# Habitat selection and grouping of beetles (Coleoptera)

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Buse, A. 1988. Habitat selection and grouping of beetles (Coleoptera). – Holarct. Ecol. 11: 241–247.

Beetles were collected by pitfall trapping for a two-year period in seven adjacent habitats in an upland site in North Wales. Positive correlations were demonstrated between number of beetle species and number and diversity of plant species. Similar correlations were shown between beetle numbers and plant species. However, only 15% of the beetle species were herbivores requiring host plants. The degree of habitat selection by individual beetle species was demonstrated, ranging from habitat specialist, being found in one habitat, to habitat generalist, being found in most habitats. Herbivores were significantly more habitat specialist than predators or scavengers. The grouping of beetles, demonstrated by ordination analysis, was similar to, but less precise than, the grouping of plant species. The beetle groups reflect habitat selection preferences by individual species rather than a functional relationship between beetle species. They provide an example of the centrifugal structure of habitat selection theory.

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## 1. Introduction

Field studies on the relationship between beetle species and habitat have been mainly descriptive. They have involved the comparison of species at contrasting sites, which were selected because they differed in habitat (Greenslade 1963, den Boer 1977), management methods (Boyd 1960, Rivard 1966, Bertwell and Blocker 1975, Jones 1976), or altitude (Pearson and White 1964). Thiele (1977) reviewed the general distribution of carabid species in relation to habitat. A contrary approach has been to define site (habitat) differences by the beetle species identified in each (Refseth 1980, Butterfield and Coulson 1983).

Recent field studies designed to examine the nature of habitat selection have been mainly on small mammals (Hallett et al. 1983, Abramsky et al. 1985). The importance of habitat selection in competition between species has been examined by Pimm and Rosenzweig (1981) and Rosenzweig (1981).

The purpose of the present study was to examine the relationship between beetle species and habitat, and, in particular, the role of habitat selection.

This study differs from most others in that habitats were interspersed at one site. Hypothetically, this allowed beetles to move from one habitat to another and thus to be evenly dispersed. Also, major abiotic factors, such as temperature, rainfall and light, were virtually the same for all habitats.

One aim of the study was to investigate the hypothesis that there was a relationship between the number of beetles or beetle species and the number or diversity of plant species. The second aim was to examine the hypothesis that the degree of habitat selection varied between beetle species and that habitat selection was related to feeding type. The third aim was to compare the spatial grouping of beetle species with the spatial grouping of plant species.

## 2. Materials and methods

### 2.1. Study site

The study site was the Anafon valley (National Grid Reference SH687712) in the mountains of Snowdonia in North Wales. The site is at an altitude of 310 to 390 m

and its area is approximately 2 km². It is grazed by sheep and ponies.

Rainfall is about 200 cm per year. The rocks are Ordovician blue-black and Glanrafon slates (Roberts 1979). The soils are mainly podzolic, formed from drift material, with areas of deep peat at higher altitudes and loose screes on the valley sides (Ball 1963).

Seven habitats were visually identified in the study area and, for brevity, will be termed herb-rich grassland, mat-grass grassland, bracken, gorse, ling heath, bilberry heath and wet flush.

## 2.2. Sampling

Pitfall trapping was the main method used to sample the beetle species. No other method could economically provide information on a wide range of species, over a two year period, and simultaneously in a number of habitats. To obtain an equally representative sample of all the habitats, equal sampling was undertaken in each. Two examples of each of the seven types were examined.

A line of approximately 30 m length was set out near the centre of each habitat and ten points selected at random along it. A 100 mm length of 58 mm inside diameter rigid plastic tube was inserted in the ground at each point. At bimonthly intervals during the period May 1977 to March 1979, a polypropylene trap of 55 mm depth and 55 mm inside diameter, and containing 20 mm depth of ethanediol, was inserted for a week in each tube. Between sampling periods, each permanent tube was sealed. There were thus ten trapping points in each of two examples of each of seven habitats: a total of 140.

The number of each species of Coleoptera collected in each trap was recorded.

Turves, each measuring 250×250 mm and of approximately 50 mm depth, were collected from one example of each habitat in September 1979 and from both examples in April, May, June and September 1980. Each turf was inverted and placed under heat in an extractor of the Tullgren funnel type.

An objective assessment of the vegetation groups in the area was required for comparison with the habitats. Therefore, in October 1979, a 1 m² quadrat was centred on each trapping point and the cover of each plant species and physical feature, such as bare rock or soil, recorded.

Many factors affect the results of pitfall trapping (Greenslade 1964, Luff 1975, Uetz and Unzicher 1976, Adis 1979, Baars 1979a). The effects of interspecific differences in behaviour and activity and of differing vegetation or physical conditions on behaviour are particularly relevant here. The heat extraction of turves was carried out to assess these effects, particularly amongst the smaller, more densely distributed species. The larger species are too dispersed to be sampled quantitatively by heat extraction. However, Gilbert

(1956) found that behaviour might have little effect as similar results were obtained for larger species by pitfall trapping and day and night searching "by eye".

Within each species, the effects of seasonal differences in activity between habitats are precluded by summing the results for the complete sampling period. The central position of traps in each habitat should eliminate the "edge" effect between habitats which might increase the mobility, and thus the catch, of beetles (Grüm 1971, Baars 1979b).

### 2.3. Analysis

#### 2.3.1. Habitat fidelity
An objective description of the distribution of each beetle species was required to compare habitat selection in different species. Braun-Blanquet (1932) used the term "fidelity" to express quantitatively the extent to which plant species were confined to certain communities. This concept was developed into a quantitative index by Goodall (1953). A "fidelity coefficient" for animal species was developed by Erdakov et al. (1979), using the numbers found in each habitat. As the summed "coefficients" for one species in all habitats equalled zero, the "coefficients" were interdependent, making comparison between species difficult.

For each species in the present study, an independent and comparable habitat fidelity value was calculated for each habitat by comparing the number of individuals found there with the number found in all others. The formula used was

$$\text{habitat fidelity} = \frac{p_{H_i} - p_{H_{i'}}}{p_{H_i} + p_{H_{i'}}}$$

where $p_{H_i} = \dfrac{n_i}{\Sigma n}$ and $p_{H_{i'}} = \dfrac{n - n_i}{(N - 1)\Sigma n}$.

$n_i$ = number of individuals in habitat i; n = total number of individuals in all habitats; N = total number of habitats; $H_i$ = habitat i; and $H_{i'}$ = all habitats except habitat i. The resultant value was in the range −1 to +1. +1 indicated that all the individuals of the species occurred in the habitat, 0 showed that the particular habitat contained an average share of the species, and −1 that no individuals were found in the habitat. The statistical significance of differences in distribution of a species between habitats was examined by comparing the actual number in each using $\chi^2$.

The degree of habitat selection demonstrated by a species can be determined by the extent to which its habitat fidelity values differ from 0. Thus, an index of habitat selection can be produced by considering negative fidelity values as positive differences and summing with the positive fidelity values. If the species was equally distributed through all the habitats, the index would be 0. If it was restricted to one habitat, the index would be 7.

beetle species (comprised of 1700 individuals) collected in pitfall traps and 6 of the 45 species (comprised of 331 individuals) collected by heat extraction are included in the consideration of habitat selection.
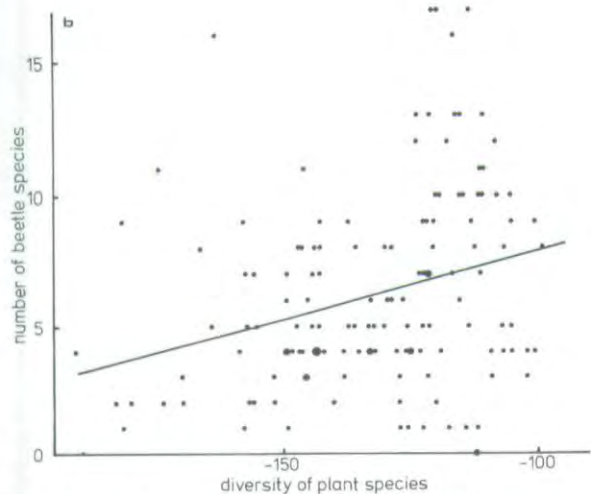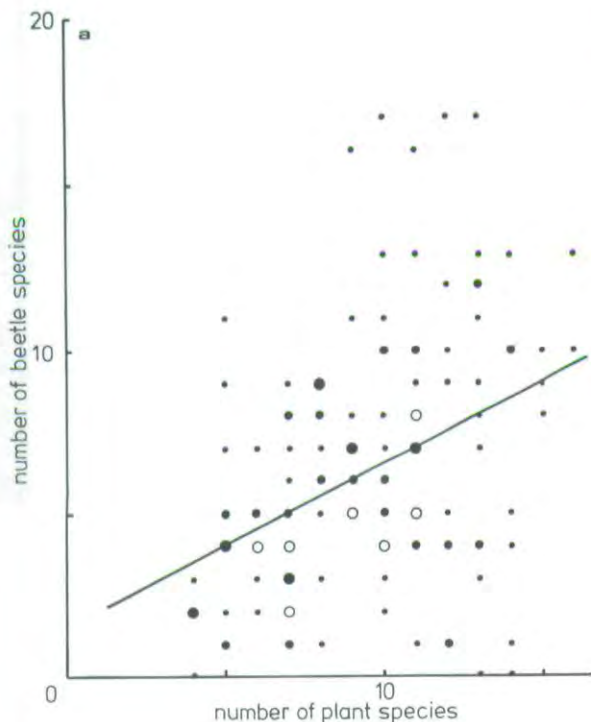


Fig. 1a. The relationship between the number of beetle species and the number of plant species ($y = 0.52x + 1.32$, $r = 0.40$, $p < 0.001$) at each trap.
b. The relationship between the number of beetle species and the diversity (Shannon Idex) of plant species ($y = 0.05x + 13.09$, $r = 0.29$, $p < 0.01$) at each trap.
The larger dots, ● ● and ○, represent 2, 3 and 4 or 5 values at the respective points.
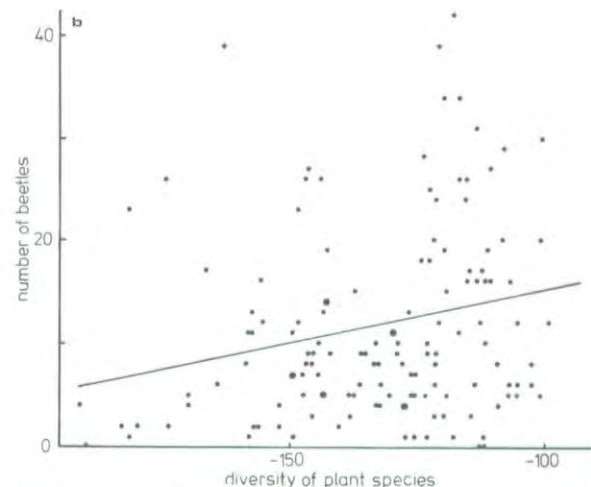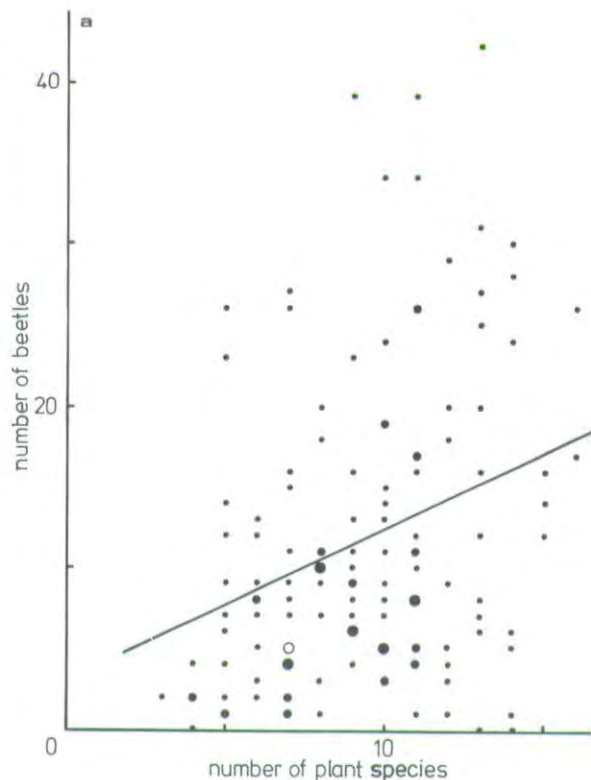
Fig. 2a. The relationship between the number of beetles (individuals) and the number of plant species ($y = 0.95x + 2.99$, $r = 0.24$, $p < 0.02$) at each trap.
b. The relationship between the number of beetles (individuals) and the diversity (Shannon Index) of plant species ($y = 0.1x + 25.11$, $r = 0.19$, $p < 0.05$) at each trap.
The larger dots, ● ● and ○, represent 2, 3 and 5 values at the respective points.

In this study, with 7 habitats, habitat fidelity values were calculated only for species with more than 14 individuals to reduce the possibility of inevitable selection of certain habitats if, say, only eight or nine individuals of the species had been found. Thus, 21 of the 154

Tab. 1. The habitat fidelity of individual beetle species in each of 7 habitats; +1 indicating that all individuals were in the habitat, −1 that no individuals were in the habitat and 0 that the mean number of individuals was in the habitat. The habitat selection index indicates the extent to which distribution differs from being equal between all habitats (the sum of the fidelity values, −ve values being converted to +ve). Collected by pitfall trapping, except *, collected by heat extraction. The seven habitats were: h herb-rich grassland, m mat-grass grassland, b bracken, g gorse, v bilberry heath, l ling heath, w wet flush. Species nomenclature as Kloet and Hincks (1977).

| | (No.) | Habitat fidelity in the 7 habitats | | | | | | | Habitat selection index |
|---|---|---|---|---|---|---|---|---|---|
| **Predators** | | | | | | | | | |
| Pterostichus nigrita | (33) | +1.0 w | −1.0 h | −1.0 m | −1.0 b | −1.0 g | −1.0 l | −1.0 v | 7.0 |
| Cicindela campestris | (26) | +1.0 g | −0.3 l | −1.0 h | −1.0 m | −1.0 b | −1.0 v | −1.0 w | 6.3 |
| Tachyporus pusillus | (21) | +0.9 h | +0.3 m | −1.0 b | −1.0 g | −1.0 v | −1.0 l | −1.0 w | 5.2 |
| T. chrysomelinus | (28) | +0.6 h | +0.5 m | −0.4 b | −0.4 w | −0.6 g | −0.6 v | −1.0 l | 4.2 |
| Abax parallelepipedus | (16) | +0.9 b | −0.1 v | −0.4 h | −0.4 g | −0.4 l | −1.0 m | −1.0 w | 4.2 |
| Pterostichus madidus | (126) | +0.8 b | +0.2 m | 0.0 h | −0.4 v | −0.7 l | −0.8 g | −1.0 w | 4.0 |
| Carabus problematicus | (117) | +0.5 g | +0.5 v | +0.2 l | −0.3 b | −0.6 m | −0.7 h | −1.0 w | 3.8 |
| Nebria salina | (199) | +0.7 h | +0.2 b | 0.0 g | −0.3 m | −0.3 l | −0.5 v | −1.0 w | 3.0 |
| **Scavengers** | | | | | | | | | |
| Anthobium unicolor | (47) | +1.0 g | −0.4 l | −0.6 v | −1.0 h | −1.0 g | −1.0 b | −1.0 w | 5.1 |
| Olophrum piceum | (15) | +0.7 g | +0.4 m | +0.2 w | −0.4 l | −1.0 h | −1.0 b | −1.0 v | 4.7 |
| Staphylinus aeneocephalus | (108) | +0.6 h | +0.5 m | 0.0 g | −0.4 w | −0.6 b | −1.0 v | −1.0 l | 4.2 |
| Xantholinus linearis | (57) | +0.7 h | +0.3 m | +0.2 g | −0.4 b | −0.8 v | −0.8 l | −1.0 w | 4.1 |
| *    " | (29) | +0.5 h | +0.4 m | +0.4 g | −0.4 b | −0.6 v | −1.0 l | −1.0 w | 4.3 |
| Staphylinus olens | (32) | +0.5 v | +0.5 l | +0.2 b | −0.2 g | −0.7 h | −0.7 m | −1.0 w | 3.7 |
| Calathus fuscipes | (47) | +0.7 h | +0.2 g | 0.0 m | −0.3 b | −0.6 v | −0.8 l | −1.0 w | 3.6 |
| Quedius nitipennis | (15) | +0.6 h | +0.4 g | 0.0 l | 0.0 w | −0.4 m | −1.0 b | −1.0 v | 3.5 |
| *    " | (41) | +0.6 m | +0.2 g | +0.1 l | +0.1 w | −0.2 h | −1.0 b | −1.0 v | 3.5 |
| Mycetoporus rufescens | (20) | +0.4 g | +0.3 v | 0.0 l | 0.0 b | −0.2 h | −0.5 w | −1.0 m | 2.6 |
| *Chaetarthria seminulum | (20) | +1.0 w | −1.0 n | −1.0 m | −1.0 b | −1.0 g | −1.0 v | −1.0 l | 7.0 |
| *Amischa analis | (37) | +0.8 h | +0.6 m | −0.5 b | −0.7 w | −1.0 g | −1.0 v | −1.0 l | 5.5 |
| *Geostiba circellaris | (23) | +0.8 g | +0.4 m | −0.3 h | −0.3 b | −0.6 w | −1.0 v | −1.0 l | 4.2 |
| *Othius angustus | (52) | +0.5 m | +0.3 b | +0.2 h | −0.2 g | −0.3 v | −0.6 l | −0.8 w | 2.9 |
| **Herbivores** | | | | | | | | | |
| Longitarsus succineus | (28) | +1.0 h | −0.6 v | −1.0 m | −1.0 b | −1.0 g | −1.0 l | −1.0 w | 6.6 |
| L. suturellus | (111) | +1.0 h | −0.2 m | −0.8 b | −0.8 w | −0.9 g | −1.0 v | −1.0 l | 5.7 |
| L. holsaticus | (93) | +0.9 h | −0.3 b | −0.5 m | −0.6 w | −1.0 g | −1.0 v | −1.0 l | 5.3 |
| Sitona regensteinensis | (26) | +0.9 g | −0.3 v | −0.3 l | −0.3 w | −1.0 h | −1.0 m | −1.0 b | 4.9 |

Tab. 2. A comparison of the significance of the U-values resulting from the Mann-Whitney U-test between ranked habitat selection indices (see legend to Tab. 1) for each species in the predator, scavenger and herbivore groups of beetles. (  ) no. of species included.

| | Feeding types | | |
| --- | --- | --- | --- |
| | Predators(11) | Scavengers(18) | Herbivores(8) |
| Predators | – | 76.0  P = 0.1 | 22.0  P = 0.05 |
| Scavengers | | – | 18.0  P = 0.001 |
| Herbivores | | | – |

### 2.3.2. Ordination

An objective assessment of the spatial grouping of beetle species was undertaken using all the species found at one trapping point as the basic unit: there were 140 such units. The relationships between these units, based on the relationships between the beetle species they contained, were assessed by ordination by reciprocal averaging using the programme DECORANA (Hill 1979). The results were plotted: closely related trapping points were close together, less related points were farther apart.

Similar analyses were undertaken using the plant species around each trap. The resultant groups could be compared with the original habitats and with the beetle groups.

### 3. Results

#### 3.1. The relationship between beetles and plant species

There was a marked correlation between the number of beetle species and the number of plant species found at each of the 140 trapping points (Fig. 1a). A similar correlation was evident between the number of beetle species and the diversity (Shannon Index) of plant species at each trap (Fig. 1b).

The number of beetles caught at each trapping point was found to be correlated with both the number and diversity of plant species (Fig 2a and b). However, this relationship was less marked than for beetle species.

#### 3.2. Habitat selection in beetles

For each beetle species, the habitat fidelity in each habitat is shown in Tab. 1. At one extreme, the species showed the greatest possible degree of habitat selection, being found only in one habitat and having a habitat selection index of 7.0. At the other extreme, the species showed little habitat selection, tending towards being spread equally through all the habitats of the study site. The least habitat selection index was 2.6. Thus the species range from "habitat specialist" to "habitat generalist" (Witowski 1978).

The predators, scavengers/omnivores, and herbivores are separated in Tab. 1. This separation is an approximation as, in some species, the proportion of different

foods varies according to availability (Luff 1974). It appears in Tab. 1 that habitat selection differed with feeding type. This hypothesis was tested by ranking the habitat selection indices for the species in Tab. 1, and additional species with a minimum of 6 records, within each feeding type. The three feeding types were then compared using the Mann-Whitney U-test (Tab. 2). Herbivores were found to be significantly more habitat specialist than scavengers/omnivores. A similar significant difference was apparent between herbivores and predators.

#### 3.3. Habitat, plant species groups and beetle species groups

Visual differences in the grouping of vegetation were used to divide the study site into habitats for the purpose of sampling. For comparison, an objective grouping of the trapping points, on the basis of the plant species around each, was undertaken by ordination. The trapping points formed similar groups to the original habitats (Fig. 3). Axis 1 demonstrated a transition from grassland groups to heath groups, whereas axis 2
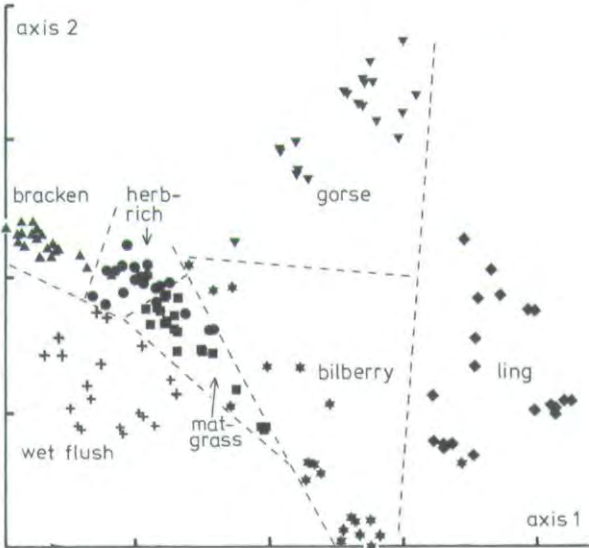


Fig. 3. The ordination of the trapping points based on the plant species around each, showing the resultant vegetation groups. The location of each trapping point in the habitats was: ● herb-rich grassland; ■ mat-grass grassland; ▲ bracken; ▼ gorse; ★ bilberry heath; ◆ ling heath; + wet flush.
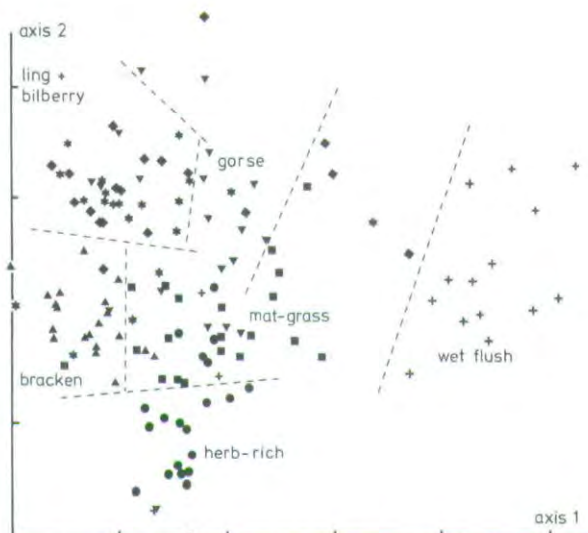
Fig. 4. The ordination of the trapping points based on the beetle species collected at each, showing the resultant beetle groups. The location of each trapping point in the habitats was: ● herb-ich grassland; ■ mat-grass grassland; ▲ bracken; ▼ gorse; ★ bilberry heath; ◆ ling heath; + wet flush.

tended to reflect a sequence from wetter to drier groups.

The groups formed by the ordination of the beetle species at each trapping point (Fig. 4) were less precise than those of the plant species. This might be expected because of the mobility of beetles and the differing degrees of habitat selection shown by the various species. However, there were beetle groups corresponding with the vegetation groups of wet flush, herb-rich grassland, mat-grass grassland and bracken. There was also a combined heath group of ling and bilberry trapping points. The wet flush group was the most distinct: the only species completely specific to one habitat in Tab. 1, *Pterostichus nigrita* and *Chaetarthria seminulum*, were in this group. In some cases, such as *P. nigrita*, this might reflect a physiological requirement for damp places, whereas in others, such as *Phyllotreta tetrastigma*, it is due to specificity to host plant species which live in wet habitats.

## 4. Discussion

There was a marked correlation between the number of beetle species found in a trap and the number or diversity of plant species around it. A similar relationship has been shown between plant-sucking bugs (Homoptera) and plant diversity (Murdoch et al. 1972). However, in the present study only 15% of the 120 beetle species found in traps were herbivores, the majority being predators or scavengers. Thus, specificity to food plants could not be a major factor here. It seems likely that the relationship is due to the greater variety of

"microhabitats" available for the beetle species when more plant species are present. It has been shown in birds (MacArthur and MacArthur 1961) that diversity of species depends upon diversity of foliage height and density rather than upon species composition. Murdoch et al. (1972) found a similar correlation between plant bug diversity and foliage height diversity in their old fields.

The beetle species, considered individually, varied from habitat specialist to habitat generalist (Witowski 1978). Within each feeding type in Tab. 1, that is predators, scavengers or herbivores, these habitat preferences are seen to be either distinct or shared with other species (Rosenzweig 1985). Thus, amongst the predators, the preference of *Pterostichus nigrita* for the wet flush habitat was distinct, whereas the preference of *Abax parallelepipedus* and *Pterostichus madidus* for bracken were shared. The latter situation is described by Rosenzweig (1986, 1987) as a centrifugal structure: both species share a preference for one habitat type, but have distinct preferences for their secondary habitat types. In this case, *A. parallelepipedus* had a secondary preference for bilberry heath, whereas *P. madidus* had secondary preference for mat-grass grassland. They also extended into other habitats.

The scavengers *Xantholinus linearis* and *Staphylinus aeneocephalus*, which might be expected to have similar requirements, showed very similar habitat preferences, sharing primary, secondary and tertiary habitat types. It would seem that centrifugal distribution was not operating here. However, the original data shows a time difference, *X. linearis* having a population peak early in the year and *S. aeneocephalus* later. Thus, time should be included as a factor in considering the role of habitat selection.

The herbivores, as a group, were shown to be significantly more habitat specialist than the predators or scavengers. The requirement of individual species for specific host plant species, themselves occurring in specific habitat types, might account for this. No significant difference in the intensity of habitat selection could be demonstrated between the predator group and the scavenger group.

The grouping of beetles by ordination was less precise than the vegetation grouping. This reflects the fundamental difference between plants and animals, recognized by Macan (1974). He observed that, between two points on an ecological gradient, one or a few plant species become dominant. Beyond such points, they give way to another species with which they cannot compete. Animals, however, each have differing ranges along the gradient: there is no animal equivalent to dominance. The degree of grouping of the beetle species is therefore surprising. Habitat selection theory can help to explain this. Each species has its own habitat preference, as demonstrated by its occurrence in its preferred habitats in the study site, and will thus form a partially fortuitous group with other species with the

same preferred habitat. The scavengers and herbivores will each be there for their own reasons, such as shelter or food requirements. Some of the predators might feed on the smaller beetle species found in the habitat. Rosenzweig's (1986) centrifugal structure explains how species of the same feeding type, with apparently the same requirements, can be found in one group. These factors all lead to the grouped structure of the beetle population.

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