farm experiment at Boxworth, UK, was largely (47%) explained by between year differences, and only secondarily (17%) by field and pesticide treatments. This analysis formed part of a wider survey of Carabidae in UK cereal fields, some results of which are now briefly considered.

5.1 Methods

Data from 149 cereals trials from eight different institutes were collated together. The earliest records were from general field surveys made by Horticulture Research International (formerly G.C.R.I. Littlehampton) in 1974. Most other institutes provided data from surveys or plot experiments made during the early to mid-1980s.

Only Carabidae were identified to species at all sites, with the full dataset for all dates containing 77 species of (adult) Carabidae. No species was ubiquitous to all sites, although *Agonum dorsale*, *Bembidion lampros*, *Notiophilus biguttatus*, *Pterostichus melanarius* and *Trechus quadristriatus* were all found at over 135 of the 149 sites. The mean starting date for sampling was 10th April, and the mean finishing date was 27th July, and so only pitfall trap records between these dates were used for the analyses.

Pitfall catches were converted to percentages of each species in the site totals and ordinated using DECORANA. The possible effects of sampling year and institute on the invertebrate community were investigated by Canonical Correspondence Analysis, using year and institute as nominal environmental variables. Detrending was not used in this analysis, as most taxa in fact occurred in many of the sites.

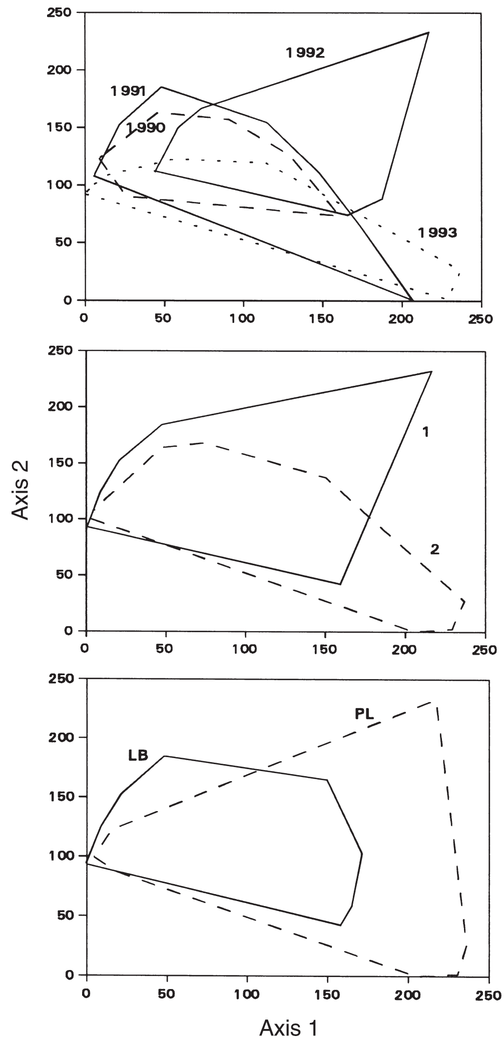

Fig. 4. First two axes of DECORANA ordinations of pitfalled sites from upland grazing land at Pwllpeiran, Wales. Polygons enclose sites grouped according to year, treatment (1 = conventional, 2 = reduced grazing, no added N) and site (LB, PL).

5.2 Results

The eigenvalues for the first two ordination axes were 0.546 and 0.369 respectively. The first ordination axis separated out several surveys made by Horticulture Research International in the late 1970's from the remainder, as well as fields in the Boxworth Project's Insurance pesticide regime. These Insurance fields also separated out from the remainder on the second ordination axis. The other two Boxworth pesticide regimes (Supervised and Integrated) did not appear to be particularly different in terms of their species composition from all the other sites in the analysis.

It was clear from the CCA that the year in which the survey was made was the most important factor affecting the Carabidae species composition at the sites. The eigenvalues for the first two ordination axes were 0.258 and 0.127 respectively; these are lower than the equivalent eigenvalues of the DCA because in CCA the ordination axes have been constrained by the environmental variables. The year of sampling had correlation coefficients with axes 1 and 2 of – 0.71 and – 0.25, respectively; the equivalent coefficients for the Institute from which the data were derived were – 0.66 and – 0.33, respectively. Again, therefore, year to year variation was the major factor affecting the carabid assemblages, even on a country-wide scale.

6. Discussion

These brief presentations of results of disparate pieces of work on ground beetles have in common the aim of facilitating better use of carabids in grasslands and cereals as indicators of the type and quality of their environment. It is clear, that if a short period of pitfall trapping is to be used to assess the carabid species richness of these habitats (as by Maelfait & Desender 1990), trapping efficiency should be as high as possible. The modified traps described here will give a larger and more diverse catch in a limited period. As species richness is one of the best discriminators between cropping systems (Booij 1994), methods that sample the full complement of species in a habitat as soon as possible are to be encouraged. The short trial data presented here are insufficient to show whether the potential species pool being sampled by the two types of trap was the same; rarefaction or other such models (see e.g. Lövei & Samu 1987) would be needed to examine this further.

Once the numbers of individuals as well as species collected from a site are considered, the species/catch relationship offers a further means of deriving information from the carabid fauna. It is perhaps not surprising that in the grassland data presented here, as for Dritschilo and Erwin (1982) in cornfields and Holliday (1993) in boreal forest, diversity statistics based largely on the relative numbers of species and log-individuals did not differ at all between habitat groups, despite the almost significant differences in evennesss. The evenness statistic tested here differs from the often used index of Hill (1973) in that it is largely dependent on the ‘tail’ of species that occur in small numbers. As these may represent occasional individuals of colonising species, the index is sensitive to site disturbance, followed by re-colonisation, as in the coastal study presented here, although it did not differ overall between the carabid assemblages of major grassland habitats.

In contrast, the residual deviance of the logarithm of numbers caught about the regression of log-catch on species numbers did respond significantly to habitat type. This statistic (in effect an analysis of covariance) would therefore merit further consideration as a measure of the extent to which the numbers of carabids caught at a site differ from the numbers expected based on the numbers of species caught. It is not based on any underlying theoretical models, other than the pragmatic transformation of catch to a logarithmic scale, but appears to be sensitive to changes in the carabid assemblages within grasslands. If it were quantified further in relation to the confidence bands around the regression, it would enable a measure of the ‘typicality’ of the species/numbers caught value for any site, analogous to typicality measurements that consider also the actual species composition of the fauna (Eyre & Rushton 1989).

Indices of diversity and evenness are based on theoretical distributions of actual population sizes among the assemblage of species present (reviewed in Magurran 1988, Loreau 1992). They do not, therefore, take account of one of the major differences between carabid species, namely their rate of movement, and hence the relationship between their density and pitfall catch. Loreau (1992) suggests that pitfall catch is a better measure than actual density of the species’ importance in a community, because it integrates population size, body mass and time of activity. However, rate of movement in any habitat is approximately correlated with body size (Thiele 1977) and taxonomic group (Forsyth 1983), so pitfall catches of each species of carabid could possibly be ‘corrected’ to a standard effective body length based on these factors, and alternative ‘diversity’ measures calculated. It remains to be seen whether these suggestions could improve the use of carabid ‘diversity’ measures in grassland habitats.

Data from the coastal grasslands at Coatham Common are an example of the possible use of carabids in short-term and small scale environmental assessments. The notable thing about the results was that only the moisture status of the ground had a major impact on the carabid assemblage (as with carabid distributions generally, Luff *et al*. 1989). The species composition had not changed consistently following the disturbance of pipeline installation, although the disturbed sites had a larger proportion of species caught singly or in low numbers, possibly because of the generally higher amount of bare ground, and the presence of possible colonising carabids. At this small scale, therefore, analysis of presence/absence species data gave little information, as occasional individuals of many species were found outside their 'normal' habitat. Analysis of assemblage 'structure' (i.e. species richness, evenness) was more helpful than assemblage 'composition' for detecting the effect of man's disturbance.

The longer-term and large scale analyses of the carabids of the Welsh upland management experiment and the UK cereal field data both suggest that the year in which the samples were collected was the most important factor affecting variation in the species composition of the fields. Sampling year probably acts as a surrogate environmental variable for the meteorological conditions of that season (and possibly the previous, over-wintering period). As well as the resulting, more or less synchronised changes in the catch of many species from year to year, there will be independent variations in each species' catch resulting from the species-specific population dynamics of each beetle species. The sensitivity of the overall assemblage to year to year variations will thus also depend in part on the variation in catch of each species from year to year (the Distribution of Population Sizes, den Boer 1977) which in turn is related to the dispersal strategies of the species involved, and the stability of their habitats. Thus in upland grasslands in northern England, the carabids of unmanaged moor and grass are stable from year to year, whereas the fauna of intensively managed 'improved' pasture varies widely according to the chance recolonisation of the fields after agricultural disturbance (Rushton *et al*. 1989).

In the wider analysis of cereal fields, however, all of which were subjected to annual cultivations, it was noticeable that, despite the plethora of pesticide and agronomic treatments that the fields had received, the only consistent pattern was that the Boxworth Insurance fields differed from the remainder. These fields received an exceptionally high pesticide load, one which would not be observed under normal agricultural practice, resulting in a very species poor invertebrate fauna (Sanderson 1994).

It would seem that the carabid assemblages of grasslands (in the widest sense) are inherently more variable than those of cereal fields; both the assemblage structure and species composition enable the use of ground beetles as environmental indicators in these habitats. The disparate topics considered in this paper attempt to show that there is still much to learn in our methodology and analysis of these carabid assemblages. Even given ideal sampling and analytical techniques, however, any short term assessments must, however, be considered within the larger, year to year changes resulting from the beetles' population dynamics: it is this area that carabidologists should be addressing in these, if not all, habitats.

Acknowledgements. The work described in this overview paper results from the efforts of many colleagues and Institutions, too numerous to list individually. In particular, thanks are due to Mick Eyre, Steve Rushton and Roy Sanderson, who have been closely involved, and to Alan Craig for field assistance. Work at A.D.A.S. farms was funded by the Ministry of Agriculture, Fisheries and Food; I am grateful to John Wildig for work at Pwllpeiran.

References

Adis, J. 1979: Problems of interpreting arthropod sampling with pitfall traps. — Zool. Anz. 202: 177–184.

Alderweireldt, M. & Desender, K. 1994: Belgian carabidological research on high-input agricultural fields and pastures: a review. — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: Ecology and Evolution: 409–415. Kluwer, Dordrecht.

Asteraki, E. J. 1993: The potential of carabid beetles to control slugs in grass clover swards. — Entomophaga 38: 193–198.

Baars, M. A. 1979: Catches in pitfall traps in relation to mean densities of carabid beetles. — Oecologia 41: 25–46.

Balduf, W. V. 1935 (reprinted 1969): The bionomics of entomophagous Coleoptera. — Classey, Hampton.

Bilde, T. & Toft, S. 1994: Prey preference and egg production of the carabid beetle Agonum dorsale. — Entomol. exp. et applic. 73: 151–156.

Booij, K. 1994: Diversity patterns in carabid assemblages in relation to crops and farming systems. — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. &

Maelfait, J.-P. (eds.), Carabid beetles: Ecology and Evolution: 425–431. Kluwer, Dordrecht.

Burel, F. 1992: Effect of landscape structure and dynamics on species diversity in hedgerow networks. — Landscape ecol. 6: 161–174.

Cárcamo, H. A., Niemelä, J. K. & Spence, J. R. 1995: Farming and ground beetles: effects of agronomic practice on populations and community structure. — Can. Entomol. 127: 123–140.

Cardwell, C. Hassall, M. & White, P. 1994: Effects of headland management on carabid beetle communities in Breckland cereal fields. — Pedobiologia 38: 50–62.

Chiverton, P. A. 1984: Pitfall-trap catches of the carabid beetle Pterostichus melanarius, in relation to gut contents and prey densities, in insecticide treated and untreated spring barley. — Entomol. exp. et applic. 36: 23–30.

— 1986: Predator density manipulation and its effects on populations of Rhopalosiphum padi (Hom.: Aphididae) in spring barley. Ann. appl. Biol. 109: 49–60.

Den Boer, P. J. 1977: Dispersal power and survival: carabids in a cultivated countryside. — Misc. Pap. Landbouwhogesch. Wageningen 14: 1–190.

Desender, K. Maelfait, J.-P., d'Hulster, M. & Vanhercke, L. 1981: Ecological and faunal studies on Coleoptera in agricultural land I. Seasonal occurrence of Carabidae in the grassy edge of a pasture. — Pedobiologia 22: 379–384.

Dritschilo, W. & Erwin, T. L. 1982: Responses in abundance and diversity of cornfield carabid communities to differences in farm practices. — Ecology 63: 900–904.

Ericson, D. 1979: The interpretation of pitfall catches of Pterostichus cupreus and Pt. melanarius (Coleoptera, Carabidae) in cereal fields. — Pedobiologia 19: 320–328.

Eyre, M. D. & Rushton, S. P. 1989: Quantification of conservation criteria using invertebrates. — J. appl. Ecol. 26: 159–171.

Forbes, S. A. 1883: The food relations of the Carabidae and Coccinellidae. Illinois State Lab. Natur. Hist. Bull. 1: 33–64.

Forsythe, T. G. 1983: Locomotion in ground beetles (Coleoptera Carabidae): an interpretation of leg structure in functional terms. — J. Zool., Lond. 200: 493–507.

Frampton, G. K., Cilgi, T., Fry, G. L. A. & Wratten, S. D. 1995: Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera, Carabidae) on farmland. — Biol. Conserv. 71: 347–355.

Halsall, N. B. & Wratten, S. D. 1988: The efficiency of pitfall trapping for polyphagous predatory Carabidae (Coleoptera). — Ecol. Entomol. 13: 293–299.

Hance, T. & Grégoire -Wibo, C. 1987: Effect of agricultural practices on carabid populations. — Acta Phytopath. Entomol. Hung. 22: 147–160.

Hill, M. O. 1973: Diversity and evenness: a unifying notation and its consequences. — Ecology 54: 427–431.

Holliday, N. J. 1993: The carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. — Can. J. Zool. 70: 440–452.

Kiss, J., Kádár, F., Kozma, E. & Tóth, I. 1993: Importance of various habitats in agricultural landscape related to integrated pest management: a preliminary study. — Landscape and Urban Planning 27: 191–198.

Kiss, J., Kádár, F., Tóth, I., Kozma, E. & Tóth, F. 1994: Occurrence of predatory arthropods in winter wheat and in the field edge. — Ecologie 25; 127–132.

Loreau, M. 1992: Species abundance patterns and the structure of ground beetle communities. — Ann. Zool. Fennici 28: 49–56.

Lövei, G. L. & Samu, F. 1987: Estimation of the number of carabid species occurring in a wet meadow. — Acta Phytopath. Entomol. Hung. 22: 399–402.

Lövei, G. L. & Sárospataki, M. 1990: Carabid beetles in agricultural fields in eastern Europe. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 87–93. Intercept, Andover.

Luff, M. L. 1987: Biology of polyphagous ground beetles in agriculture. Agric. Zool. Rev. 2: 237–278.

— 1990: Spatial and temporal stability of carabid communities in a grass/arable mosaic. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 191–200. Intercept, Andover.

Luff, M. L., Eyre, M. D. & Rushton, S. P. 1989: Classification and ordination of habitats of ground beetles (Coleoptera, Carabidae) in north-east England. — J. Biogeog. 16: 121–130.

— 1992: Classification and prediction of grassland habitats using ground beetles (Coleoptera, Carabidae). — J. Env. Management 35: 301–315.

Lys, J.-A. & Nentwig, W. 1991: Surface activity of carabid beetles inhabiting cereal fields. — Pedobiologia 35: 129–138.

— 1992: Augmentation of beneficial arthropods by strip-management 4. Surface activity, movements and activity density of abundant carabid beetles in a cereal field. — Oecologia 92: 373–382.

Lys, J.-A., Zimmerman, M. & Nentwig, W. 1994: Increase in activity density and species number of carabid beetles in cereals as a result of strip management. — Entomol. exp. appl. 73: 1–9.

Maelfait, J.-P. & Desender, K. 1990: Possibilities of short-term carabid sampling for site assessment studies. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 217–225. Intercept, Andover.

Magurran, A. 1988: Ecological diversity and its measurement. — Croom Helm, London.

Mauremooto, J. R., Wratten, S. D., Worner, S. P. & Fry, G. L. A. 1995: Permeability of hedgerows to predatory carabid beetles. — Agric. Ecosys. and Envir. 52: 141–148.

Niemelä, J., Ranta, E. & Haila, Y. 1985: Carabid beetles in lush forest patches on the Åland Islands, south-west Finland: an island-mainland comparison. — J. Biogeog.

12: 109–120.

Niemelä, J., Halme, E., Pajunen, T. & Haila, Y. 1986: Sampling spiders and carabid beetles with pitfall traps: the effect of increasing sampling effort. — Ann. Entomol. Fennici 52: 109–111.

Rushton, S. P., Luff, M. L. & Eyre, M. D. 1989: Effects of pasture improvement and management of the ground beetle and spider communities of upland grasslands. — J. appl. Ecol. 26: 489–503.

Rushton, S. P., Eyre, M. D. & Luff, M. L. 1990: The effects of management on the occurrence of some carabid species in grassland. — In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies: 209–216. Intercept, Andover.

Rushton, S. P., Luff, M. L. & Eyre, M. D. 1991: Habitat characteristics of grassland Pterostichus species (Coleoptera, Carabidae). — Ecol. Entomol. 16: 91–104.

Sanderson, R. A. 1994: Carabidae and cereals: a multivariate approach. — In: Desender, K., Dufrêne, M., Loreau, M., Luff, M. L. & Maelfait, J.-P. (eds.), Carabid beetles: Ecology and Evolution: 457–463. Kluwer, Dordrecht.

Sotherton, N. W. 1985: The distribution and abundance of predatory Coleoptera overwintering in field boundaries. — Ann. appl. Biol. 105: 423–429.

Southwood, T. R. E., Brown, V. K. & Reader, P. M. 1979: The relationships of plant and insect diversities in succession. — Biol. J. Linn. Soc. 12: 327–348.

Sunderland, K. & Vickerman, G. P. 1980: Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields. — J. appl. Ecol. 17: 389–396.

Sunderland, K. D., de Snoo, G. R., Dinter, A., Hance, T., Helenius, J., Jepson, P., Kromp, B., Lys., J. A., Samu, F., Sotherton, N. W., Toft, S. & Ulber, B. 1996: Density estimation for invertebrate predators in agroecosystems. — In: Toft, S. & Riedel, W. (eds.), Arthropod natural enemies in arable land. Density, spatial heterogeneity and dispersal: 133–164. Acta Jutlandica 70(2). Aarhus University Press, Aarhus.

Ter Braak, C. J. F. 1988: CANOCO – a FORTRAN program for canonical community ordination by partial detrended canonical correspondence analysis, principal components analysis and redundancy analysis. — Groep Landbouwwiskunde, Wageningen.

Thiele, H.-U. 1977: Carabid beetles in their environments. — Springer-Verlag, Berlin.

Thomas, M. B., Wratten, S. D. & Sotherton, N. W. 1991: Creation of "island" habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. — J. appl. Ecol. 28: 906–917.

Wallin, H., Chiverton, P. A., Ekbom, B. S. & Borg, A. 1992: Diet, fecundity and egg size in some polyphagous predatory carabid beetles. — Entomol. exp. appl. 65: 129–140.

Winder, L., Hirst, D. J., Carter, N., Wratten, S. D. & Sopp, P. I. 1994: Estimating predation of the grain aphid Sitobion avenae by polyphagous predators. — J. appl. Ecol. 31: 1–12.