Aspects of the ecology of some invertebrates on limestone outcrops in Moorland

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How to cite:

Lloyd, Louise Jane (1987) *Aspects of the ecology of some invertebrates on limestone outcrops in Moorland*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/6875/

ABSTRACT

In 1984-5 the carabids and staphylinids on ten isolated limestone outcrops and intervening blanket peat within the Moor House Reserve, Cumbria, were investigated. In 1986 a subsidiary study on similar habitats was made at Tailbridge Hill, Cumbria. Pitfall and window traps sampled beetles from the ground and air respectively. Numbers and alpha diversities of carabids and staphylinids were higher on the Moor House limestone outcrops than on the blanket peat. The outcrops acted as isolates to many species, but also suffered considerable contamination by adjacent peat faunas. Limestone species taken on outcrops exhibited a positive species:area relationship consistent with island biogeographical theory. Peat species taken on outcrops showed a negative species:area relationship. Overall, species of staphylinid were positively, and carabid, negatively, correlated with outcrop size. Dispersal of species between habitats was influenced by body size, degree of hygrophily and flight activity. Flight by carabids was negligible, but most staphylinids could fly. Weather conditions were probably the primary cause of this difference between taxa. Flight by staphylinids was related to the stability of the habitat or resources involved. All Nomadic species could fly whereas flight by Peat species was negligible. Limestone species showed relatively high levels of flight activity attributable to the need of many rarer species for regular dispersal between outcrops to spread the risk of extinction. The aerial fauna at Moor House had three components, with species deriving from the immediate habitat, moorland habitats nearby, or regions beyond the Reserve. A considerable influx of staphylinids (and aphids) onto the Reserve occurred in July-October as aerial plankton was carried in from the west by prevailing winds. The applicability of island biogeography theory to the Moor House system, and to 'habitat islands' in general, is discussed.

ASPECTS OF THE ECOLOGY OF SOME INVERTEBRATES ON LIMESTONE OUTCROPS IN MOORLAND

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A thesis presented in candidature for
the degree of Doctor of Philosophy
in the University of Durham, 1987.

I certify that all material in this thesis which is not my own work has been identified and that no material is included for which a degree has previously been conferred upon me.

For Ma and Pa.

ACKNOWLEDGEMENTS

Above all, my thanks are due to John Coulson for all his sound advice, constructive criticism, and constant encouragement throughout his supervision of this study. I also thank the many friends and colleagues, especially Tusi Butterfield and Nicholas Aebischer, who proved an endless source of daily help and inspiration. The Durham University Zoology Department provided facilities and materials and a particularly obliging team of technicians. My thanks go to all of them, and particularly to Eric Henderson for his invaluable assistance with fieldwork. The research was supported by a grant from the Natural Environment Research Council. Permission to work on the Moor House National Nature Reserve was given by the Nature Conservancy Council, which also kindly allowed access to meteorological records from, and maps of, the Reserve. I am indebted to Peter Hammond for help with the identification of elusive staphylinids, and for many valuable comments. I am obliged to Maureen Dupuch and colleagues at Rothamsted Experimental Station for identifying the aphid species taken at Moor House. I thank my father for his painstaking proof-reading of the text and helpful suggestions. Finally, I thank my family, at home and abroad, for all their moral support and encouragement.

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CHAPTER 1 GENERAL INTRODUCTION

A larger area of a given habitat usually contains more species than a smaller area of the same habitat. This is a commonly observed phenomenon which aroused much statistical interest at the beginning of this century (Arrhenius 1921, Gleason 1922) and was finally shown to conform most satisfactorily to a power function model (Connor and McCoy 1979). More recently, however, it is the biological nature of this simple species:area relationship which has become the focus of most discussion and controversy, generated initially by the publication of MacArthur and Wilson's theory of island biogeography (1963, 1967). In their theory, MacArthur and Wilson developed the ideas of Preston (1962), who regarded the observed species:area relationship as a dynamic equilibrium of species exchange between isolates. The island biogeography theory states that the number of species on islands of similar habitat in the same latitude depends on the size and isolation of the islands, and is a balance between rates of immigration and extinction. The former rate is predicted to decrease with increasing isolation, and the latter to increase with decreasing area. Thus the lowest equilibrium numbers of species are to be expected on the smallest and most distant islands.

As formerly extensive natural habitats become progressively fragmented by the activities of man, increasing attention has been focussed upon the application of classical island biogeography theory to terrestrial systems and whether it can be usefully employed in the understanding of the faunas of 'habitat islands' (MacArthur and Wilson 1967, Simberloff and Wilson 1969, Boecklen 1986), especially with regard to the design of future nature reserves (Simberloff 1976, Simberloff and Abele 1982, Wright and Hubbell 1983). Isolated patches of habitat, like islands, contain distinctive species which are confined to those or similar patches in the region but are absent from the intervening expanse of dissimilar habitat (Levenson 1981, Mader 1984, Webb and Hopkins 1984). If such habitat islands are truly acting as isolates, then the same processes of immigration and extinction which are considered to dictate the species complement of island communities can be expected to apply to them.

However, the contrast in environment between a habitat patch and its surrounds is rarely so marked as between a real island and the encompassing ocean. In the latter system the surrounding expanse of water presents a formidable barrier to casual dispersal by the majority of terrestrial species on the island. Only a handful of amphibious or beach species can exploit both habitat types, and even most of them will be unable to survive for long in the water without regular recourse to land for breeding, feeding or shelter. Within a wholly terrestrial system, on the other hand, the change in environment across the boundary of the habitat island is never so marked, and there is inevitably an invasion onto the patch of species originating on the surrounding habitats together with a converse efflux of species from the patch into adjacent habitats (Janzen 1983, Mader 1984, Webb and Hopkins 1984). Many of these species will not wander far from their respective habitats, being dependent upon them for food, shelter or other ecological requirements (Grum 1971), but some may be sufficiently eurytopic to survive for considerable periods within the less favourable environment (Den Boer 1970).

Although this interdispersal of species across the habitat boundary is recognized as having an important effect on the local fauna of a habitat island (Mader 1984, Webb and Hopkins 1984) little detailed investigation has been conducted into its nature or magnitude. In most instances no formal attempt has been made to discriminate between species representative of and vagrant on a habitat respectively. As a result, the species:area relationships recorded have often proved highly confusing and misleading, based on a species list which includes residents and vagrants alike. The picture is often further complicated by the fact that most studies have concentrated on habitats only relatively recently fragmented and restricted to isolated patches where the local faunas are unlikely to have reached a stable equilibrium within their new environmental context (Webb and Hopkins 1984). Moreover, in such systems where a formerly extensive habitat has been reduced to a scattering of isolated fragments, a large species pool, analogous to that present on a nearby continent in a true island situation, from which suitable colonization can arise is lacking, and the predicted balance between immigration and extinction rates is upset.

The Pennine moorlands in northern England, however, provide an excellent natural system within which the faunas of habitat islands may be comprehensively studied: amidst the general expanse of blanket peat typifying this region there are many isolated and discrete patches of contrasting limestone grassland where the underlying bedrock has outcropped. This pattern of habitat types has been in existence for thousands of years with negligible interference from outside (Johnson and Dunham 1963, Godwin 1981) and the resident faunas may be expected to be in a stable equilibrium state overall. Although these grasslands are very patchily distributed within the moorland in question, in other localities nearby they form a much more extensive and continuous habitat which may serve as a source for immigrating species.

In order to study this moorland system, two animal taxa were selected: the ground beetles (Carabidae) and the rove beetles (Staphylinidae). Both groups are abundant and represented by numerous species on the moor, and form distinctive species assemblages on blanket peat and limestone grassland respectively (Houston 1970, Coulson and Butterfield 1979). The majority of their species are surface-active generalist predators easily sampled by simple trapping methods. Many of the species in both taxa are flightless, and hence will have limited powers of dispersal away from their original habitat (Houston 1970, Hammond pers. comm.). Other species, on the other hand, have been shown to be capable of flight elsewhere, and, if they possess that ability on the moor, will have the potential for considerable and long-range dispersal (Den Boer 1971, Hanski and Koskela 1977).

In this thesis the patterns and processes characterizing the carabid and staphylinid communities on limestone grassland habitat islands are investigated in detail. To achieve a thorough understanding of the system in operation, the species representative of limestone grassland and blanket peat respectively are first distinguished and examined, and their capacity for flight determined. The nature and extent of the interchange of species between the two habitats is then investigated, and its consequencies for the species diversity and composition of the grassland habitat islands considered. Finally, the relative isolation of the staphylinid and carabid faunas on the limestone outcrops is examined with respect to their respective powers for dispersal, and the applicability of the classical island biogeography model to such habitat islands is discussed.

CHAPTER 2 THE STUDY AREAS AND SAMPLING SITES

2:1 Location and general physiography

Most of the work described in this thesis was conducted on the Moor House National Nature Reserve, Cumbria (National Grid Reference NY 758329). A subsidiary study was carried out on Tailbridge Hill, Cumbria (National Grid Reference NY 808046). The location of these study areas in relation to Durham is shown in Figure 2.1.

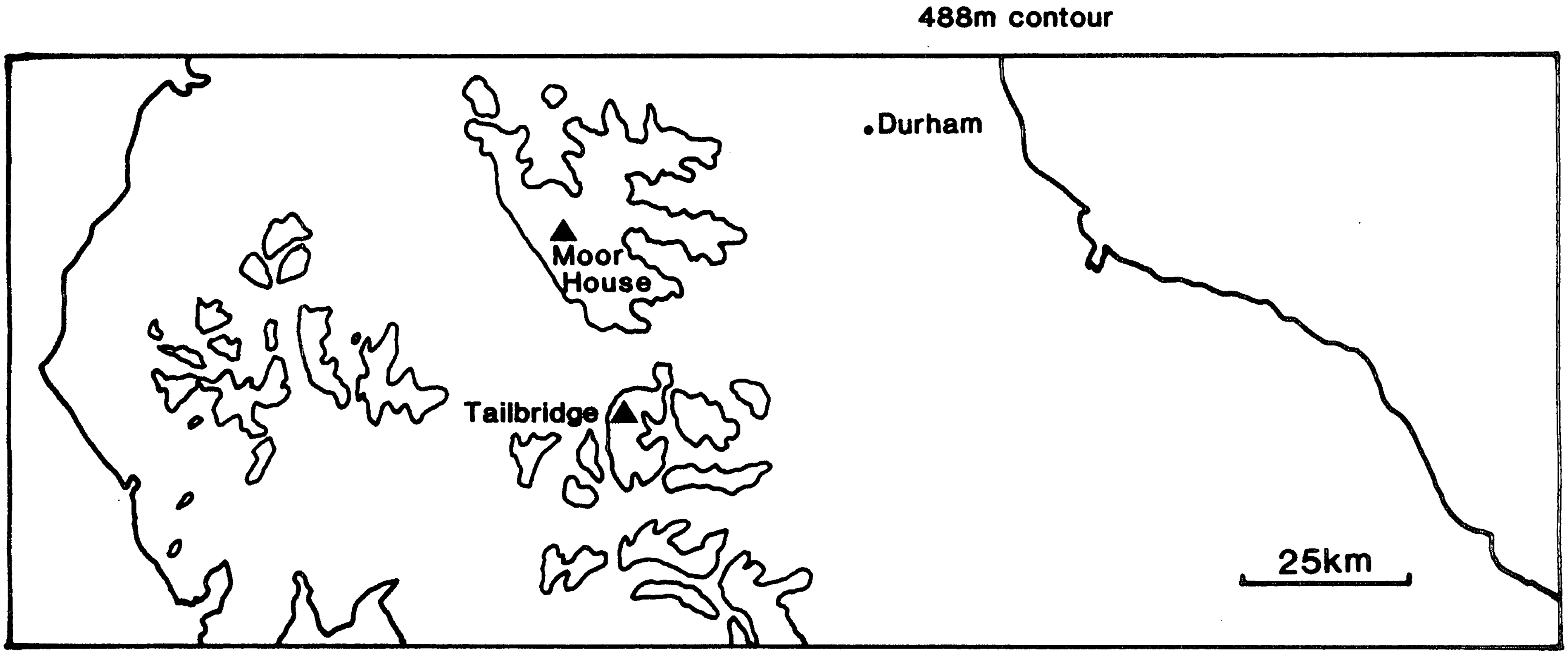
2:1.1 The Moor House Reserve

The Moor House Reserve occupies nearly 4000ha of moorland typical of the northern Pennines. To the west a steep scarp slope rises from about 300m on the edge of the Vale of Eden, forming a summit ridge comprising the three principal fells, Knock Fell (794m), Great Dun Fell (845m) and Little Dun Fell (842m). These form a continuum with the highest peak of the Pennines, Cross Fell (984m), which lies just outside the Reserve's northern boundary. The greater part of the Reserve is composed of a gently sloping plateau-like area at about 500-600m on the eastern side of the ridge, which has been dissected by numerous small fast-flowing streams draining into the Tees on the northern and eastern edges of the Reserve.

The bedrock underlying the Reserve and dominating its surface geology consists of a series of almost horizontal alternating beds of limestone, sandstone and shale of Carboniferous age, the differential weathering of which has produced the stepped topography of the west-facing escarpment. The solid geology of most of the gentle dip slope is obscured by an almost continuous mantle of glacial drift which becomes thin and discontinous on

Figure 2.1

Map of northern England, showing the location of the Moor House National Nature Reserve and Tailbridge Hill in relation to Durham.



the summit ridge and steeper slopes.

Blanket peat with a surface vegetation of *Calluneto-Eriophoretum* forms the dominant soil type, covering over half of the Reserve to a depth of about 1m wherever the underlying boulder clay has impeded drainage and caused waterlogging. In certain areas the peat reaches 3m in depth and its greater instability has led to extensive erosion (10-15%) of the almost continuous peat cover on the eastern plateau. Where blanket peat is absent and glacial drift thin, soil formation has been influenced by the underlying bedrock to produce iron podsols dominated on the summits by *Festuca* spp., and a variety of peaty and mineral soils on the western slope dominated by *Festuca* spp., *Nardus stricta*, or *Juncus squarrosus*. On the eastern dip slope, small patches of alluvial soils have developed along the larger streams, and a number of isolated patches of calcareous soil of varying sizes supporting an *Agrosto-Festucetum* vegetation type have resulted from the outcropping of the limestone strata. Sheep-grazing on the Reserve during the late spring and summer months is preferentially concentrated on these latter areas, producing a short even sward. Past mining activity has produced localized pockets of 'made ground'. General descriptions of the Reserve have been given by Conway (1955) and Cragg (1961). Detailed accounts of the geology and a soil map have been produced by Johnson and Dunham (1963) and Hornung (1969), and the nature of the surface vegetation has been detailed by Eddy *et al*. (1969). A comprehensive overview of all these aspects has been presented by Heal and Smith (1978).

2:1.2 Tailbridge Hill

At Tailbridge Hill the escarpment rises from an altitude of about 250m on the south-easterly edge of the Vale of Eden to form a ridge at 547m. A plateau of moorland over 100ha in total area extends behind the ridge, characterized by a mosaic of extensive grasslands with exposed limestone pavements and areas of eroding blanket bog dominated by Eriophorum. Occasional patches of Juncus squarrosus with Nardus stricta occur along the edges of the peat hags where the underlying millstone grit has been exposed. The Agrosto-Festucetum sward on the mineral soils is heavily grazed by sheep.

2:2 The Sampling Sites

From the areas described, sampling sites were selected for study. These divided into three main groups:(i) limestone sites, (ii) Juncus moor sites, and (iii) blanket peat sites.

2:2.1 Moor House

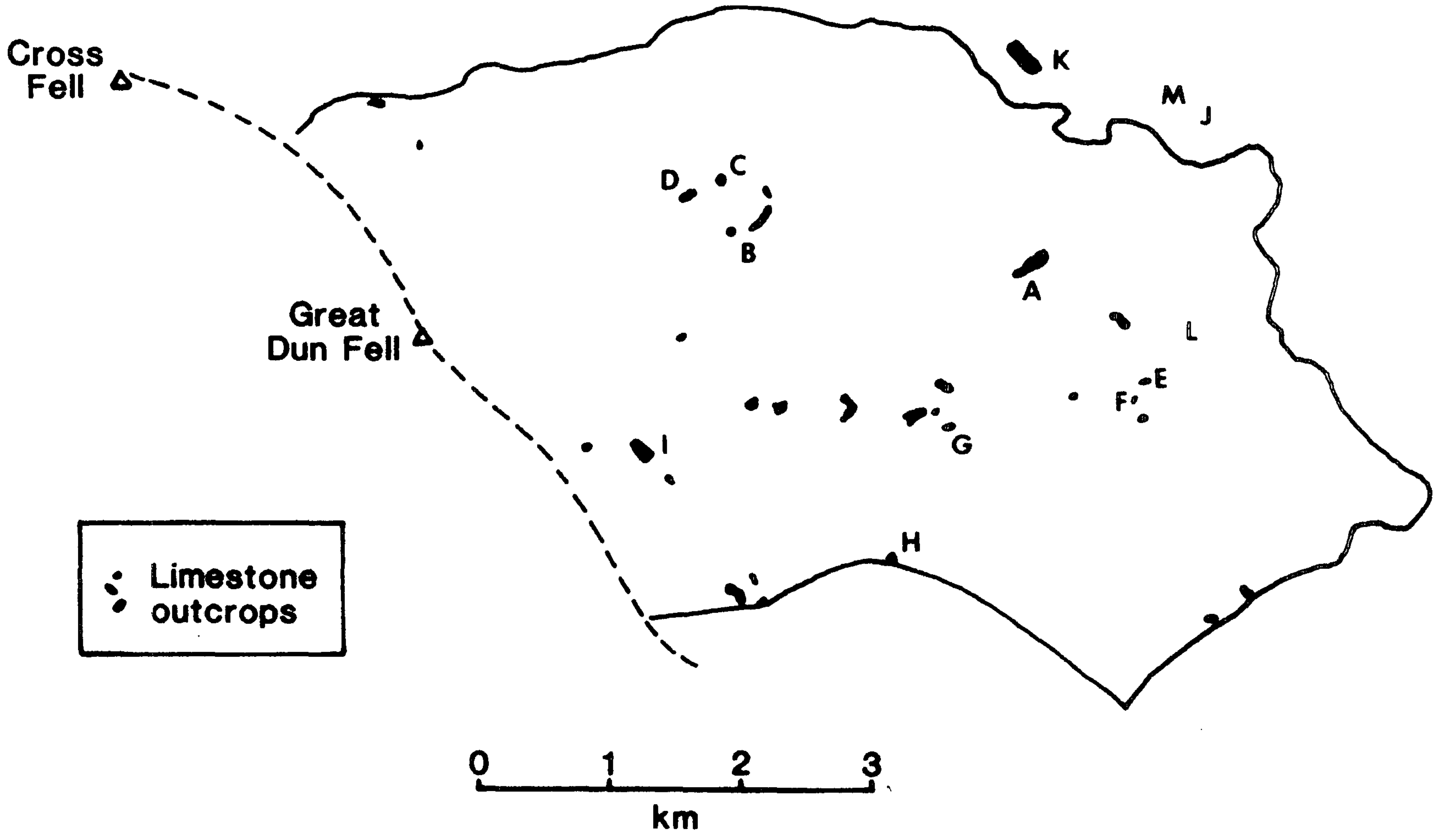
All of these sites occurred either on the eastern dip slope of the Reserve or on the summit ridge itself. Their locations are shown in Figure 2.2.

i. Limestone sites

The ten sites in this group included one (Site A) previously used by Coulson and Butterfield (1979) and described by Rawes and Welch (1969). Each site was typified by limestone bedrock, often exposed as weathered clints and grykes or boulders, which was overlain by a thin (less than 0.5m in depth) base-rich and well-drained brown earth soil supporting an Agrosto-Festucetum sward. The turf was heavily and closely grazed by sheep during the spring and summer months. All but one of these outcrops were

Figure 2.2

Map of the eastern dip slope of the Moor House Reserve, showing the locations of the sampling sites.



totally surrounded by peat moorland; Site A alone bordered a water-course, Moss Burn. Site K was located just outside the Reserve, on its north-eastern boundary. The sites varied greatly in their extent, elevation and relative isolation: their individual characteristics and the vegetational nature of their immediate surrounds are given in Table 2.1.

ii. Juncus moor sites

This was an extensive area of fairly shallow (less than 1m in depth) but poorly-drained peat moor on the north-eastern side of the Tees (just outside the Reserve) at an altitude of 550m. Its vegetation was dominated by Juncus squarrosus and Nardus stricta. Since 1977 a large portion of the area (16ha) had been 'improved' according to the standard practice of burning, fertilizing and liming, reseeding with an upland grass mixture and draining. It had been enclosed and was stocked with sheep during the summer. A detailed account of this area and of the improvement measures applied to it has been given by Tracey (1980). Site J was located on this 'pseudo-limestone grassland' area, whilst Site M was situated on an unimproved region of the original moor adjacent to it.

iii. Blanket peat sites

The sites in this group were all located on blanket peat at least 1m thick which was dominated by Calluna and Eriophorum spp., and was very poorly drained. The sites differed from one another only in their relative distances from the nearest limestone outcrops (with the exception of Sites g and d which were at different altitudes to the rest), as indicated in Table 2.2.

Table 2.1

Altitude, size and surrounding vegetation of the limestone sites at Moor House. Local vegetation type was quantitatively assessed from vegetational maps of the Reserve (after Eddy *et al*. 1969). Vegetation bordering Site K, which lay outside the Reserve, was not quantitatively assessed.

Outcrop	Altitude (m)	Area (ha)	% vegetation type in 100m radius of site			
			Agrosto-Festucetum	*Calluneto-Eriophoretum*	*Juncetum/Festucetum*	Other vegetation
A	560	4.9	43	49	4	4
B	670	1.6	5	59	24	11
C	660	1.4	4	86	10	0
D	660	1.4	4	52	39	5
E	580	0.2	3	81	16	0
F	580	0.4	3	85	12	0
G	650	2.0	7	77	2	14
H	730	1.0	14	33	53	0
I	750	9.8	35	8	57	0
K	540	14.0	nd	nd	nd	nd

Table 2.2

Altitude and location of the blanket peat sites at Moor House.

Blanket peat site	Altitude (m)	Distance from nearest limestone outcrop (m)
L	580	400
LE	580	40
LF	580	40
FE	580	40
EX	580	2
EY	580	2
FX	580	2
FY	580	2
g	540	5
d	660	150

2:2.2 Tailbridge

These sites all occurred at an altitude of 518m on the plateau behind Tailbridge Hill, and their locations in the study area are shown in Figure 3.2. They were arranged along a transect which passed from an area of limestone grassland over 10ha in extent (Sites TA, TB, TC and TD) and adjacent to a much larger area of limestone pavement, across a relatively narrow band (40m) of shallow peat underlain by millstone grit and dominated by _Juncus squarrosus_ and _Nardus stricta_ (Sites TE and TF), onto an extensive area of blanket peat more than 1.5m in depth (Sites TG and TH). The sites on each habitat type differed from one another only in their relative distances from the mineral soil/peat interface (Table 2.3).

2:3 _The climate at Moor House_

Meteorological records have been kept at Moor House since 1952, and a summary of some monthly long-term climatic averages is given in Table 2.4. The Reserve lies on the highest part of the Pennine upland, on the most consistently elevated region in England, and its general climate is severe by British standards: cool, wet and windy (Heal and Smith 1978). It is typical of the montane regions of Britain (Pearsall 1950), oceanic and subarctic rather than temperate, and having many features comparable to those at sealevel in southern Iceland (Manley 1936, 1942, 1943). Rainfall is high (about 1900mm/year) and irregularly distributed throughout the year, with late autumn being the wettest period. Snow cover lasts for an average of 70 days, and frost usually occurs in every month. Summer temperatures exceed 10°C only in July and August, and the maximum solar radiation, occurring in June, is only 5.8h/day of bright sunlight. Windspeeds are

Table 2.3

Characteristics of the sites at Tailbridge.

Habitat	Site	Distance from habitat interface (m)
Limestone	TA	100
	TB	50
	TC	25
	TD	2
Juncus moor	TE	2
	TF	25
Blanket peat	TG	50
	TH	100

Table 2.4

Long-term climatic averages at Moor House (from Heal *et al*. 1975).

	Month												Yearly
	J	F	M	A	M	J	J	A	S	O	N	D	average
Daily duration of bright sun (h)													
1954-1972	1.0	1.7	2.6	4.0	5.2	5.8	4.6	4.2	3.4	2.5	1.3	0.9	3.1
Air temperature 1/2(max+min) (0°C)													
1953-1973	-0.4	-1.0	1.1	3.5	6.7	9.6	11.0	10.8	9.3	6.8	2.6	0.8	5.1
Rainfall (mm)													
1953-1967	177	150	134	120	128	113	144	170	160	180	200	206	1883
Number of days with snow lying													
1953-1972	16.5	17.4	11.6	4.0	0.6	0	0	0	0	0.2	6.0	10.4	66.7
Wind velocity (m/s)													
1956-1972	8.1	8.0	8.0	6.7	6.3	5.9	5.9	5.9	6.4	7.4	7.5	8.2	7.0

Figure 2.3

Seasonal pattern of rainfall, temperature and hours of sunshine at Moor House in 1984 and 1985. Values are daily averages during fortnightly periods. Rainfall data are incomplete for 1984. Sunshine is measured as daily duration of bright sun. Temperatures are daily (maximum + minimum)/2 air temperatures.

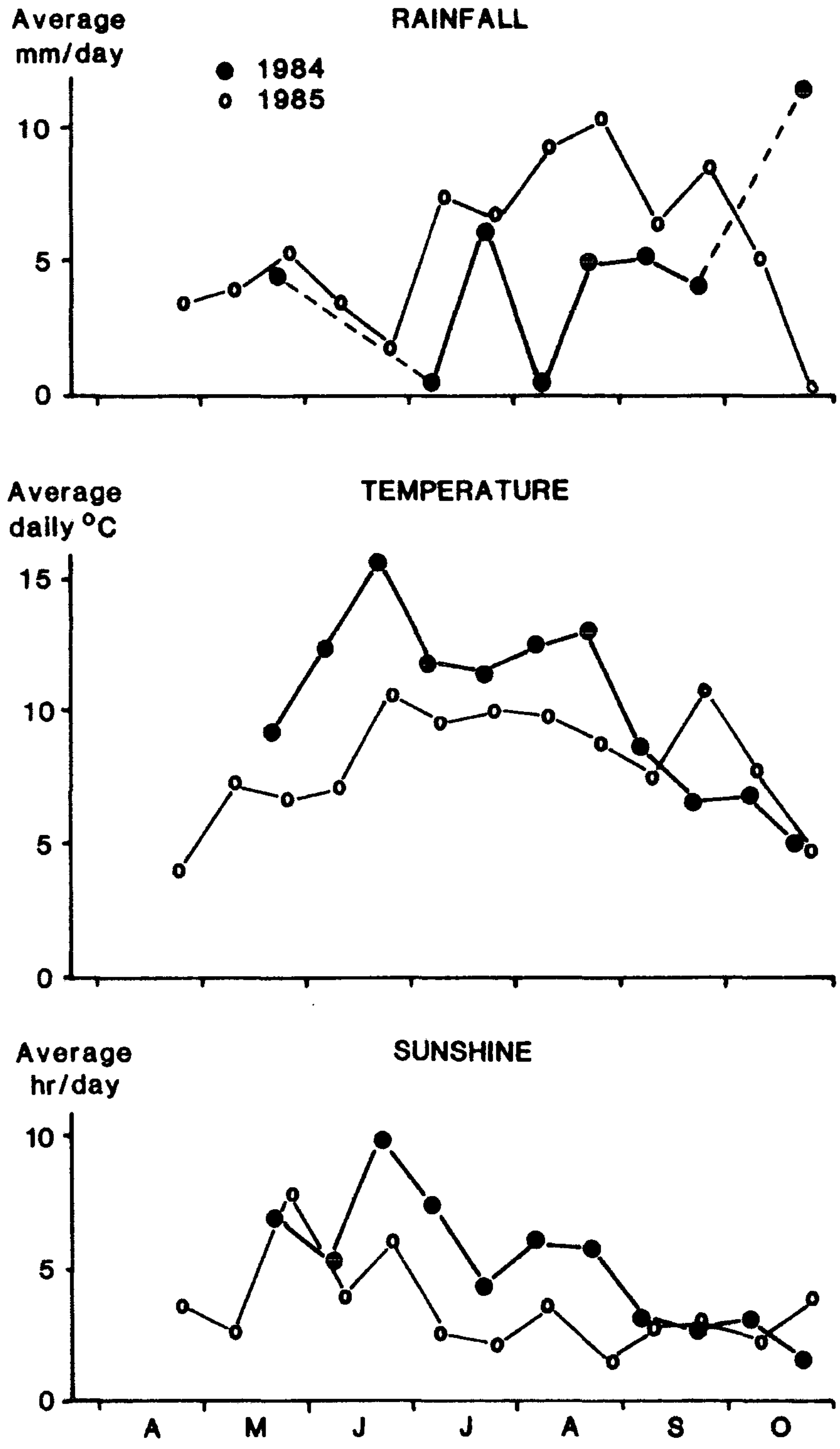


Table 2.5

Comparison of climatic data from Moor House during May-October in 1984 and 1985 with the long-term averages for the same period (calculated from Table 2.4).

	1984	1985	Long-term average
Daily duration of bright sun (h)	5.6	3.5	4.6
Air temperature 1/2(max+min)(°C)	11.5	8.1	9.5
Rainfall (mm)	702 *	845	715
Wind velocity (m/s)	3.3	3.6	6.1

* based on incomplete data

high, particularly in February and March (about 8.0m/s) when easterly winds are frequent.

Data on weather conditions on the Reserve during the growing season (May to October) in 1984 and 1985 have been extracted from the Nature Conservancy's records (Figure 2.3), and a summary of this data is compared with the long-term averages for Moor House over this period in Table 2.5. During the growing season of 1984, the average daily number of sunshine hours was 1h greater than the long-term average (4.6h), and the mean air temperature was 2°C higher than the long-term mean (9.5°C). In contrast, in 1985, the average daily duration of sun (3.5h) was more than 1h shorter than the long-term average, and the mean air temperature (8.1°C) was 1.4°C lower than the long-term average. Rainfall during this period was close to the long-term average in 1984 (7.1mm), but higher than average in 1985 (8.1mm). Windspeeds were lower than average (6.1m/s) in both years, and though showing no consistent direction in the first part of the field season, became prevailing westerly from mid-summer onwards.

Thus, to summarize, the 1984 growing season was characterized by higher than average daily hours of sunshine and air temperatures, average rainfall, and lower than average wind velocities, whilst the same period in 1985 featured lower than average daily hours of sun, air temperatures and wind velocities, but higher than average rainfall. Seasonal patterns of prevailing winds were similar in both years.

CHAPTER 3 THE SAMPLING METHODS

3:1 Pitfall traps

3:1.1 General overview

Pitfall trapping constitutes one of the simplest and most economical methods of continuously sampling surface-active invertebrates such as carabids and staphylinids, and has been used extensively by many investigators (eg Williams 1959, Duffey 1962, Pearson and White 1964, Coulson and Butterfield 1979). Although their ease of use commends them as a potentially valuable means of sampling certain animal populations (Luff 1975), pitfall traps must be used with discretion. Catch size has been shown to be influenced by many factors apart from population size (Briggs 1961, Mitchell 1963, Greenslade 1964, Luff 1975), particularly by the relative activity of the animals which may be affected by weather conditions (Mitchell 1963), the nature of the habitat, and the sex, age and condition of the individuals (Petruska 1968). This makes pitfall traps of limited value for the direct estimation of populations or the comparison of different community types (Briggs 1961, Greenslade 1964). However, providing that due attention is paid to these potential sources of variation, pitfall trapping still provides valuable information on species communities, and Greenslade (1964) considered the method quite adequate to assess the relative numbers of a carabid species in different vegetation types in an investigation not dissimilar to the one being undertaken at Moor House. As the present study is concerned largely with intra-specific and inter-habitat differences in specific taxa (carabids and staphylinids), and not with overall community structure within an area, pitfall trapping was considered the most appropriate method to use for sampling the surface-active animals on the study areas in question (cf Chapter 2).

The traps used were standard polythene bottles with an aperture diameter of 45mm, which had the dual advantage over glass jars of not being a hazard to sheep if damaged, and having screw-tops which allowed them to be easily transported back to the laboratory for sorting. Their potentially lower catching efficiency relative to glass jars (Luff 1975) was counteracted by the addition of 50ml of a 2% formalin-detergent solution to each trap which quickly killed specimens, so preventing their escape and predation of other animals caught. The role of formalin as an attractant or deterant for a few species (Luff 1968) was not considered an important biassing factor since catches were made for comparison between and not within local communities.

3:1.2 Trapping at Moor House

A set of ten bottles formed the basic trapping unit at each site. In each case the traps were positioned to form a 2 x 5 grid, with 3m between traps in the same row and 2m between the two rows. This design allowed sampling to be localized and compact, yet with a minimum of interference between traps. Each trap was dug into the ground so that its rim was flush with the ground surface; trap catches can be qualitatively and quantitatively affected by the level of the rim of the trap above the ground (Greenslade 1964), so a precise fit between trap lip and ground surface was imperative.

In 1984, regular pitfall trapping was in operation from 27 April until 30 November. Sets of ten traps were placed on all limestone sites, both <u>Juncus</u> moor sites, and blanket peat site L. The traps were left in place during the winter months until April of the following year.

In 1985, regular pitfall trapping took place between 5 April and 31 October. Trapping was discontinued on limestone sites G and H, and the number of traps in operation on limestone site K, _Juncus_ moor site M, and blanket peat site L was doubled, effectively giving two basic trapping units (ie KX and KY, MX and MY, LX and LY) on each of these sites. In addition, a row of five traps was set in operation on each of the blanket peat sites LE, LF, EX, EY, FX, and FY, and ten traps on site FE (Table 3.2). These latter sets of traps, in association with blanket peat site L and limestone sites E and F, formed a transect passing from limestone grassland onto blanket peat and from one limestone outcrop to another (Figure 3.1). When considered together, traps at equivalent locations on the blanket peat (ie LE+LF, EX+EY, FX+FY) formed the standard ten-pitfall trapping unit. Data from them were used in the analysis of interchange of beetles between habitats in Section 6:6. All traps were left in place during the winter months, and finally taken up in April 1986.

3:1.3 Trapping at Tailbridge

A set of ten traps also formed the basic trapping unit on this study area, but here the traps were placed in a single line on each site with 3m between each trap. The lines ran perpendicular to the transect line crossing the habitat interface, and hence parallel to the interface itself (Figure 3.2). Trapping was in operation during 1986 from 14 April until 25 August.

Figure 3.1

Schematic layout of the sampling transect across limestone and blanket peat habitats at Moor House in 1985. Letters in upper and lower case refer to locations of pitfall and window traps respectively.

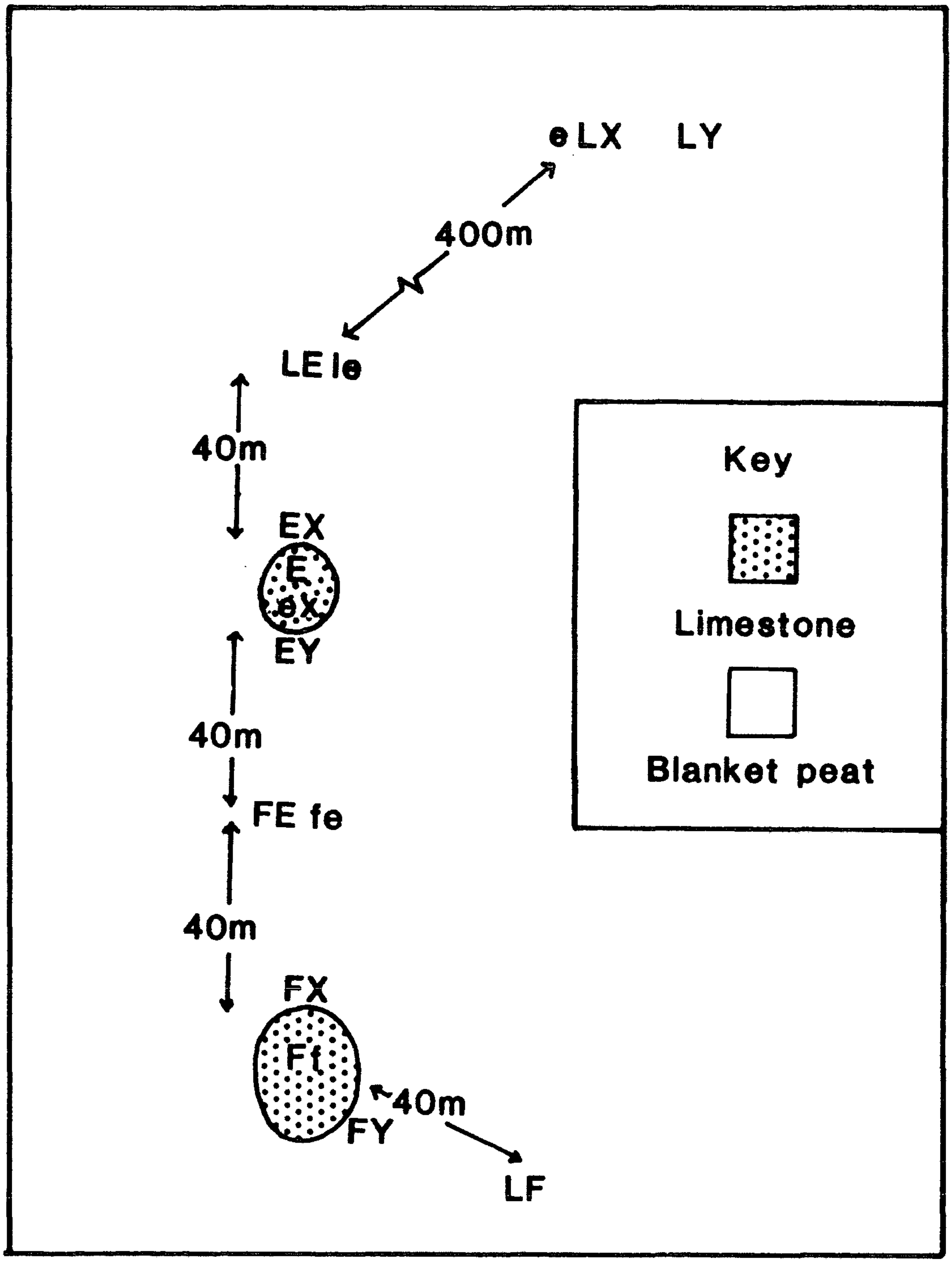
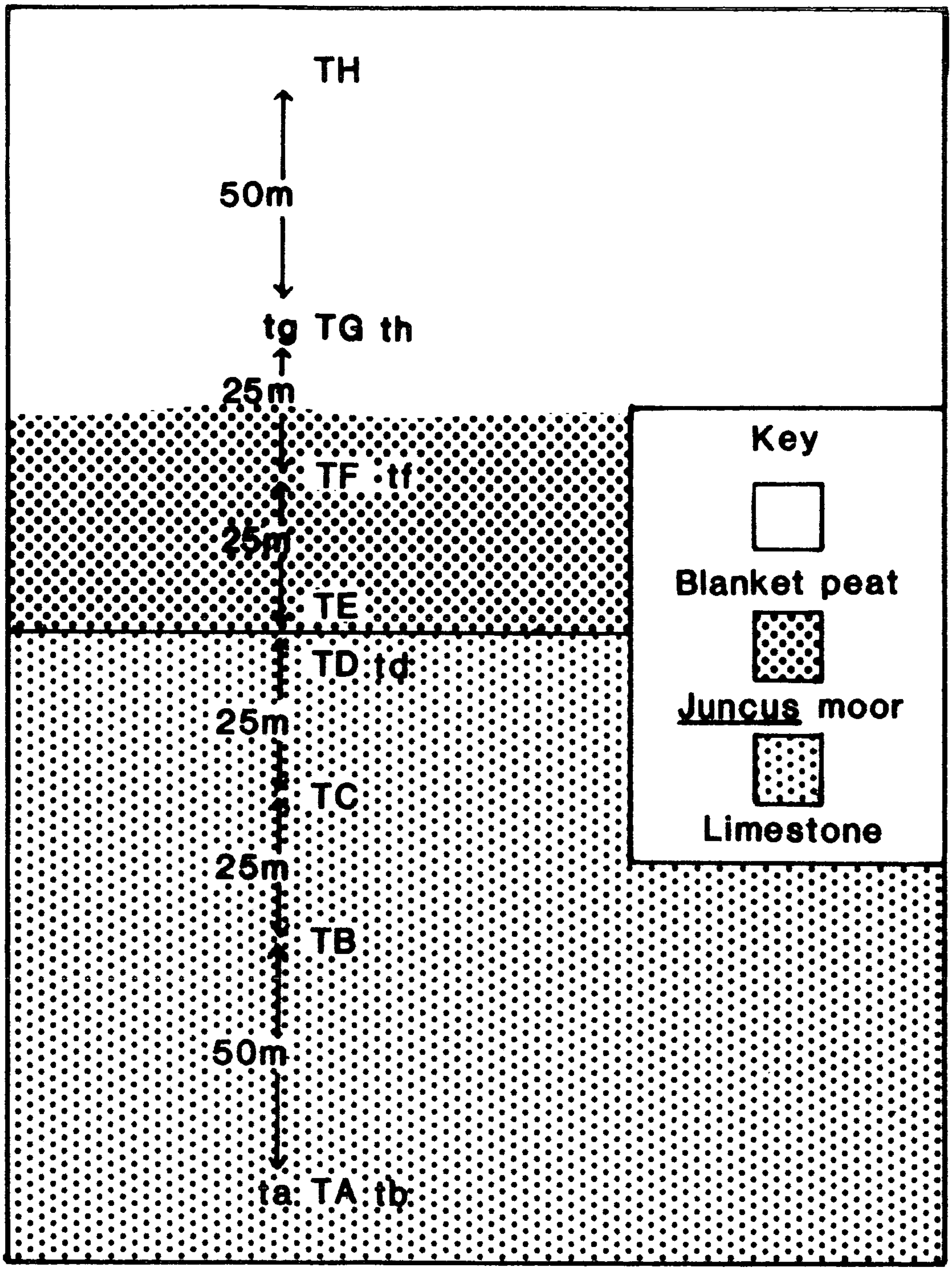


Figure 3.2

Schematic layout of the sampling transect across limestone and blanket peat habitats at Tailbridge in 1986. Letters in upper and lower case refer to locations of pitfall and window traps respectively.



3:1.4 The collection of samples

All traps were emptied and reset at fortnightly intervals throughout the field season (April-November), and their contents sorted, labelled and stored in 70% alcohol. Samples from each trapping unit were labelled with the letter of the site they were taken from, and material from the individual traps was kept separate, so that levels of within-site variability could be assessed. All carabid and staphylinid individuals were identified to species, counted, and stored separately.

3:2 Window traps

3:2.1 General Overview

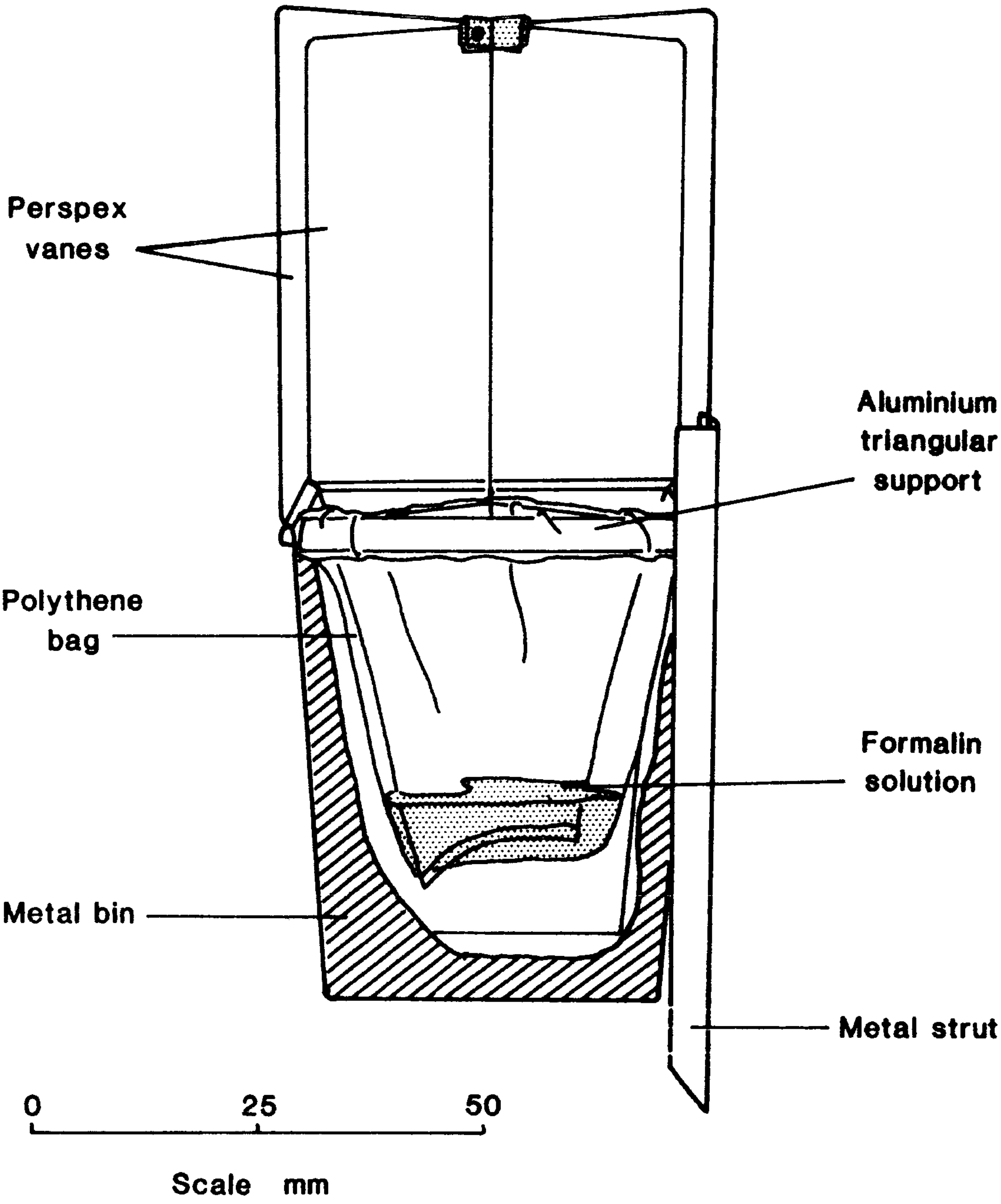
Flying beetles and other heavy-bodied insects tend to fall upon hitting an obstacle during flight. The window trap is designed to exploit this principle. It basically consists of a large pane of glass or clear perspex held vertically over a collecting trough containing a solution of preservative and wetting agent (Chapman and Kinghorn 1955, Van Huizen 1977, 1980), and functions because the insects flying against the pane generally drop into the collecting fluid before they can recover and regain flight.

Chapman and Kinghorn (1955) found that light-bodied forms such as midges and aphids were not taken efficiently in window traps, but that most Coleoptera and many Hymenoptera, Diptera, Lepidoptera and other winged insects were frequently captured. Wind conditions influenced trap performance, and the flight behaviour of the insects was a significant factor in the effectiveness of their capture, with some insects apparently avoiding the trap because of the visual obstruction presented by the supporting structures and trough. They concluded that the traps nevertheless took a sufficient sample of many of the insects common in an area to permit satisfactory determinations of seasonal abundance, site distribution and the relationship of flight to weather conditions. Window traps have been used extensively, and to good effect, to sample flying carabids in the Netherlands in a variety of habitat types (Den Boer 1970, 1971, Meijer 1971, 1974, Van Huizen 1977). They have an advantage over other designs such as light traps, in that they do not appear to attract or repel the airborne insects but intercept them more-or-less at random (Van Huizen 1980), thus (theoretically) allowing indices of absolute population and directions of flight to be more easily obtained (Southwood 1978). Like pitfall traps, they are also relatively simple and inexpensive to construct, and may be left unattended for many days at a time with the animals effectively sampling themselves. The height above ground at which sampling normally occurs (0.5-3.0m) has been demonstrated not to bias the catchabilty of different carabid species (Van Huizen 1980).

The conventional design of window trap described above was not considered suitable or robust enough for the rigorous conditions of climate and sheep interference experienced at Moor House, and a new model (Figure 3.3) was constructed. Two 0.5 x 0.5m sheets of clear perspex interlock perpendicularly to one another, and are wedged upright into a standard metal bin, giving a total of 1m of sampling surface located 0.5m above the ground. Removable polythene bags supported on metal rims slot into each of the 4 sections of the bin delimited by the 'window'. A solution of 2% formalin and detergent in each bag quickly kills and preserves trapped specimens. During 1984, the traps were fastened down with guy-ropes, but in 1985 and 1986 these were abandoned in favour of four short metal struts positioned at each corner of the bin, and which firmly held it

Figure 3.3

Diagram of the window trap used at Moor House, Tailbridge and Durham during 1984-6. Only one metal strut and the contents of one sector are shown.



in place. The 'Moor House' design of trap possesses several features that make it superior to the earlier designs for use on the moorland sites in question. Its interlocking vanes provide mutual support and rigidity for one another; this dispenses with the need for an elaborate (or simple) frame, thus rendering the portion above the bin quite inconspicuous from a distance. They also allow all four compass directions to be sampled (and kept separate) at the same time. The shallow troughs used in the earlier designs (Chapman and Kinghorn 1955, Van Huizen 1977) would quickly become flooded by the high levels of precipitation occurring on the moorland, or their contents would be blown out by the strong winds or sampled by curious sheep. The bags used in the 'Moor House' model were each of at least three litre capacity, and well protected from wind and sheep by the metal bin. They seldom flooded completely. Bags occasionally leaked, or were badly nibbled by sheep, but this problem could be overcome in future by the replacement of bags with fitted metal or plastic containers.

3:2.2 Trapping at Moor House

Eight window traps were in operation on the Reserve during 1984 and 1985, sampling concurrently with the pitfall traps. In 1984, five were located adjacent to the pitfall sets on the limestone sites A, B, C, F and I respectively, one was positioned beside the pitfall traps on blanket peat site L, and the other two operated independently on blanket peat sites g and d (Table 2.2). All window traps were positioned with the bin sides facing N, S, E and W compass directions. During 1985, window trapping on limestone sites C and I was discontinued, and further traps positioned on limestone site E and *Juncus* moor site J. Trapping on blanket peat site g was discontinued, but additional window traps were set in operation on blanket peat sites LE and FE. Sampling was in operation from April to October in both years.

3:2.3 Trapping at Tailbridge

Six window traps were set up on the study area; two (ta and tb) were positioned on the limestone grassland and corresponded to the pitfall traps on limestone site TA, one (td) was located on the mineral soil-peat interface next to site TD, one (tf) was sited close to the <u>Juncus</u> moor site TF, and the other two (tg and th) were positioned alongside the pitfall traps on the blanket peat site TG.

3:2.4 Trapping at Durham field station

During 1984 and 1985, an additional window trap (s) was in operation in a small area of pasture behind the Durham field station (National Grid Reference NZ 274405, altitude 76m). The field was grazed by cows and sheep for most of the field season, and bounded by deciduous woodland. The trap operated concurrently with those at Moor House, and provided a lowland comparision of the aerial fauna present.

3:2.5 The collection of samples

Window traps were emptied and reset at fortnightly intervals in parallel with the changing of the pitfall traps. During 1984, samples from the N-, S-, E- and W- facing sections of the traps were kept separate, but in 1985 and 1986 these components were combined at the time of emptying to give single fortnightly samples for each window trap. The trap contents were sorted into major insect groups, counted, and stored in 70% alcohol. Samples from each window trap were labelled in lower case with the letter of the site they were taken from. All carabid and staphylinid individuals were identified to species, counted, and stored separately.

3:3 Soil samples

During 1984, soil samples were taken with a view to obtaining an estimate of the absolute densities of certain species on a site, as a supplement to other methods of collection. Owing to the meagre extent of the limestone outcrops under study, and the fragility of the grassland habitat, only very restricted sampling was possible here, and was limited to the two relatively large limestone sites A and I. Sampling on these sites took place in early May (site A) and late October- November (sites A and I). On each occasion, soil cores were taken randomly using a 102mm diameter corer to as great a depth as the thin soil would allow. Similar samples were taken from _Juncus_ moor site M in early May for comparison. The cores were initially hand-sorted and then placed in Berlese funnels to extract any remaining animals. Material was sorted, labelled and stored in 70% alcohol.

3:4 Dung samples

Sheep dung was collected from the limestone grassland at Tailbridge Hill on several occasions during the field season of 1986. Any beetles present were extracted by flotation (in water) and hand-sorting in the laboratory. Material was identified, labelled and stored in 70% alcohol.

Chapter 4 THE BEETLE FAUNAS ON LIMESTONE GRASSLAND AND BLANKET PEAT

4:1 The carabid and staphylinid species present

Totals of 5417 carabids belonging to 43 species and 22544 staphylinids of 157 different species were taken in pitfall and window traps at Moor House and Tailbridge during 1984-86. A list of the species, their relative abundances in pitfall traps on the different habitat types in each study area, and their capacities for flight, is given in Table 4.1. In the following sections, the carabid and staphylinid composition of catches made on different sites during one year's sampling are overviewed.

4:2 The surface fauna (pitfall trap catches)

4:2.1 Moor House

a) Carabids

Average numbers of carabid species were over twice, and average numbers of individuals over five times as high in catches from the limestone grassland as in those from the surrounding blanket peat (Table 4.2a). Of the eleven commonest species (Table 4.3), six were present on both habitat types, five were taken only on limestone, and none were found solely on blanket peat. The three species contributing most to the increased densities on the limestone, *Patrobus assimilis*, *Carabus problematicus* and *Loricera pilicornis*, were also present on the peat, and only *C. problematicus* was significantly less abundant on this latter habitat than on the limestone (Table 4.4). The two most abundant species on the peat, *Carabus glabratus* and *Leistus rufescens*, were significantly more abundant

Table 4.1

Carabid and staphylinid species recorded at Moor House and Tailbridge during 1984–6. Nomenclature after Kloet and Hincks (1977).

HABITAT

Lime = limestone grassland
Impr = improved _Juncus_ moor
Untr = untreated _Juncus_ moor
Peat = blanket peat

ABUNDANCE (mean numbers taken in ten pitfalls/year)

A = abundant (> 30 individuals)
F = frequent (6-30 individuals)
S = scarce (< 6 individuals)
- = absent

FLIGHT ACTIVITY

* = present in window traps at Moor House/Tailbridge

Table 4.1 (cont.)

Species	Moor House				Tailbridge		
	Lime	Impr	Untr	Peat	Lime	Untr	Peat
CARABIDAE							
Cychrus caraboides	S	–	–	S	–	–	–
Carabus glabratus	S	–	–	F	–	–	–
C. nitens	–	–	–	–	–	S	–
C. problematicus	F	–	S	S	S	F	F
C. violaceus	S	–	S	–	S	S	S
Leistus rufescens	S	–	S	F	–	S	–
Nebria gyllenhali	S	–	–	–	–	–	–
N. salina	S	F	–	–	F	A	A
Notiophilus aestuans	–	–	–	–	S	S	–
N. aquaticus	F	–	S	–	A	F	S
N. biguttatus	F	S	S	–	S	S	S
N. germinyi	S	–	–	–	S	S	S
• *Loricera pilicornis*	F	F	S	S	S	F	S
Dyschirius globosus	–	–	–	–	S	S	F
Clivina fossor	–	–	–	–	F	S	S
Patrobus assimilis	F	S	S	S	S	F	A
P. atrorufus	C	S	S	–	A	S	–
Trechus micros	S	–	–	–	–	–	–
T. obtusus	S	S	–	–	F	S	S
• *T. quadristriatus*	–	–	–	–	S	S	–
Bembidion aeneum	–	F	S	–	–	–	–
B. bruxellense	S	–	–	–	–	–	–
• *B. guttula*	S	S	–	–	–	–	–
Pterostichus adstrictus	F	S	S	–	F	A	A
P. diligens	S	S	S	–	S	F	A
P. madidus	S	–	S	–	S	S	–
P. melanarius	S	–	–	–	–	–	–
P. nigrita	S	S	F	–	S	S	A
P. oblongopunctatus	S	–	–	–	–	–	–
P. strenuus	S	–	S	–	–	–	–
Calathus fuscipes	–	–	–	–	F	S	S
C. melanocephalus	S	–	–	–	A	F	S
C. micropterus	F	–	S	S	–	–	S
Olisthopus rotundatus	–	–	–	–	–	S	S
Agonum fuliginosum	S	S	–	S	S	S	F
A. muelleri	–	S	–	–	–	–	–
• *Amara apricaria*	–	–	–	–	–	–	–
• *A. familiaris*	–	–	–	–	S	S	–
A. lunicollis	S	S	F	–	S	S	–
A. ovata	–	S	S	–	–	–	–
Trichocellus cognatus	S	–	–	–	–	–	–
• *Bradycellus harpalinus*	–	–	–	–	–	–	–
B. ruficollis	S	–	–	–	–	–	–

Species	Moor House				Tailbridge		
	Lime	Impr	Untr	Peat	Lime	Untr	Peat
STAPHYLINIDAE							
• *Megarthrus depressus*	S	–	S	–	–	–	–
Anthobium unicolor	–	–	S	F	–	–	–
Olophrum assimile	F	S	–	–	–	–	–
O. piceum	F	F	S	A	S	A	A
• *Deliphrum tectum*	–	–	–	–	–	–	–
Arpedium brachypterum	F	–	–	F	S	S	S
• *Acidota crenata*	S	–	S	S	S	–	S
A. cruentata	S	–	–	–	S	–	–
• *Lesteva longoelytrata*	S	S	–	–	–	F	–
L. monticola	A	A	S	A	S	F	A
L. pubescens	S	–	–	–	S	S	–
L. punctata	–	–	–	S	–	–	–
• *Anthophagus alpinus*	–	–	–	–	–	–	–
• *A. caraboides*	–	–	–	–	–	–	–
• *Phyllodrepa floralis*	–	–	–	–	–	–	–
• *Dropephylla grandiloqua*	–	–	–	–	–	–	–
• *D. vilis*	–	–	–	–	–	–	–
• *O. exiguum*	S	–	–	–	–	–	–
O. laticolle	S	–	–	–	–	–	–
• *O. rivulare*	–	–	–	–	–	–	–
• *O. rugatum*	–	–	–	–	–	–	–
• *Xylodromus concinnus*	–	–	–	–	S	–	–
• *Coryphium angusticolle*	–	–	–	–	–	–	–
Syntomium aeneum	S	–	–	–	S	–	–
• *Carpelimus pusillus*	S	–	–	–	–	–	–
• *Platystethus arenarius*	S	–	–	–	S	–	–
• *Anotylus rugosus*	S	S	–	–	–	–	–
• *A. sculpturatus*	S	–	–	–	–	–	–
• *A. tetracarinatus*	S	S	S	S	–	–	–
• *Oxytelus laqueatus*	S	–	–	–	–	–	–
Stenus brevipennis	S	–	S	S	S	–	S
S. brunnipes	S	–	S	S	S	S	S
• *S. canaliculatus*	S	–	–	–	–	–	–
S. impressus	S	–	–	S	–	S	–
S. melanarius	S	–	–	–	–	–	–
• *S. nanus*	–	–	–	–	–	–	–
S. nitidiusculus	S	–	–	–	–	–	–
S. picipes	S	–	–	S	–	–	–
S. pusillus	–	–	–	–	–	S	S
Euaesthetus laeviusculus	S	–	S	–	–	S	F
Lathrobium brunnipes	S	–	S	S	S	S	F
L. fovulum	S	–	S	–	S	S	–
L. fulvipenne	S	S	–	S	S	F	S
Othius angustus	S	–	S	–	F	S	–
O. myrmecophilus	S	–	S	–	F	S	S
O. punctulatus	F	–	S	S	S	S	S
Gyrohypnus angustatus	S	S	–	–	–	–	–
G. punctulatus	S	–	–	–	–	–	–
Xantholinus glabratus	–	S	–	–	–	–	–
X. linearis	S	F	–	–	F	S	–
X. longiventris	–	–	–	–	S	–	–
X. tricolor	S	–	–	–	–	–	–

Table 4.1 (cont.)

Species	Moor House				Tailbridge		
	Lime	Impr	Untr	Peat	Lime	Untr	Peat
STAPHYLINIDAE (cont.)							
* *Philonthus cognatus*	–	–	–	–	–	S	–
P. decorus	S	S	–	–	–	S	–
* *P. discoideus*	–	–	–	–	–	–	–
* *P. ebeninus*	–	–	–	–	–	–	–
* *P. fimetarius*	–	S	–	–	–	–	–
* *P. laminatus*	S	F	S	–	S	S	–
* *P. marginatus*	S	S	–	–	–	–	–
* *P. nigriventris*	S	–	–	–	–	S	S
* *P. puella*	–	–	–	–	–	–	–
* *P. rectangulus*	–	–	–	–	–	–	–
* *P. splendens*	–	S	–	–	S	–	–
* *P. umbratilis*	–	–	–	–	–	–	–
* *P. varians*	S	S	–	–	1	–	–
* *P. varius*	S	S	S	–	F	F	S
* *Gabrius subnigritulus*	S	S	S	–	–	–	–
* *G. trossulus*	S	S	S	–	S	–	–
Staphylinus aeneocephalus	F	F	A	–	F	F	–
Quedius boopoides	S	–	S	–	–	–	–
Q. boops	F	–	S	S	S	S	F
Q. curtipennis	S	S	F	–	S	S	–
Q. fulvicollis	S	–	–	–	–	–	–
Q. molochinus	F	S	S	F	S	F	F
Q. nitipennis	F	S	–	–	S	–	S
Q. umbrinus	S	S	S	S	–	–	–
* *Mycetoporus clavicornis*	S	–	–	S	S	S	S
* *M. lepidus*	S	–	S	–	S	–	S
* *M. longulus*	S	–	S	–	S	S	–
* *M. punctus*	S	–	S	S	–	–	–
M. rufescens	S	–	–	S	S	S	S
* *Bryoporus rugipennis*	S	–	–	–	–	–	–
* *Bolitobius cingulatus*	S	S	S	–	–	–	S
B. inclinans	S	–	–	F	–	–	S
Tachyporus atriceps	S	–	–	–	S	–	–
* *T. chrysomelinus*	S	F	F	S	F	F	S
* *T. hypnorum*	–	–	–	–	–	–	–
* *T. nitidulus*	–	–	–	–	–	–	–
* *T. pusillus*	F	S	–	–	F	–	–
Tachinus corticinus	–	–	–	–	S	–	–
T. elongatus	S	S	S	S	S	–	S
* *T. marginellus*	S	S	S	S	S	S	–
* *T. signatus*	S	F	S	S	S	–	–
* *Cypha laeviuscula*	S	S	S	–	S	–	S
Myllaena brevicornis	–	–	–	S	–	–	–
* *Autalia puncticollis*	S	–	–	–	–	–	–
* *A. rivularis*	–	S	–	–	S	–	–
Schistoglossa curtipennis	S	S	–	–	–	–	S
* *S. gemina*	S	–	–	–	S	–	–
* *Boreophila islandica*	S	–	S	–	S	S	F
* *Aloconota gregaria*	S	F	S	–	–	–	–
* *Amischa analis*	F	F	S	S	F	S	S
A. cavifrons	–	–	–	–	S	–	–
Geostiba circellaris	S	–	S	–	F	S	F
Liogluta nitidula	A	S	–	S	–	S	–

Species	Moor House				Tailbridge		
	Lime	Impr	Untr	Peat	Lime	Untr	Peat
STAPHYLINIDAE (cont.)							
* *Atheta aquatica*	–	–	–	–	–	–	–
A. arctica	S	–	–	S	S	S	F
* *A. atramentaria*	S	S	S	–	F	S	S
* *A. atricolor*	S	S	–	–	S	S	–
* *A. cadaverina*	S	–	S	–	–	–	S
* *A. cauta*	S	S	–	–	–	–	–
* *A. celata*	S	–	–	–	–	S	–
* *A. cinnamoptera*	–	–	–	–	–	–	–
* *A. cribrata*	S	–	–	–	–	–	–
* *A. debilis*	–	–	–	–	–	–	–
* *A. diversa*	–	–	–	–	–	–	–
* *A. elongatula*	S	–	S	–	–	–	–
* *A. excellens*	F	S	S	–	S	S	S
A. exigua	S	S	–	–	–	–	–
* *A. fungi*	S	S	–	–	–	–	–
* *A. fungicola*	–	–	–	–	–	–	–
* *A. hybrida*	S	–	–	–	–	–	–
* *A. hypnorum*	S	–	–	S	–	–	–
* *A. indubia*	S	S	S	–	S	S	–
* *A. longicornis*	S	–	S	–	S	–	S
* *A. macrocera*	–	–	–	–	–	–	–
* *A. marcida*	–	–	–	–	–	–	–
* *A. monticola*	–	–	–	–	–	–	–
* *A. nigricornis*	–	–	–	–	–	–	–
* *A. nigripes*	–	S	–	S	–	–	–
* *A. nigritula*	–	–	–	–	–	–	–
* *A. palustris*	–	S	–	–	–	–	–
* *A. paracrassicornis*	–	–	–	–	–	–	–
* *A. parvula*	–	–	–	–	–	–	–
* *A. procera*	–	–	–	–	–	–	–
* *A. setigera*	S	S	–	–	–	–	–
* *A. sodalis*	S	–	–	–	–	–	–
* *A. sordidula*	–	–	–	–	–	–	–
* *A. subsinuata*	–	–	–	–	–	–	–
A. tibialis	A	F	S	–	A	F	S
* *A. triangulum*	–	–	–	–	–	–	–
* *A. trinotata*	–	–	–	–	–	–	–
* *A. xanthopus*	–	–	–	–	–	–	–
* *Aleuonota rufotestacea*	–	–	–	–	–	–	–
Ocalea picata	S	S	–	–	–	–	–
Ocyusa hibernica	S	–	–	–	S	–	S
* *Oxypoda elongatula*	S	–	S	–	S	S	–
O. induta	–	–	–	–	–	–	–
O. islandica	–	–	–	–	A	S	–
* *O. opaca*	S	–	–	–	S	–	–
O. soror	S	–	S	–	A	S	–
* *O. spectabilis*	S	–	–	–	–	–	–
O. tirolensis	S	–	–	S	–	–	–
* *O. umbrata*	S	A	S	–	S	–	–
* *Tinotus morion*	S	S	–	–	S	–	–
* *Aleochara bipustulata*	S	S	–	–	S	–	–
* *A. lanuginosa*	S	S	S	–	S	–	–

Table 4.2

Average numbers of carabids and staphylinids taken in pitfall traps on limestone and blanket peat sites.

a)Moor House	Mean numbers in ten pitfalls				Significant
	LIMESTONE (n=19)		BLANKET PEAT (n=3)		difference
	mean	se	mean	se	($p < 0.05$)
CARABIDS					
Species	13.2	0.4	6.0	0.5	+
Individuals	157.6	18.4	30.7	5.1	+
STAPHYLINIDS					
Species	38.8	0.9	19.7	1.6	+
Individuals	802.4	102.2	256.0	38.1	+

b)Tailbridge	Mean numbers in ten pitfalls				Significant*
	LIMESTONE (n=2)		BLANKET PEAT (n=2)		difference
	mean	se	mean	se	($p < 0.05$)
CARABIDS					
Species	12.5	0.4	16.0	0.8	+
Individuals	233.0	56.3	345.5	28.2	+
STAPHYLINIDS					
Species	29.0	0.8	26.0	4.1	
Individuals	762.0	80.0	183.0	49.0	+

* calculated using mean numbers in sets of five pitfalls

Table 4.3

Carabid and staphylinid species averaging at least five individuals in ten pitfall traps on limestone or blanket peat sites at Moor House, listed in order of descending abundance on limestone.

	Mean numbers in ten pitfalls				Significant
	LIMESTONE (n=19)		BLANKET PEAT (n=3)		difference
	mean	se	mean	se	($p < 0.05$)
CARABIDS					
Patrobus assimilis	26.6	11.5	3.3	1.3	
Carabus problematicus	24.3	4.0	1.0	0.5	+
Loricera pilicornis	21.3	9.3	3.3	2.5	
Patrobus atrorufus	15.8	6.5	abs		+
Pterostichus adstrictus	14.4	5.9	abs		+
Notiophilus aquaticus	11.7	2.1	abs		+
Calathus micropterus	6.8	4.9	5.7	1.6	
Notiophilus biguttatus	6.0	1.2	abs		+
Nebria gyllenhali	5.6	2.5	abs		+
Leistus rufescens	3.1	1.0	9.0	2.3	+
Carabus glabratus	1.7	0.8	8.0	1.8	+
STAPHYLINIDS					
Atheta tibialis	449.0	79.7	abs		+
Liogluta nitidula	61.4	11.8	1.3	1.1	+
Lesteva monticola	55.5	15.7	38.7	12.9	
Olophrum assimile	27.5	18.9	abs		+
O. piceum	26.4	6.6	131.3	19.8	+
Staphylinus aeneocephalus	24.4	15.2	abs		+
Amischa analis	13.7	2.9	0.3	0.3	+
Atheta excellens	10.6	2.2	abs		+
Quedius boops	9.6	2.5	5.0	2.2	
Othius punctulatus	7.5	1.9	2.0	0.9	+
Quedius molochinus	7.5	1.7	21.7	1.8	+
Tachyporus pusillus	7.1	1.6	abs		+
Quedius nitipennis	6.5	1.2	abs		+
Mycetoporus lepidus	5.9	1.2	abs		+
Cypha laeviuscula	5.9	2.4	abs		+
Tachyporus chrysomelinus	5.7	1.5	0.3	0.3	+
Othius angustus	5.4	0.8	abs		+
Oxypoda umbrata	5.4	1.3	abs		+
Anthobium unicolor	abs		28.0	7.4	+

abs = absent from pitfall trap catches

here than on the limestone, whilst the third main contributor, Calathus micropterus, was equally abundant on both peat and limestone habitats. The five species taken solely on the limestone, Patrobus atrorufus, Pterostichus adstrictus, Notiophilus aquaticus, N. biguttatus and Nebria gyllenhali, comprised only a third (mean numbers per site = 52.5) of the total carabids taken on this habitat.

b) Staphylinids

Limestone grassland catches contained twice as many staphylinid species, and three times as many individuals, as those from the blanket peat (Table 4.2a). Of the 19 most common species (Table 4.3), eight were common to both habitat types, one species, Anthobium unicolor, was present only in blanket peat catches, and ten species were taken solely on the limestone. Over half of the staphylinids present in catches from limestone were of a single species, Atheta tibialis, which was totally absent in catches on the blanket peat. The second most abundant species on the limestone, Liogluta nitidula, though present on the blanket peat, was significantly less abundant here, whilst the third major contibutor, Lesteva monticola, occurred in equally great numbers on the blanket peat (Table 4.3), where it was the second most abundant species. The commonest species in peat catches, Olophrum piceum, was also present on the limestone, but in significantly lower numbers. Two other species relatively abundant on the peat, Quedius molochinus and Q. boops, were also common on the limestone, and only the former species was significantly more abundant on the blanket peat. The ten species present solely on the limestone comprised only one eighth (mean numbers per site = 99.2) of the total staphylinids taken on this habitat.

c) Summary

The limestone grasslands at Moor House were richer in numbers of species and densities of individuals of both carabids and staphylinids than the blanket peat. Over half (15) of such species common on these habitats were present solely on limestone whilst only one species was restricted to the blanket peat (Table 4.5a). Five species were common on both habitats.

4:2.2 Tailbridge

a) Carabids

The limestone grassland catches more than 25m from the habitat interface averaged only two-thirds the species and three-quarters the individuals of blanket peat samples (Table 4.2b.). Of the twelve commonest species eight were present on both habitats, but only one of these species, *Nebria salina*, was common on both (Table 4.4). Three species were taken solely on the blanket peat, and only one, *Patrobus atrorufus*, occurred on the limestone alone. The three most abundant species on the limestone, *Patrobus atrorufus*, *Calathus melanocephalus* and *Notiophilus aquaticus*, together comprising over two-thirds of the total individuals taken there, were absent from or significantly less abundant on the blanket peat. *Trechus obtusus* was the only other common carabid occurring in significantly greater numbers on the limestone than on the blanket peat. Of the three major contributors to the high carabid densities on the blanket peat, *Pterostichus adstrictus*, *P. diligens*, and *P. nigrita*, which together represented nearly two-thirds of the total carabids taken from this habitat, the latter two species were completely absent from the limestone catches, and *P. adstrictus* was significantly less abundant on the limestone than on the blanket peat. Of the other two species occurring in relatively high

Table 4.4

Carabid and staphylinid species averaging at least ten individuals in ten pitfall traps on limestone or blanket peat sites 50m or more from the habitat interface at Tailbridge, listed in order of descending abundance on limestone.

	Mean numbers in ten pitfalls				Significant
	LIMESTONE (n=2)		BLANKET PEAT (n=2)		difference*
	mean	se	mean	se	(p < 0.05)
CARABIDS					
Patrobus atrorufus	85.0	42.4	abs		+
Calathus melanocephalus	43.0	4.9	4.0	1.6	+
Notiophilus aquaticus	38.5	2.0	2.0	1.6	+
Clivina fossor	21.5	11.0	3.0	1.2	
Nebria salina	14.0	8.2	49.0	18.0	
Trechus obtusus	13.0	3.3	5.5	1.2	+
Pterostichus adstrictus	2.5	0.4	85.5	12.7	+
Carabus problematicus	1.5	1.2	10.0	1.6	+
Discychus globosus	1.5	1.2	22.0	9.0	+
Patrobus assimilis	abs		33.5	4.5	+
Pterostichus nigrita	abs		50.5	7.8	+
P. diligens	abs		59.5	5.3	+
STAPHYLINIDS					
Atheta tibialis	465.5	42.0	4.0	3.3	+
Oxypoda soror	79.5	2.9	abs		+
O. islandica	77.0	28.6	abs		+
Amischa analis	28.0	0.8	3.0	2.4	+
Othius angustus	13.5	3.7	abs		+
Xantholinus linearis	11.5	3.7	abs		+
Othius myrmecophilus	10.5	1.2	2.0	0.8	+
Geostiba circellaris	10.0	5.7	10.0	6.5	
Quedius boops	5.0	0.8	11.5	0.4	+
Atheta arctica	abs		10.5	2.0	+
Euaesthetus laeviusculus	abs		16.5	3.7	+
Olophrum piceum	abs		41.0	3.7	+
Lesteva monticola	abs		42.5	4.5	+

abs = absent from pitfall trap catches

* calculated using mean numbers in sets of five pitfalls

Table 4.5

Common carabid and staphylinid species at Moor House and Tailbridge classed using relative abundances in pitfall traps. (Species totals bracketed.)

MOOR HOUSE

ON LIMESTONE ONLY (15)

Nebria gyllenhali
Notiophilus aquaticus
N. biguttatus
Patrobus atrorufus
Pterostichus adstrictus
Olophrum assimile
Othius angustus
Staphylinus aeneocephalus
Quedius nitipennis
Mycetoporus lepidus
Tachyporus pusillus
Cypha laeviuscula
Atheta excellens
A. tibialis
Oxypoda umbrata

ON BLANKET PEAT ONLY (1)

Anthobium unicolor

MOSTLY ON LIMESTONE (4)

Carabus problematicus
Othius punctulatus
Amischa analis
Liogluta nitidula

ON PEAT AND LIMESTONE (5)

Loricera pilicornis
Patrobus assimilis
Calathus micropterus
Lesteva monticola
Quedius boops

MOSTLY ON BLANKET PEAT (4)

Carabus glabratus
Leistus rufescens
Olophrum piceum
Quedius molochinus

TAILBRIDGE

ON LIMESTONE ONLY (5)

Patrobus atrorufus
Othius angustus
Xantholinus linearis
Oxypoda islandica
O. soror

ON BLANKET PEAT ONLY (7)

Patrobus assimilis
Pterostichus diligens
P. nigrita
Olophrum piceum
Lesteva monticola
Euaesthetus laeviusculus
Atheta arctica

MOSTLY ON LIMESTONE (6)

Notiophilus aquaticus
Trechus obtusus
Calathus melanocephalus
Othius myrmecophilus
Amischa analis
Atheta tibialis

ON LIMESTONE AND PEAT (3)

Nebria salina
Clivina fossor
Geostiba circellaris

MOSTLY ON BLANKET PEAT (4)

Carabus problematicus
Dyschirius globosus
Pterostichus adstrictus
Quedius boops

numbers on the blanket peat, Patrobus assimilis and Dyschirius globosus, only the latter was present on the limestone, and in significantly lower abundance than on the blanket peat.

b) Staphylinids

The average number of staphylinid individuals taken from the limestone more than 25m from the habitat interface was four times as high as from the blanket peat, but numbers of species showed no significant difference between habitat types (Table 4.2b.). Of the thirteen most common species, five occurred on both habitats, but only one species, Geostiba circellaris was common on both. Four species were taken on the limestone only, and four were sampled solely on the blanket peat (Table 4.5b). The most abundant species on the limestone, Atheta tibialis, which comprised over half the total individuals taken on this habitat, was also present on the blanket peat but in significantly lower numbers, whilst the other two major contributors, Oxypoda soror and O. islandica, were totally absent from the peat. The three most abundant species on the blanket peat, Olophrum piceum, Lesteva monticola and Euaesthetus laeviusculus, which together represented over half the total individuals taken on this habitat, were all absent from the limestone catches, and of the next two main contributors, Atheta arctica and Quedius boops, only the latter was present on the limestone and in significantly fewer numbers than on the blanket peat.

c) Summary

The limestone grassland at Tailbridge was richer in staphylinid species and individuals than the blanket peat, but poorer in numbers of carabid species and individuals. Nearly half (12) of the species common on these habitats were found solely on the limestone or on the blanket peat, and only three species were common on both habitats (Table 4.5).

4:2.3 Comparison between study sites

The average number of carabids taken at Tailbridge was considerably higher than at Moor House, especially on the blanket peat (Table 4.2). At Moor House the limestone represented the more carabid-rich habitat, whereas at Tailbridge the peat possessed the greater abundance of species and individuals. Average numbers of staphylinids taken on like habitats were similar on both study areas, with numbers being substantially higher on limestone than peat. The limestone at Moor House was considerably more, and the blanket peat markedly less, species-rich in staphylinids than the same habitats at Tailbridge.

Despite possessing spectra of common species which differed fundamentally in overall species composition, both study areas showed a similar separation of faunas into species found predominantly on the limestone grassland, and species typically occurring on the blanket peat (Table 4.5). Moor House was characterized by having relatively more common carabid and staphylinid species (15) present only on the limestone, and fewer species (1) restricted to the blanket peat, whereas at Tailbridge relatively more common species (7) occurred only on the peat, and less species (5) were taken solely on the limestone. Eleven species were common on both study areas, five of which were most abundant on the limestone, and one of which was most abundant on the blanket peat in both areas. The other six species had differing distributions at Moor House and at Tailbridge. The exact nature of the interaction between the limestone and blanket peat faunas on these two study areas, and the reasons behind other apparent anomalies in species distributions, are considered in later chapters.

4:3 The aerial fauna (window trap catches)

4:3.1 Carabids

A total of 16 carabids of six species was taken in window traps at Moor House and Tailbridge (Table 4.6). Three species (81% individuals) were totally absent from pitfalls in the locality, and the other three represented only 7% of species sampled on the ground in these study areas. Only one species, Loricera pilicornis, was a common moorland species (cf Table 4.3).

4:3.2 Staphylinids

Of the 119 staphylinid species captured on the ground at the two study areas, 55% were also taken in window traps (Table 4.1). However, a major difference exists in the contributions of these species which were capable of flight to the faunas on limestone and peat respectively (Table 4.7). On the limestone at Moor House, such species represented over half the total species present in pitfalls on this habitat, but only 14% of the species similarly taken on blanket peat. Likewise at Tailbridge, relatively more species caught on the limestone could fly than could those on the peat. At Moor House, average numbers of such species and individuals were significantly higher on the limestone than on the blanket peat in both trap types (Table 4.8). A similar trend existed in the Tailbridge data. The overall percentage contribution of such individuals to the total individuals taken in pitfalls was low on both habitats, however, not exceeding 11% on limestone or blanket peat (Table 4.7). Of the total 99 staphylinid species taken in window traps on the study areas, 38% were completely absent from

Table 4.6

Carabid species taken in flight at Moor House and Tailbridge.

	Total numbers taken in window traps			
	MOOR HOUSE		TAILBRIDGE	
Loricera pilicornis	1	*	-	*
Trechus quadristriatus	8		-	*
Bembidion guttula	1	*	-	
Amara apricaria	1		-	
A. familiaris	-		1	*
Bradycellus harpalinus	3		1	
Total species	5		2	
Total individuals	14		2	

* present in pitfall traps

Table 4.7

The percentage of staphylinid species capable of flight in limestone and blanket peat faunas.

% in pitfall traps

	LIMESTONE		BLANKET PEAT	
	mean	se	mean	se
MOOR HOUSE				
Species	50.8	13.7	13.6	7.7
Individuals	10.9	1.1	3.4	1.5
TAILBRIDGE				
Species	45.0	9.2	32.7	9.2
Individuals	9.4	1.1	9.6	2.2

Table 4.8

Numbers of staphylinid species capable of flight in traps on limestone and blanket peat.

a)Window traps	Mean numbers per trap				Significant
	LIMESTONE		BLANKET PEAT		difference
	mean	se	mean	se	$(p < 0.05)$
MOOR HOUSE					
Total species	29.0	2.8	14.4	1.2	+
Total individuals	123.4	24.8	29.3	4.2	+
TAILBRIDGE					
Total species	19.0	0.8	14.0	0.0	
Total individuals	125.5	21.6	64.0	8.2	

b)Pitfall traps	Mean numbers in ten traps				Significant
	LIMESTONE		BLANEKT PEAT		difference
	mean	se	mean	se	$(p < 0.05)$
MOOR HOUSE					
Total species	19.7	0.8	4.0	0.5	+
Total individuals	87.4	6.4	5.0	0.5	+
TAILBRIDGE					
Total species	13.0	0.0	8.5	1.2	+
Total individuals	72.0	2.4	17.5	8.6	

pitfall traps.

4:3.3 Summary

Very few carabid species flew at Moor House or Tailbridge, and seldom, whereas the majority of staphylinid species present in the same areas were able to fly. A major distinction existed between the faunas on limestone and peat with regard to the levels of flight activity exhibited, with over twice as many species being capable of, and active in, flight on the former habitat as on the latter. Abundances of individuals of flying species were low in comparison with their non-flying counterparts. Over a third of the total species sampled from the air were not taken on the ground at all. The significance of these between-habitat differences in flight activity, and the nature of the species involved, are considered in future chapters.

4:4 The underground fauna at Moor House (Soil samples)

A single carabid and 46 staphylinid individuals were extracted from soil cores during 1984 (Table 4.9). The carabid, an adult *Pterostichus strenuus*, was taken on limestone site A where it was also frequently caught in pitfall traps. Only 13% (6) of the staphylinids taken were adults, and all species identified (a third of the larvae could not be) were commonly present in pitfall traps on the sites from which they were taken. Averages of 1.3 (± 0.4) adults and 6.5 (± 1.2) larvae were taken per ten cores on the grassland sites, giving average densities of 1.6 (± 0.5) and 7.7 (± 1.3) individuals per square metre respectively. One adult staphylinid and eight larvae were taken in cores from the *Juncus* site, giving densities of 1.3 and 10.2 individuals per square metre respectively. The paucity of data

Table 4.9

Carabids and staphylinids taken in soil at Moor House during 1984.

	Limestone site			*Juncus* moor site
	A (May)	A (Oct)	I (Nov)	M (May)
Number of cores	10	25	10	10
CARABIDS				
Pterostichus strenuus	-	1	-	-
STAPHYLINIDS				
Acidota cruentata	-	-	1	-
Othius angustus larva	4	1	-	-
O. myrmecophilus larva	-	1	-	-
O. punctulatus larva	-	2	-	-
Xantholinus sp. larva	3	-	-	-
Quedius sp. larva	-	1	-	-
Atheta arctica	-	1	-	-
A. tibialis	1	-	-	1
Boreophila islandica	-	-	1	-
Amischa analis	-	1	-	-
Unidentified larvae	-	16	4	8
Total adults	1	2	2	1
Total larvae	7	21	4	8

involved precludes any further quantitative analysis or interpretation of these soil faunal results.

4:5 The dung fauna at Tailbridge (Dung samples)

A total of 299 staphylinids of 12 different species was extracted from sheep dung at Tailbridge in 1986 (Table 4.10). All species were also taken by window trap and were present in pitfall trap catches on the same study area or at Moor House. No carabids were present in the dung. The implications of these findings are considered in Chapter 6.

Table 4.10

Staphylinids taken in sheep dung at Tailbridge during 1986.

Species	No. of individuals
Platystethus arenarius	3
Oxytelus laqueatus	5
Tachinus marginellus	14
Aleochara bipustulata	6
A. lanuginosa	4
Tinotus morion	1
Atheta atramentaria	255
A. cauta	3
A. celata	1
A. cribrata	2
A. longicornis	1
A. macrocera	4
Total species	12
Total individuals	299

Chapter 5 THE FAUNAL DIVERSITY AND CATEGORIZATION OF THE MOOR HOUSE SITES

5:1 Introduction

The general overview of the carabids and staphylinids present on limestone grassland and blanket peat at Moor House given in Chapter 4 indicated a fundamental difference between these habitats, both in characteristic numbers of species and individuals, and in the species composition of their faunas. This chapter deals with both aspects of this diversity as revealed by pitfall trap catches. The data concerned give only a comparative indication of actual numbers and densities of species on a site, since pitfall trap catches are a function of animal activity as well as abundance (cf Section 3:1). Absolute densities have been assessed by soil sampling (Section 4:4). Each set of data collected by a sampling unit (ten pitfall traps) on a site in one year is considered a discrete entity. Thus, sites may have one, two or three such data sets associated with them (Section 3:1).

When all of the Moor House sites are considered (Table 5.1), a substantial amount of intra- as well as inter-habitat variation in total numbers of species and individuals taken in a year is evident. A scatterplot of total species against the logarithm (base 10) of total individuals caught on each site reveals considerable deviation from the overall straight-line relationship (Figure 5.1): samples taken from eight different sites each contained 13 carabid species, but in numbers ranging from 43 to 308 total individuals - a six-fold difference. Conversely, samples from two sites contained 42 and 43 carabid specimens of 7 and 13 different species respectively - a two-fold variation in species numbers. Likewise, on two sites 39 staphylinid species were taken in samples of 200

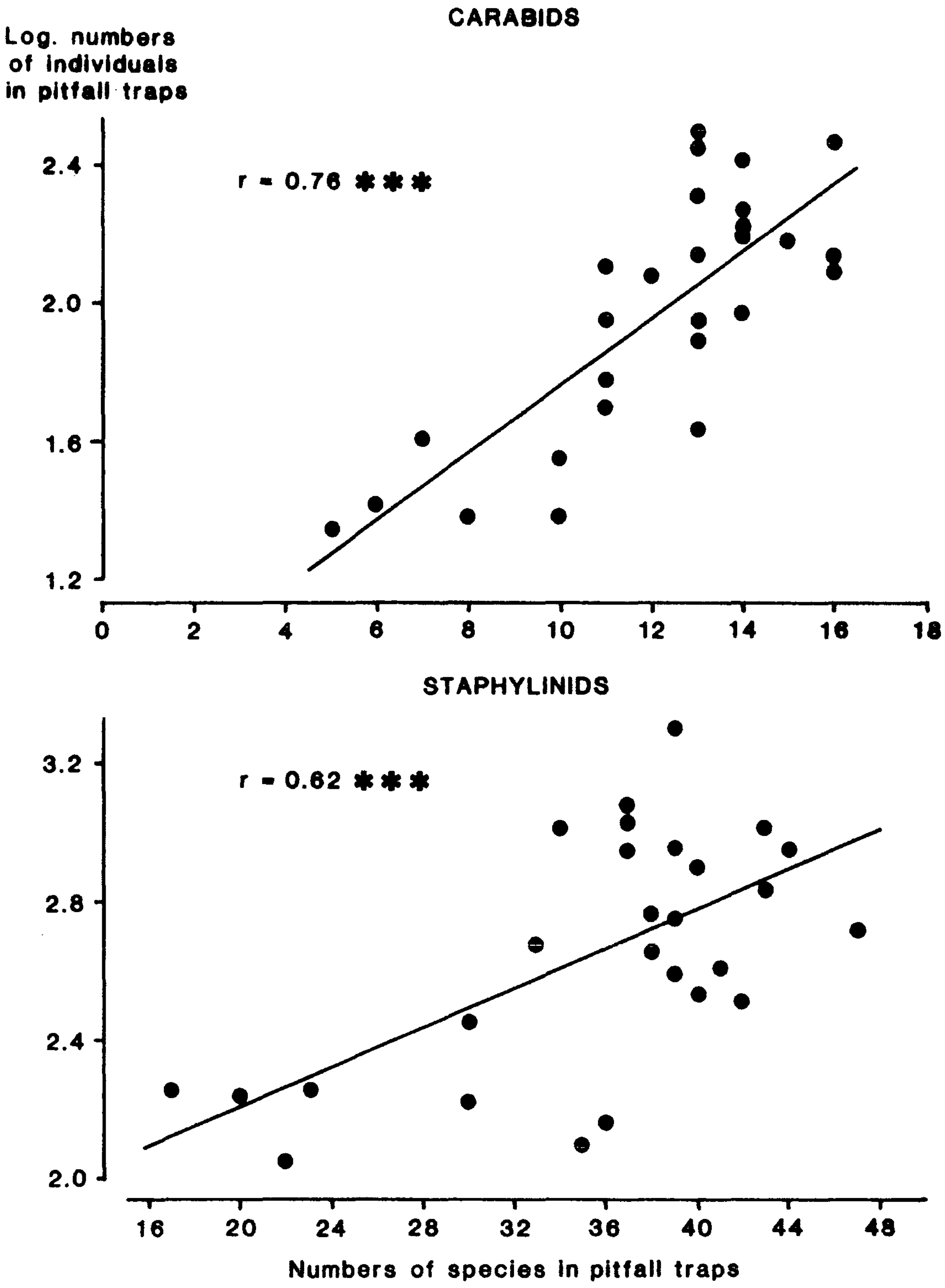
Table 5.1

Total numbers of carabids and staphylinids taken in pitfall traps at Moor House during 1984 and 1985.

	Limestone sites											*Juncus* sites			Peat sites	
	A	B	C	D	E	F	G	H	I	KX	KY	J	MX	MY	LX	LY
STAPHYLINIDS																
Species																
1984	39	34	36	36	39	38	44	37	39	43	-	40	24	-	16	
1985	36	41	39	33	31	43	-	-	42	42	46	36	32	39	21	22
Individuals																
1984	406	1021	1098	883	558	567	890	1161	2025	672	-	478	177	-	177	
1985	340	950	850	517	308	336		-	1658	464	542	140	231	200	312	306
CARABIDS																
Species																
1984	12	14	11	16	13	16	14	14	13	10	-	13	10	-	5	-
1985	11	13	13	13	16	15			14	13	11	8	11	13	6	7
Individuals																
1984	125	93	93	123	207	138	164	258	308	36	-	96	24	-	22	-
1985	128	145	180	283	297	156			164	43	54	24	61	77	28	42

Figure 5.1

Abundance of carabid and staphylinid individuals in relation to number of species taken on sites at Moor House. Data are for annual catches from sets of ten pitfall traps in 1984 and 1985. Significance levels given by ***: $p < 0.001$.



and 2025 individuals (a ten-fold difference), whilst on other sites similar-sized samples of staphylinids (306 and 308 individuals) contained 22 and 31 different species respectively. Each sample taken from a site in one year possessed a unique combination of numbers of species and individuals, quite apart from any special features in its species composition. How can this diversity peculiar to each sample be evaluated, and a meaningful comparison be made between sites from different habitats, and in different years?

Whittaker (1972) has proposed a useful classification of species diversity:-

i) Alpha diversity: the diversity of species within a community or habitat;
ii) Beta diversity : a measure of the rate and extent of change in species along a gradient from one habitat to others.

These different components of diversity are considered in turn as they apply to the system at Moor House, and a categorization of sites according to species composition is derived on the basis of them.

5:2 Alpha diversity

5:2.1 The general concept

'The prime value of a descriptive measure or index lies in its usefulness for investigating quantitatively some intuitively recognized property' (Kempton and Taylor 1974). The spectrum of habitats and sites investigated on the Moor House Reserve, and the wide variation in species abundances recorded from them, demand the imposition of some such measure to assess the differences in diversity which obviously exist. The measure used must behave consistently within a stable species population, responding to changes within, and differences between, habitats in such a way that any superficial intra-site variation is minimized while inherent differences between sites are maximized. Which diversity index possesses the high and efficient discriminant ability required? As Taylor (1978) remarks, 'The criterion for selecting a diversity statistic must be that it performs the function required of it'. Only a review of the possible alternatives applicable to the Moor House situation will reveal the best approach.

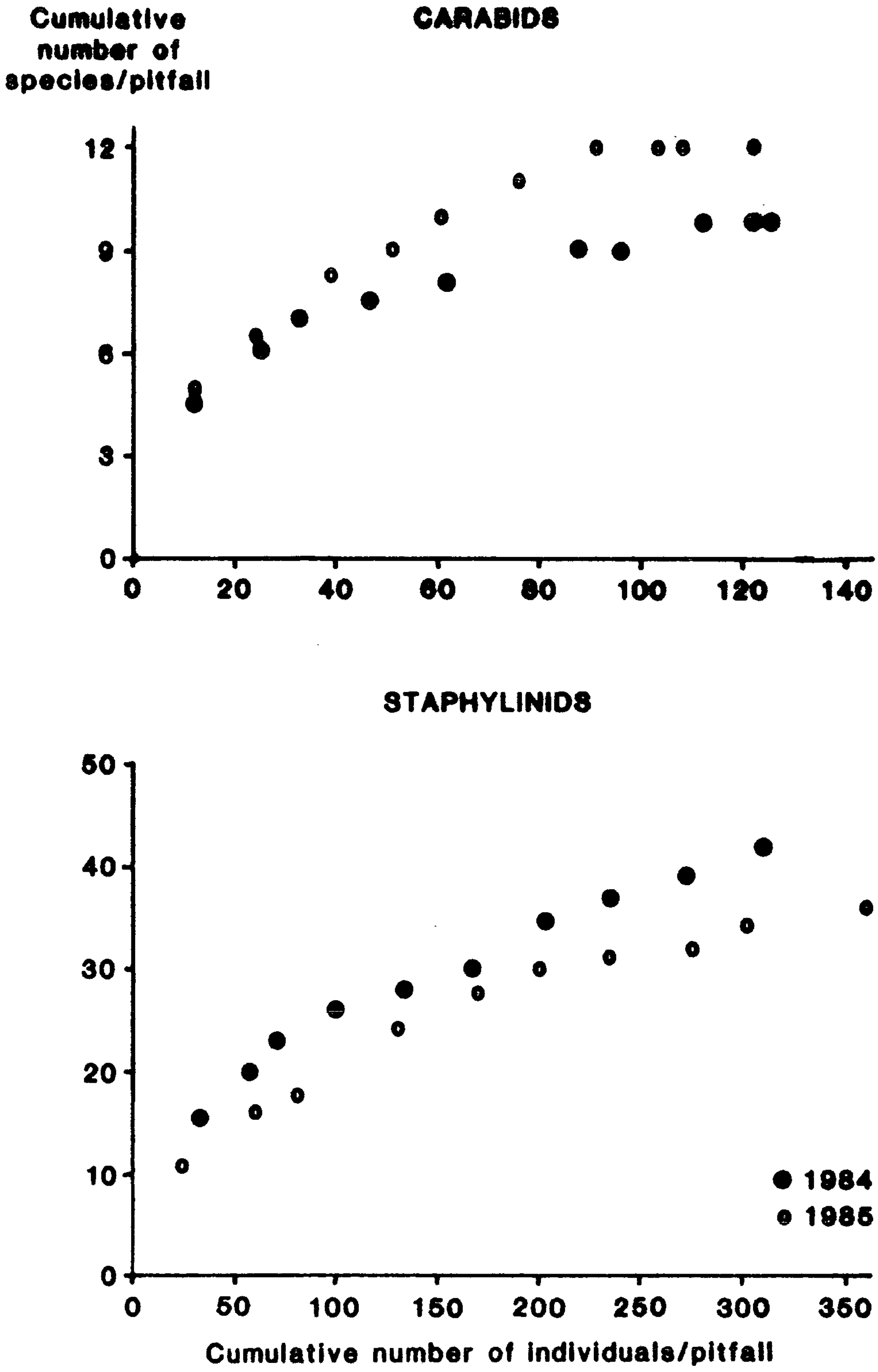
5:2.2 Species richness

If a series of concurrent samples is taken from a defined habitat, and the cumulative total of species plotted against that of individuals, a graph of the type shown in Figure 5.2 is obtained. In a well-defined stable population, a point is reached at which further sampling produces no new species, and the curve on the graph reaches an asymptote at a value which represents the total number of species ($\underline{S}$) present in that area. This parameter, $\underline{S}$, has often been taken as a simple but straightforward measure of alpha diversity (e.g. Coulson and Butterfield 1979). But however attractive such an index may be in theory, in practice it is often almost impossible to calculate satisfactorily, owing to its heavy dependence upon three important factors: a) the intensity of sampling, b) the duration of sampling, and c) the stability and discreteness of the population under consideration.

To obtain an accurate value of $\underline{S}$, ideally a complete survey of the fauna in question is required, which with insect populations in particular is virtually impossible to realise. The problems of insufficient sampling are fully evident in the data portrayed in Figure 5.2. Although an

Figure 5.2

Species:abundance curves for carabids and staphylinids when plotted using annual catches from ten successive pitfall traps. Data are from limestone site A at Moor House for 1984 and 1985.



'equilibrium' number of 12 species might be considered to have been attained for carabids in 1985, (since after sampling 90 individuals no new species were added, even when the total sample was increased by one third this size), no obvious upper asymptote was reached for carabids in 1984 or for staphylinids in both years; one must suspect that more intensive sampling (eg 12 traps as oppposed to 10) would have produced additional species. For such 'undersampled' cases S cannot be satisfactorily determined.

Sampling duration also affects the value of S. If a series of successive samples (fortnightly totals throughout the season) is used in a plot of the cumulative total of species against that of individuals (Figure 5.3), the total number of species sampled rises progressively thoughout the sampling period in a manner not dissimilar to that arising from increasing sampling intensity (Figure 5.2). Irregularities in the shapes of the curve may be largely attributed to the seasonal occurrence of different species (the steeper portions of the curve reflecting spring and autumn peaks of beetle abundance). Clearly, if one is to obtain an accurate value of S for a habitat, a minimum of a complete year of sampling, or at least a time period known to span the activity periods of all potential species present, is essential in order to rule out any seasonality effects on the total numbers of species caught.

If continuous sampling is maintained throughout the season, then can any apparent discrepancy in the value of S between samples from the same site in consecutive years be assumed to be merely the result of inadequate sampling intensity in one or both years? If the real value of S for carabids on site A was 12, and any lower values simply indicated under-sampling, then combining data for both years from this site should merely produce a graph with a better defined plateau at an S value of 12. The evidence (Figure 5.4) does not bear this out: there is even less

Figure 5.3

Species:abundance curves for carabids and staphylinids when plotted using successive fortnightly catches from ten pitfall traps combined. Data are from limestone site A at Moor House for 1984 and 1985.

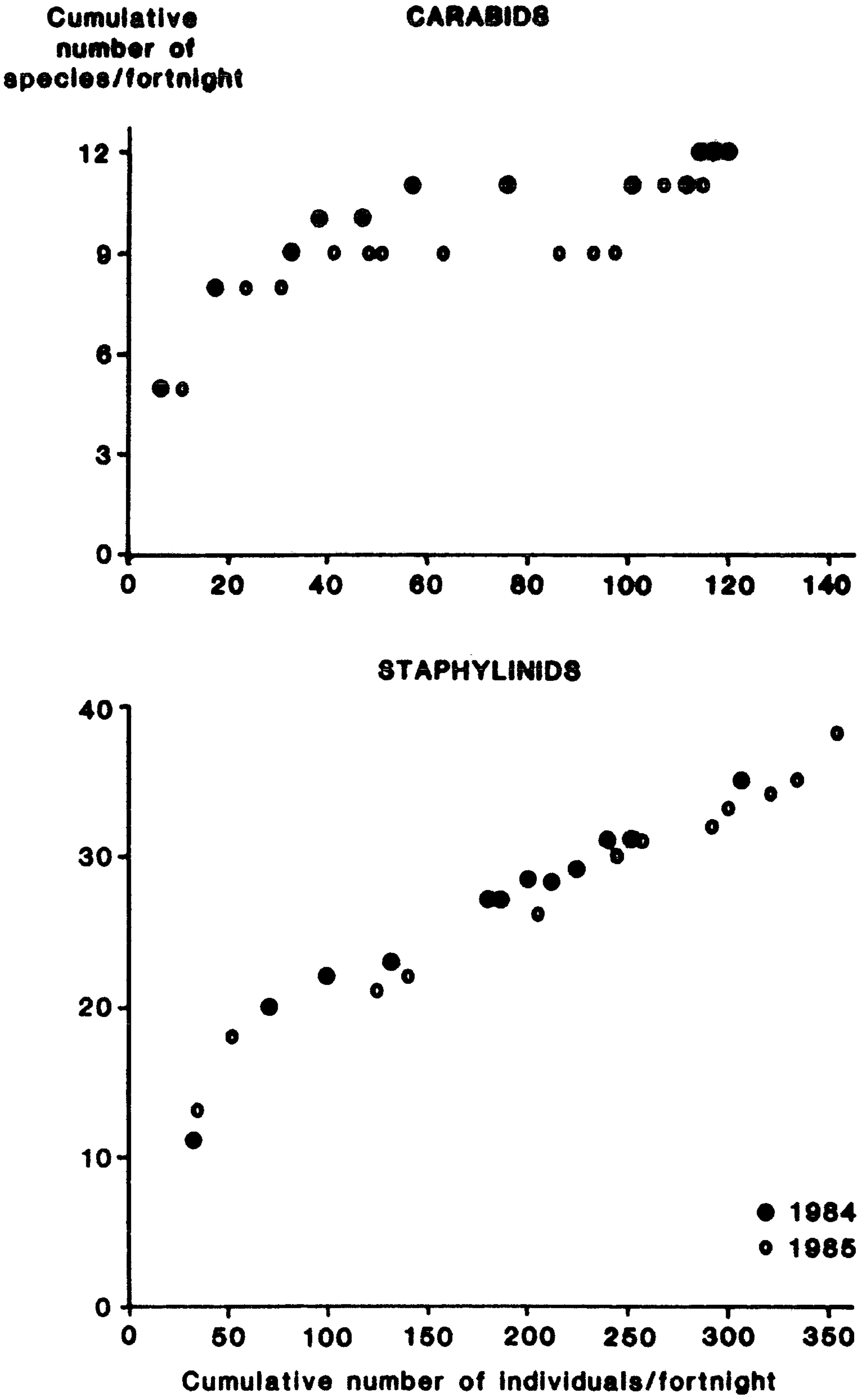
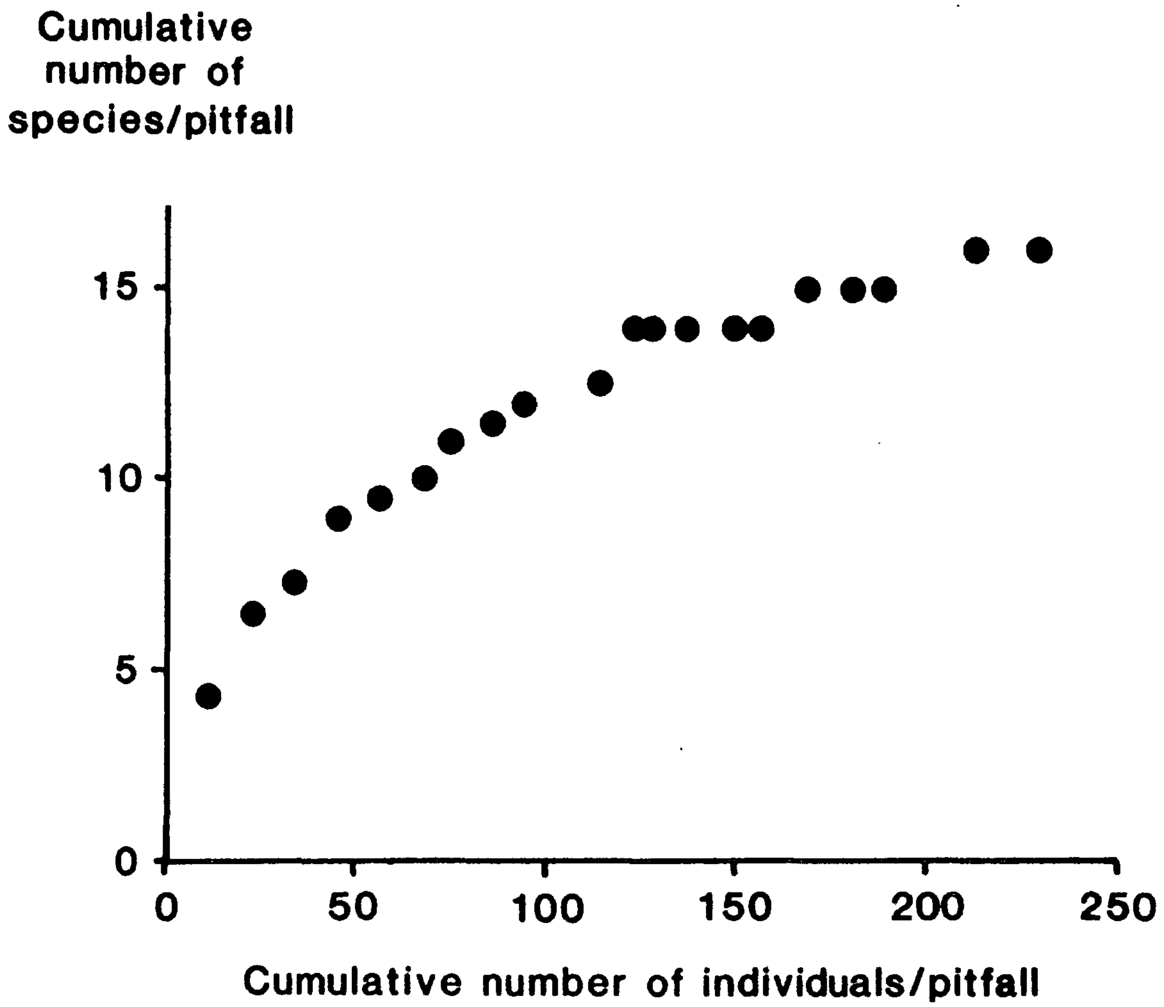


Figure 5.4

Species:abundance curve for carabids when plotted using annual catches from twenty successive pitfall traps (data from both years combined). Data are from limestone site A at Moor House.



evidence of the curve reaching an asymptote for the combined data, and, moreover, the proposed S value of 12 has risen to 16+. But is considerable under-sampling of the resident fauna in both years the only explanation?

A third factor which may greatly influence the value of S is the durational stability of the habitat concerned, and of its species equilibrium between (and within) years. A limestone outcrop such as site A is unlikely to undergo any significant changes from one year to the next in habitat characteristics such as vegetation structure. It may, however, be sufficiently small and isolated for its fauna to include species atypical of the limestone grassland habitat which have originated from different habitats bordering the site, or are immigrants from regions further afield. Such species may be represented by only a handful of vagrant individuals on the site, whose chances of being sampled in two consecutive years (if present in both) are relatively low. A simple index like S makes no allowance for the inclusion of such occasional non-resident species, treating all species alike. Moreover, the value of S for two years' data combined is effectively only taking account of the 'colonization' component of any compositional change in the fauna: the 'extinction' element is ignored. This gives a cumulative diversity index which increases from year to year although the average 'annual' diversity is much lower and may even be quite consistent (as the carabid and staphylinid data from Site A suggest). This omission is of profound importance when considering the diversity of a habitat where the annual influx of vagrant species is high or erratic. The data for site A illustrate this point (Table 5.2). Less than half of the total carabid and staphylinid species taken during 1984-5 were present in the samples taken in both years: the majority (9 carabids, 30 staphylinids) occurred in one year only. Additional sampling between July and November on the same site in 1983 contributed one more carabid and two more staphylinid species to the total. The cumulative effect of this successive annual sampling is to raise the carabid *S* value by over half as much again, and that of the staphylinids by a third as much again, when sampling is extended from one to three years (Table 5.3). If however, one makes the crude assumption that any species sampled less than six times and in one year only (ie in numbers not statistically distinguishable from zero) are vagrants and are not true members of the limestone grassland community, the revised values of *S*, although considerably reduced, are relatively consistent from one year to the next (Table 5.3).

To conclude, *S* in its unrevised form is not a very sensitive measure of species diversity. By giving equal weight to the contributions of all species, on a presence/absence basis, irrespective of differences in abundance, a very biased index is obtained : it is heavily dependent upon sample size and the inclusion of rare or immigrant species, and may be inconsistent from one year to the next. Because of its crudeness in these respects, *S* can have little value *per se* as a measure of alpha diversity in such a complex ecological system as the Moor House limestone grasslands, where sample sizes are small and the resident faunas often ill-defined or subject to sporadic contamination by immigrant species from neighbouring habitats.

5:2.3 Species equitability.

All other alpha diversity measures attempt to accommodate the differences in abundances of species by incorporating a second diversity element into their formulae, that of species equitability or evenness. Thus the species:abundance relationship has two components:

Table 5.2

Numbers of carabids and staphylinids taken in pitfall traps on limestone site A in 1984 and 1985.

	Numbers of species caught			
	1984 only	1985 only	Both years	Total
Carabids	5	4	7	16
Staphylinids	16	14	22	52

Table 5.3

The effect of sampling duration on S for carabids and staphylinids on limestone site A.

	Cumulative total species			% Increase in S
	1985	1984-85	1983-85	over 3 years
ALL SPECIES				
Carabids	11	16	17	55
Staphylinids	40	52	54	35
VAGRANT SPECIES OMITTED				
Carabids	7	8	8	14
Staphylinids	23	23	23	0

i. Species richness - the total number of species present in an area;

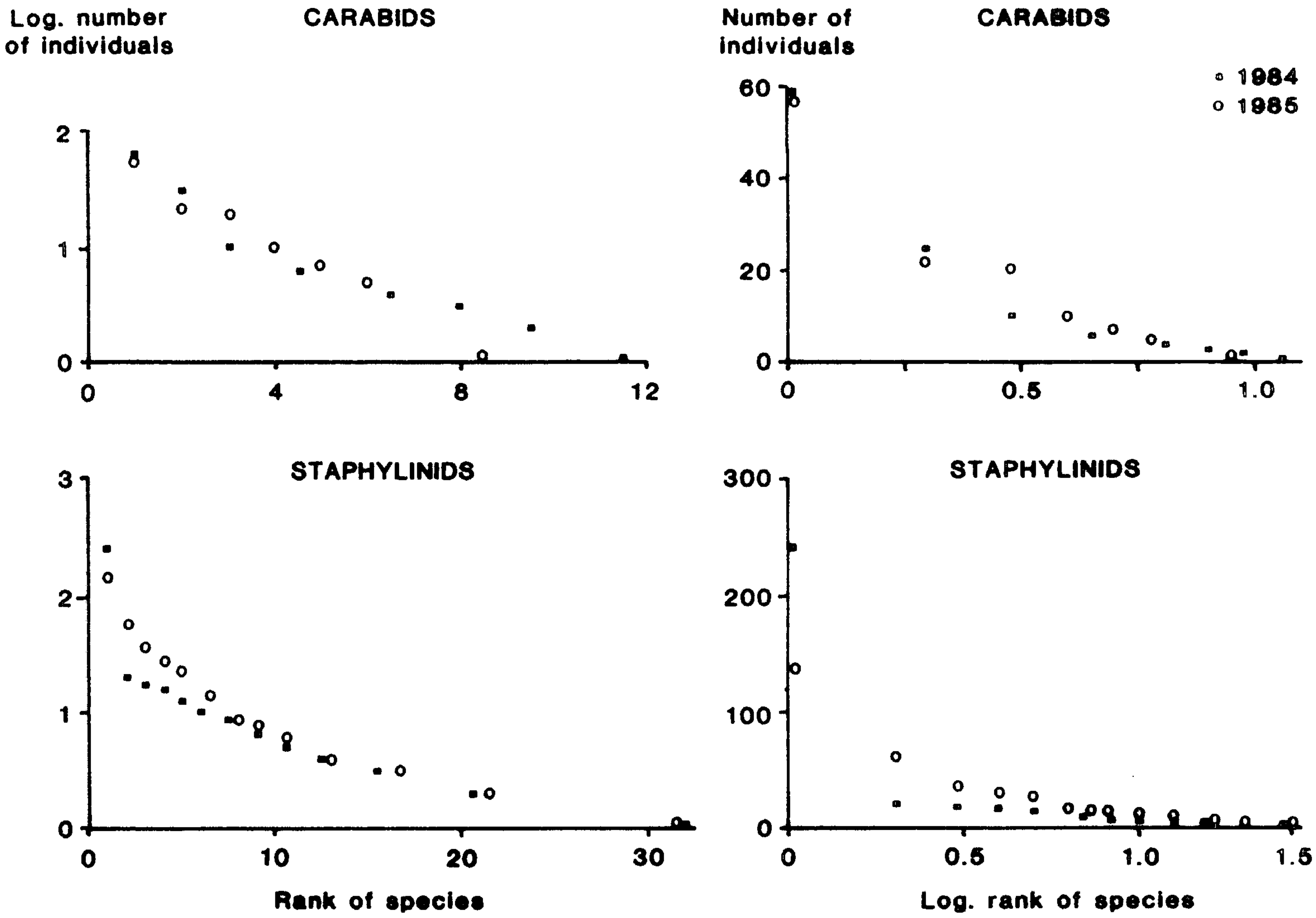
ii. Species equitability - the pattern of distribution of the individuals between the species.

When a community is sampled, it is almost invariably found that a few species are very common, several are only represented by one or two individuals, and the rest are of an intermediate abundance. This phenomenon may be illustrated by ranking the individual species according to the logarithms (base 10) of their abundances (Figure 5.5). Southwood (1978) states that the relative abundances of species can be taken to represent 'the basic pattern of niche utilization in the area', and many attempts have been made either simply to describe this pattern as accurately as possible or, alternatively, to expose the underlying distributions which have given rise to such a species pattern. In so doing the hope is that a robust measure of diversity may be obtained which is not so subject to the vagaries of sample size or rare species as is S alone.

'The equitability of the species:abundance relationship will be a reflection of the underlying distribution' (Southwood, 1978). Over the years, four main groups of mathematical models have been advanced and employed to describe the various patterns of species equitability encountered in animal communities: the geometric series, the logarithmic series (logseries), the logarithmic normal (lognormal), and MacArthur's 'broken stick' model. In a comprehensive review of the mathematical properties, applications, and relative merits of the different models, May (1975) summed up the relationships between the four types of models thus; 'If the pattern of relative abundance arises from the interplay of many independent factors, as it must once S is large, a lognormal distribution is both predicted by theory and usually found in nature. In relatively small

Figure 5.5

Rank:abundance curves for carabids and staphylinids when plotted with the logarithmic scale on different axes. Data are from pitfall traps catches on limestone site A at Moor House in 1984 and 1985.



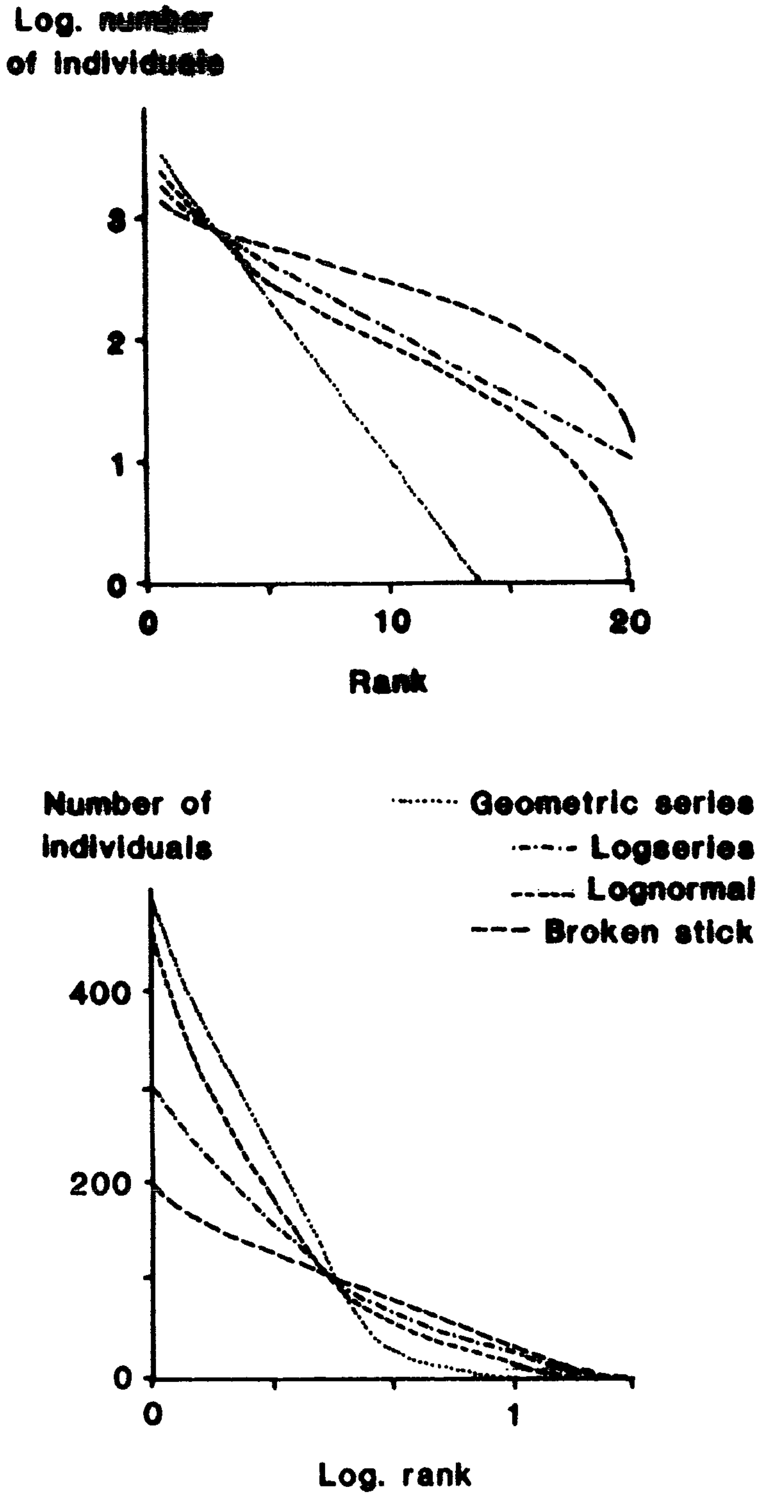
and homogeneous sets of species, where a single factor can predominate, one limiting case (which can be idealized as a perfectly uniform distribution) leads to MacArthur's broken stick distribution, whereas the opposite limit (which may be idealized as a geometric series) leads to a logseries distribution. These two extremes correspond to patterns of relative abundance which are respectively, significantly more even, and significantly less even, than the lognormal pattern'. Thus the models can be arranged in a series ranging from a highly uniform allocation of resources to a state where niche pre-emption is maximized:

(Even) MacArthur, lognormal, logseries, geometric series (Uneven).

If the logarithm (base 10) of the abundance of individuals is plotted against species rank, the geometric and logarithmic series will give approximately straight lines, whereas the broken stick model gives a straight line when the logarithm (base 10) of species rank is taken and total abundance plotted against it (Figure 5.6). When these 'model' distributions are compared with the actual rank:abundance plots for site A (Figure 5.5), it is difficult to decide which of the models most closely fits the data. Neither the carabids nor the staphylinids in either year conform to the high equitability demanded by the broken stick distribution. Such a model underestimates both the number of rare species and the abundance of the common ones in the two taxa. The same applies to the geometric series model at the other end of the equitability scale, with its strongly hierachical 'niche pre-emption' hypothesis. The markedly concave shape of the rank:abundance curve for the staphylinids, resulting from the combination of a single highly abundant 'dominant' species and many 'singleton' species, and the similar but less exaggerated rank:abundance

Figure 5.6

Model rank:abundance curves for different underlying distributions when plotted with the logarithmic scale on different axes (after Whittaker 1972).



curve for the carabids suggest that either the lognormal or the logseries model gives the closest approximation. Is it possible to differentiate between these alternatives?

When Preston (1948) first advocated the use of the lognormal distribution for obtaining the most satisfactory description of species:abundance patterns, he recognised that in practice few, if any, samples of a fauna displayed the theoretical bell-shaped curve when number of species was plotted against abundance class (using 'octaves' (logarithms to base 2) to correspond to an assumed geometric pattern of population growth). He attributed this to sample sizes typically being too small to obtain the species in the lower (rarer) octaves, and proposed that such species were hidden behind the 'veil line' (Figure 5.7). Field data would initially only represent those species to the right of the veil line, but further sampling could be predicted to shift the veil left towards the lower octaves. A logseries distribution, on the other hand, would show no such transition, since as May (1975) points out,'It <the logseries> has the elegant property that samples taken from a population distributed according to a logseries are themselves logseries' and so the logseries distribution would simply be perpetuated by further sampling.

In the case of the carabid and staphylinid data from site A, with one exception, after one year's sampling the greatest number of species occurred in the first octave (using Preston's procedure) (Figure 5.8). When the data from both years are combined for each taxon to give a larger sample size, there is no obvious change in the shape of the distribution, and it remains impossible to tell whether this is due to the sample size still being inadequate to reveal the full nature of a lognormal distribution, or because the fauna is structured according to a logseries distribution instead. Thus, although of the four conventional models proposed the lognormal and

Figure 5.7

The lognormal representation of species:abundance relationships (after May 1975). N_o marks the abundance of the species at the peak of the distribution. R represents the abundance octaves (logarithms to base 2). The solid arrow marks the direction of movement of the veil line with increasing sample size.

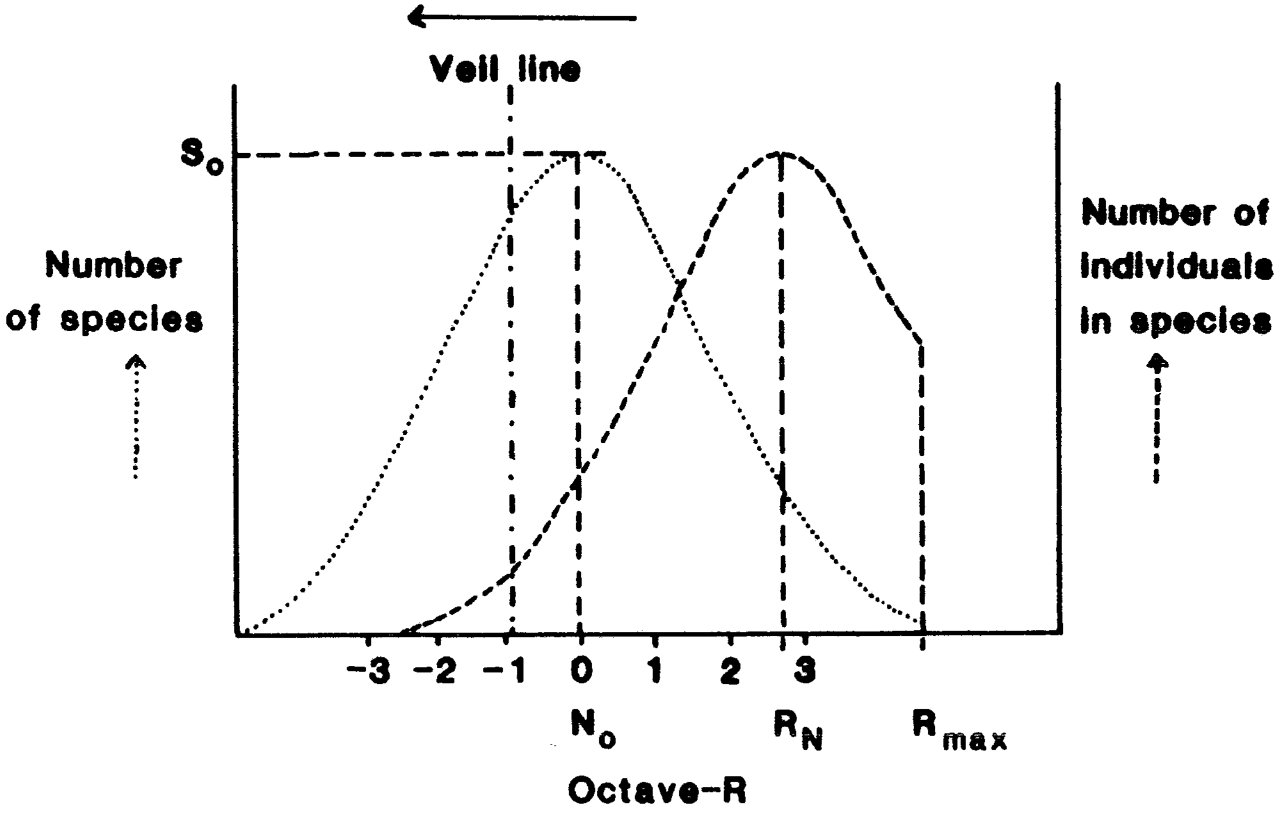
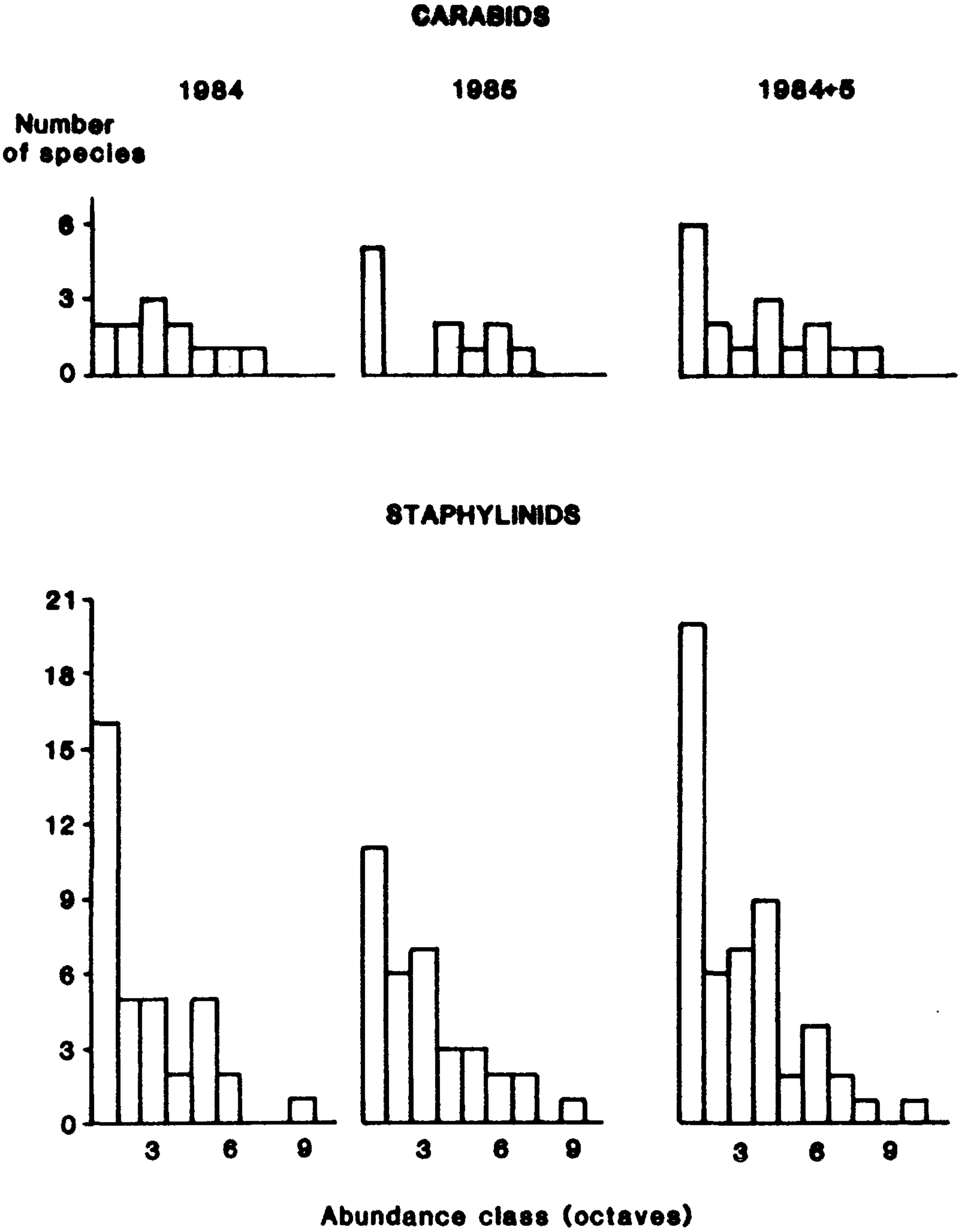


Figure 5.8

The species:abundance pattern for carabids and staphylinids where abundance is expressed in octaves (logarithms to base 2). Data are from pitfall trap catches on limestone site A at Moor House in 1984 and 1985, and for both years combined.



logseries give the best fit for the Moor House carabid and staphylinid data, the samples in question are too small and incomplete for the full nature of the species distribution to be revealed. As a result, no conclusive decision can be made as to which of the latter two models is most appropriate. The relative mathematical and philosophical merits of assuming the underlying existence of one model as opposed to the other are returned to in section 5:2.4.

5:2.4 Nonparametric indices

So far in this consideration of species diversity, attention has mainly focused on describing the nature of the complete species:abundance distribution. In practice, most workers have endeavoured to find a single parameter which satisfactorily summarizes and characterizes the distribution: a single value to describe whether the individuals are relatively evenly distributed between the species, or concentrated into a few dominant species. Many indices have been proposed and employed in such a role, and may be classed as either nonparametric or parametric. Hurlbert (1971) advocates the use of empirical measures only (ie those calculated directly from the observed relative species abundances in a sample) in the study and definition of species:abundance relations. He maintains that theoretical indices such as parameters of the model series considered earlier are inadequate for critical comparison, since the fit of the actual data to the model is always less than perfect (as the data from site A testify): hence any interpretation of the numerical values yielded by theoretical indices, or of differences in them between different samples, is of dubious value. Nonparametric indices may have the advantage of making no prior assumptions as to the fit of the species:abundance curve to a particular model, but this does not exempt them from being profoundly influenced by the nature of the underlying species:abundance distribution.

The simplest nonparametric measure of species diversity is the Dominance Index of Berger and Parker, *d*, where

d = Nmax / Ntotal where Nmax = number of individuals of the
most abundant species
Ntotal = total individuals in sample

Whereas *S*, when used as an index, gives equal importance to every species in the community, *d*, in the other extreme, considers solely the relative abundance of a single species. May (1975) concluded that it characterizes a species:abundance pattern 'as well as any <index> and better than most', on account of its relative independence from the underlying distribution and value of *S*, and thus of sample size too (see Figure 5.9). The relevance of such a finding to the Moor House data will be reviewed later.

Whatever the merits May associates with this index, the *d* values calculated from the carabid and staphylinid data for the Moor House sites (Table 5.4) suggest that it does not function very well as a diversity discriminant in this context: wherever pitfall trap data for two years are available from the same site, the value of *d* is inconsistent from one year to the next, and often shows as much if not more variation than it does between sites in the same year. For staphylinids, the *d* value is almost invariably lower in 1985 than in 1984 on the same site, whereas for carabids the relative abundance of the 'dominant' species appears to fluctuate wildly

Table 5.4

d values for carabids and staphylinids in pitfall traps at Moor House.

	CARABIDS			STAPHYLINIDS		
Site	1984	1985	1984+5	1984	1985	1984+5
Limestone						
A	0.48	0.45	0.46	0.60	0.42	0.50
B	0.41	0.27	0.28	0.79	0.59	0.69
C	0.23	0.53	0.39	0.66	0.44	0.57
D	0.36	0.58	0.51	0.71	0.42	0.60
E	0.43	0.32	0.33	0.38	0.39	0.27
F	0.21	0.24	0.21	0.58	0.34	0.49
G	0.68	-	-	0.49	-	-
H	0.35	-	-	0.64	-	-
I	0.69	0.45	0.68	0.73	0.50	0.63
K	0.58	0.28	0.41	0.41	0.41	0.40
KY	-	0.37	-	-	0.37	-
Juncus moor						
J	0.35	0.29	0.34	0.30	0.19	0.27
M	0.29	0.51	0.45	0.58	0.29	0.41
MY	-	0.49	-	-	0.29	-
Blanket peat						
L	0.55	0.29	0.34	0.53	0.41	0.45
LY	-	0.33	-	-	0.56	-

and inconsistently from year to year. The major cause of these discrepancies lies in the erratic levels of abundance of the commonest species taken on many sites, such that their order of 'dominance' on a site is rarely exactly the same from one year to the next (Table 5.5).

Of the eleven sites sampled in successive years at Moor House, less than half (5) retained the same dominant carabid species in pitfall trap catches from one year to the next, and on only eight of the sites was the dominant species in 1985 one of the three most abundant species there in the previous year. Thus although overall at least two out of the three most abundant carabid species in the catches from a site were common to both years, and on three sites the three most common species were the same from one year to the next, their order of dominance was not necessarily predictable. The situation was more consistent for the staphylinids, where besides there being at least two out of the three most abundant species present in both years at all sites save one, the relative abundances of these species were much less changeable, with catches from ten out of the eleven sites retaining the same dominant species from one year to the next.

Thus at Moor House, although the spectrum of species (particularly the common species) may have remained fairly consistent between years on the same site, yet the relative abundances of these species often altered markedly from one year to another, resulting in any one of a 'pool' of common species being 'dominant' in one year but only ranking second or less in another year. It may be argued that these shifts in relative abundance can be moderated by considering the combined data from two years' sampling, when the fluctuations will compensate each other to give a more representative average (Table 5.4). Although these combined $\underline{d}$ values do indeed tend to fall somewhere between those for each year taken separately, an added complication is introduced in that sites where sampling took place

Table 5.5

Order of abundance of the three commonest species in pitfalls at Moor House. Numbers 1-3 denote the three most abundant species in 1984. Numbers 4-5 denote species present in 1984 but not amongst the three most abundant. Numbers do not relate between sites.

		CARABIDS			STAPHYLINIDS		
		Most abundant species			Most abundant species		
Site	Year	1st	2nd	3rd	1st	2nd	3rd
Limestone							
A	84	1	2	3	1	2	3
	85	1	3	4	1	3	4
B	84	1	2	3	1	2	3
	85	4	1	2	1	3	4
C	84	1	2	3	1	2	3
	85	4	1	3	1	2	3
D	84	1	2	3	1	2	3
	85	1	2	3	1	2	4
E	84	1	2	3	1	2	3
	85	3	1	2	3	4	2
F	84	1/2	1/2	3	1	2	3
	85	3	1	4	1	3	4
I	84	1	2	3	1	2	3
	85	1	4	2	1	2	3
K	84	1	2	3	1	2	3
	85	4	1	2	1	2	3
<u>Juncus</u> moor							
J	84	1	2	3	1	2	3
	85	1	2	3/4	1	4	5
M	84	1	2/3	2/3	1	2	3
	85	1	2	4	1/4	1/4	2
Blanket peat							
L	84	1	2	3/4	1	2	3
	85	2	4	1	1	4	2/3

in one year only can no longer be directly equated with those where the *d* value derives from two years' sampling. Moreover, sceptisism must still remain regarding the accuracy afforded by only two years' data; a third season's sampling would no doubt alter the picture again. To conclude, *d* cannot be regarded as a very powerful index of diversity for the Moor House sites, since beyond the contribution made by the most abundant species in the community at the time of sampling, it takes no account of the pattern of relative abundance of the other species.

Amongst other popular nonparametric diversity indices are the Shannon-Weaver function, *H*, devised to determine the amount of information in a code and defined as

$$\underline{H} = \sum_{i=1}^{\underline{S}} pi\ (\ln pi)$$

where pi = proportion of individuals in the ith species

$\underline{S}$ = total species

and the Simpson-Yule index, *D*, which describes the likelihood of the second individual drawn from a population belonging to the same species as the first, and is defined as

$$\underline{D} = 1 / \sum_{i}^{\underline{S}} (Ni / Nt)^2$$

where Ni = the number of individuals in the ith species

Nt = total individuals

Unlike *d*, both of these measures seek to take the relative contributions of all species present in the sample into account. Even so, they have been severely criticized (May 1975, Taylor *et al.* 1976) on account of their dependence on the character of the underlying species:abundance pattern. May (1975) has described the full nature of the relationship between total species (S) and index value for H, D and d, in the context of the model distributions described earlier, and plots of his results are shown in Figure 5.9. He concludes from these that H is an insensitive measure of the distribution, being dominated by the abundant species and strongly influenced by the value of S. Likewise D is very reliant on the underlying pattern of distribution, with the lognormal type giving a D value which rises rapidly with increasing values of S, while the logseries type settles to some characteristic constant independant of the value of S. In the case of d, as the value of S becomes large, the logseries manifests its pattern of stong dominance in a d value that achieves a steady figure irrespective of increasing values of S, whilst the more even lognormal distribution shows a d value tending towards zero as the value of S increases. When one considers the Moor House data, however, some of these critisizms become rather academic and irrelevant. The numbers of species involved were never sufficiently great for anything but the very beginning of the relationship between S and H, D and d to be shown (Figure 5.10). Since at values of log S of less than 1.5-2.0 it is virtually impossible to discriminate between the different model distributions for any of the indices (because all indices are similarly greatly influenced by a changing value of S, one has to conclude that H, D and d are all equally unsatisfactory as measures of the diversity on the small and very variable Moor House sites. But is there any alternative index which can still retain its efficiency when dealing with such small, hollow-curved samples?

Figure 5.9

The diversity indices H, D, a and d, in relation to species richness, S, according to the underlying model (after May 1975). For the logseries a = 5, for the lognormal y = 1 (y = 0.7 and 1.3 also shown in the plot for H).

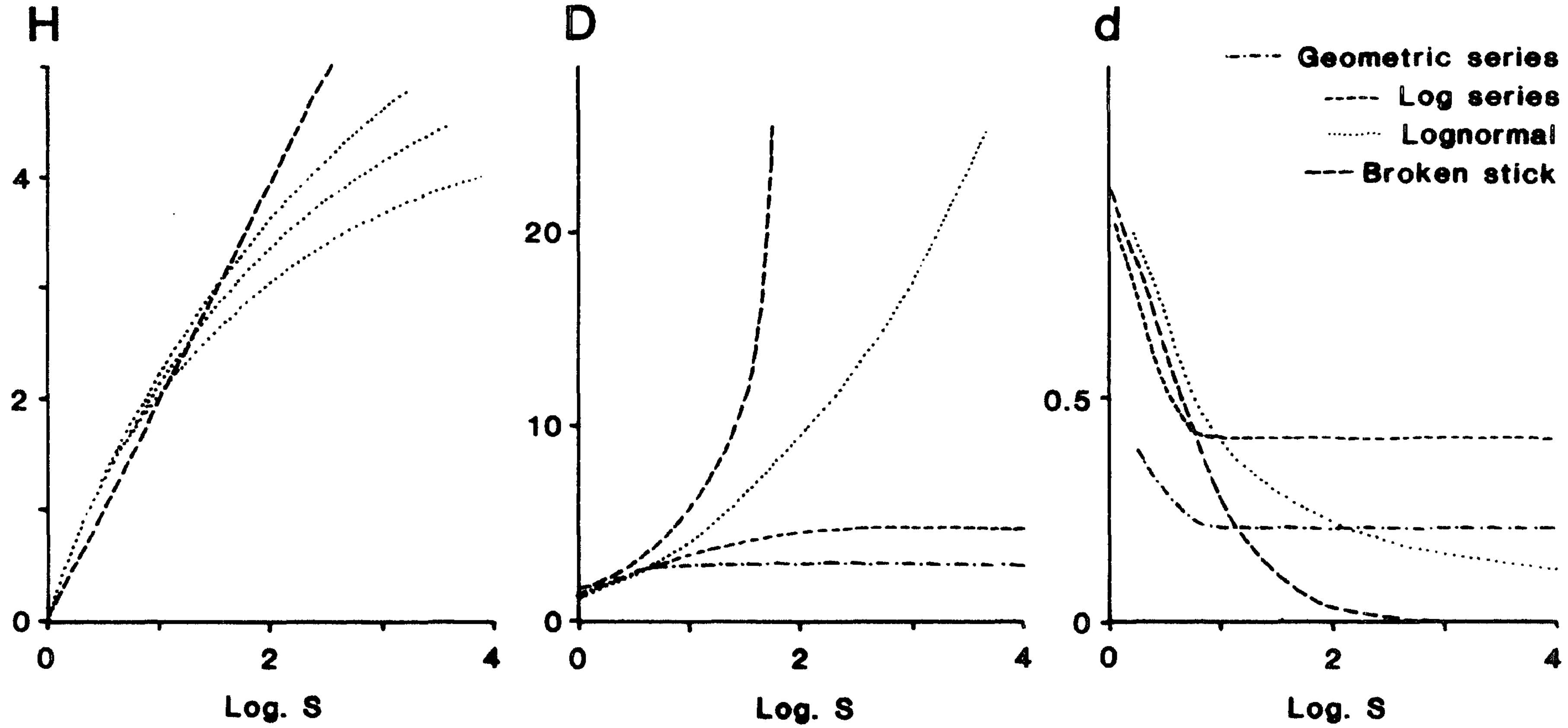
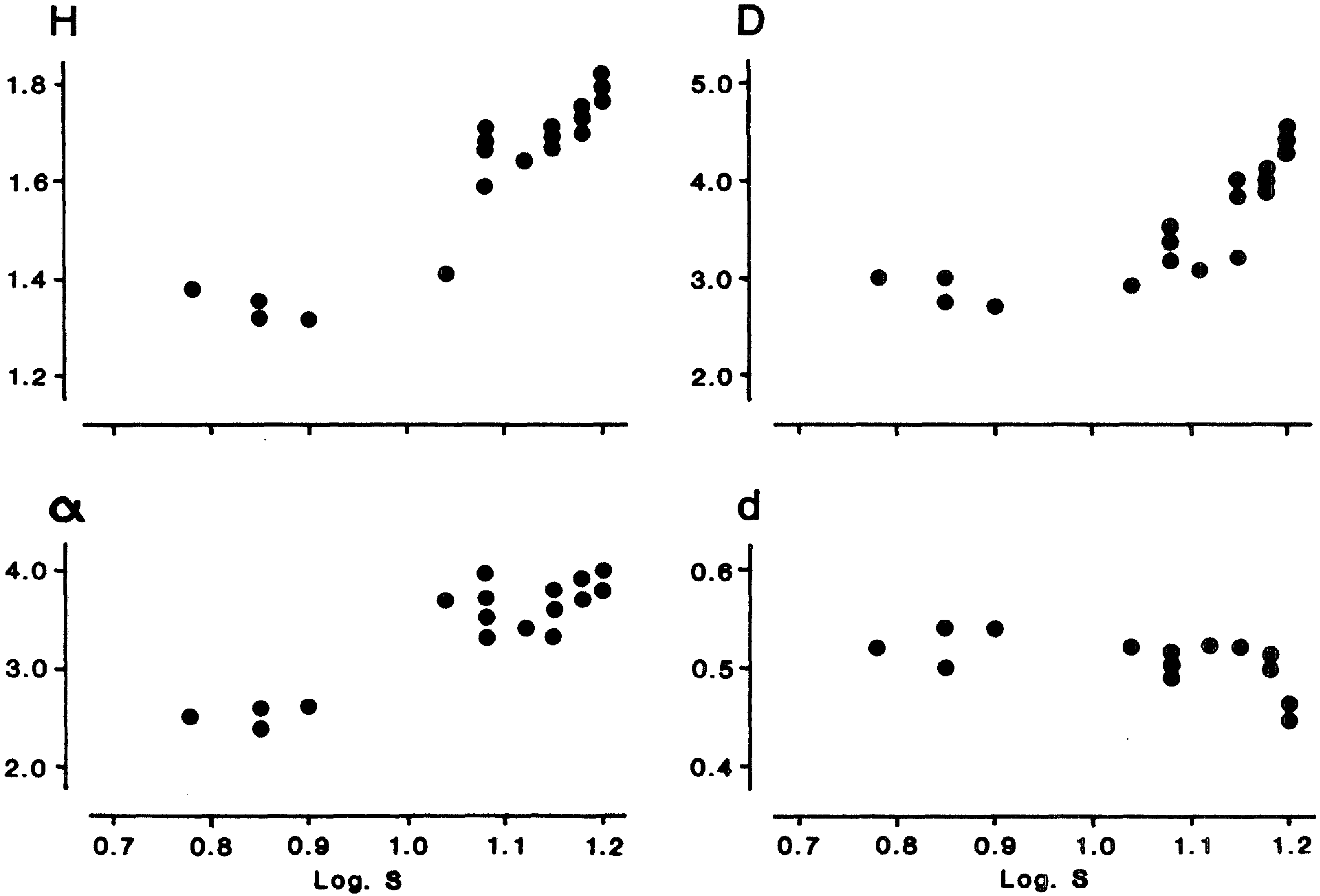


Figure 5.10

The diversity indices H, D, a and d, in relation to species richness, S, of carabids. Data are from pitfall traps catches on limestone site A at Moor House in 1984-5.



5:2.5 Parametric indices; Williams' a

The range and variety of species populations which a particular habitat or site supports can be regarded as a basic reflection of the fundamental environmental structure of that site. Therefore, it may be said that for the ecologist the importance of a diversity discriminant lies primarily in its ability to reflect, consistently, differences and changes in the environmental characteristics between the sites, which are consequently manifested in their faunas. On this premise, Kempton and Taylor (1974, 1976) argue (in direct contrast to Hurlbert (1971)) that some assumption about the mathematical form of the species:frequency distribution is essential in order that use may be made of the information on the mid-range, moderately common species, for it is these species which 'reflect most closely the nature of the environment' and are less prone to the violent fluctuations from year to year that the most abundant species exhibits. Kempton and Taylor propose that the logseries is the best model for this role, since its rank:abundance plot is almost linear over this mid-region. The slope of this region represents Williams' a, the descriptive parameter of the logseries distribution (Williams 1947).

In their consideration of the parameters of both the lognormal and logseries models as diversity discriminants, Kempton and Taylor recognized that populations in an established stable environment fitted the logseries most closely. In changing environments, less stable populations composed largely of migrant species associated with an ephemeral flora tended to fit the lognormal best, because of the more extreme skewness in the distribution of their abundances. Kempton and Taylor interpreted these findings thus, 'Because of the movement inherent in all species, samples from impoverished sites, where the resident population is at a very low density, may be overweighted by single immigrant individuals from many vagrant species bordering the impoverished zone. The resulting distribution then has a very high proportion of singletons and is strongly concave.'. However, they concluded, 'These curves tend to project unrealistic values for S*/o <the diversity parameter of the lognormal model> using the lognormal.....In this instance the less flexible logseries gives a diversity value less subject to the vagaries of the non-resident species, whose mobility provides the constantly changing succession of singletons, and is more dependent on the mid-range species resident at, and therefore more representative of, the site.' Thus even when the fit of the logseries to a set of data is not ideal, the robustness of a to deviation in either tail of the distribution may be considered to justify its use and provide a meaningful index of diversity.

The attractiveness of this philosophy as a new approach to diversity with regard to the Moor House sites is immediately apparent. Many of the unresolved problems encountered with the other indices were with precisely those aspects of the species:abundance relationship on which a places little emphasis: the wildly fluctuating abundances of the commonest species which made the nonparametric indices H, D, and d unreliable, and the long tail of rare and vagrant species which biased the value of S so heavily, rendering it inconsistent between years on the same site and unable satisfactorily to distinguish changes in diversity between sites.

The a values for carabids and staphylinids on the Moor House sites for seperate years, and for both years combined (Table 5.6), are calculated from the equation

$$S = a \ln (1 + N / a)$$

where S = total species in sample

N = total individuals in sample

According to Fisher's original theory, 'any population should have a constant value of a for samples of any size taken from it under identical conditions' (Williams 1947). Taylor (1978) insists that a must be statistically independent of the logarithm (base 10) of the total individuals in a sample before its biological dependence can be assessed. If a comparison is made between the plots of cumulative abundance against index value on the carabid data from site A (both years combined) for the various indices considered so far (Figure 5.11), it is found that a (and d) is quite independent of increasing sample size beyond an initial number of about 60 individuals, while H and D continue to rise steadily in value after this number. If the first five points on the graphs are excluded (on the premise that, in every case, the sample sizes are insufficent to give an accurate index), the slopes of a and d alone are statistically indistinguishable from zero. Similarly, a consideration of the plots of the logarithm of S against index value presented in Figure 5.10, reveals that, excepting d, a is the index most resistant to change in the face of an increasing value of S. As a consequence of this stable relationship between a and the two fundamental components of the species:abundance distribution of the samples, the a values are less influenced by perturbations to the system than are the other indices (Table 5.7): changes in index value for

Table 5.6

a and â values for carabids and staphylinids in pitfall traps at Moor House.

	CARABIDS					STAPHYLINIDS				
Site	1984	1985	1984+5	Common		1984	1985	1984+5	Common	
	a	a	a	â	se	a	a	a	â	se
Limestone										
A	3.3	2.9	3.8	3.1	0.4	10.6	10.2	12.7	10.4	1.4
B	4.6	3.5	3.9	4.0	0.6	6.8	8.7	9.1	7.7	0.8
C	3.3	3.2	3.1	3.3	0.4	7.2	8.5	8.2	7.8	0.8
D	4.9	2.8	3.6	3.7	0.5	7.6	7.9	8.2	7.7	0.9
E	3.1	3.6	3.1	3.4	0.4	9.6	8.6	10.4	9.1	1.2
F	4.7	4.1	4.6	4.4	0.6	9.2	13.1	12.3	10.9	1.5
G	3.7		-	-		9.7	-	-	-	
H	3.2			-		7.3	-	-		
I	2.8	3.7	3.5	3.2	0.4	6.9	7.8	8.8	7.3	0.7
K	4.6	6.4	5.5	5.5	1.3	10.3	11.2	12.9	10.7	1.3
KY		4.2		-			12.0	-	-	
Juncus moor										
J	4.1	4.2	4.6	4.2	0.8	10.4	15.7	13.9	12.2	1.9
M	6.5	4.0	5.3	4.8	1.1	7.5	10.1	13.7	8.9	1.4
MY	-	4.5		-		-	14.5	-	-	
Blanket peat										
L	2.1	2.4	1.8	2.2	0.4	4.3	5.9	6.5	4.7	0.6
LY	-	2.4		-			5.4	-	-	

Figure 5.11

The diversity indices H. D. a and d. in relation to the cumulative numbers of carabid individuals. Data are from pitfall traps catches on limestone site A at Moor House in 1984-5.

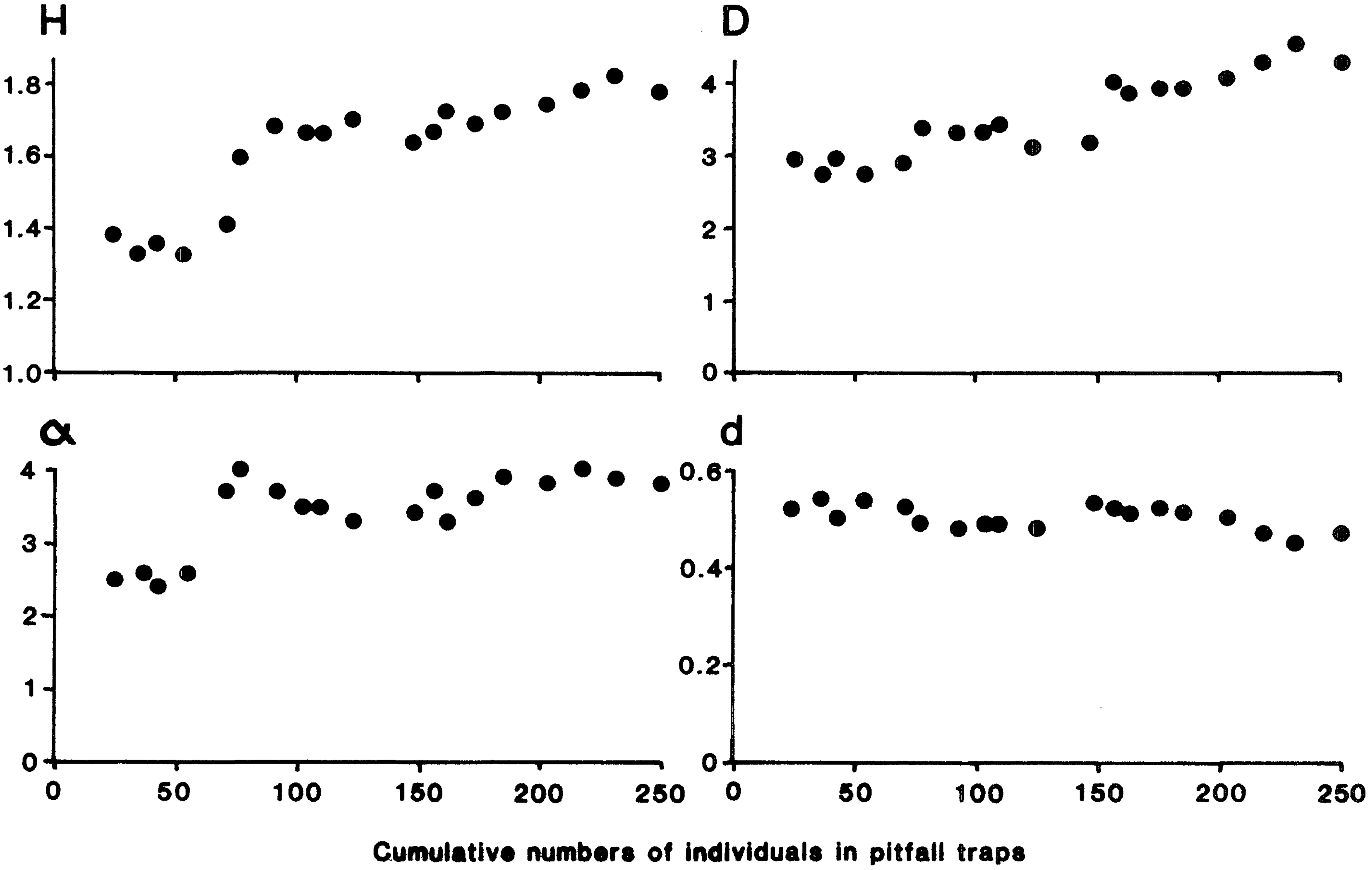


Table 5.7

Comparison of robustness of diversity indices S, d and a.

a)Constancy between years*

	CARABIDS			STAPHYLINIDS		
	S	d	a	S	d	a
Mean %	84.7	66.6	80.6	71.0	82.6	87.1
se	2.9	5.0	4.0	4.7	3.3	2.3

b)Constancy with doubled sampling duration**

	CARABIDS			STAPHYLINIDS		
	S	d	a	S	d	a
Mean %	80.9	90.4	92.5	75.2	93.6	85.5
se	2.7	1.8	1.9	1.2	2.5	2.8

c)Degree of separation of sites***

		CARABIDS			STAPHYLINIDS		
		S	d	a	S	d	a
1984	mean	12.4	0.43	3.9	35.8	0.57	8.3
	var	8.6	0.01	1.3	59.0	0.02	3.5
1985	mean	11.7	0.39	3.7	35.9	0.04	10.0
	var	8.7	0.03	1.1	56.5	0.01	9.3

Table 5.7 (cont.)

d)Significant differences between indices ($p < 0.05$)

i)Between years

	S	*d*	*a*	
S	-	3.22	ns	CARABIDS
d	-3.22	-	-2.58	
a	1.50	ns	-	

STAPHYLINIDS

ii)Between 1 and 2 years

	S	*d*	*a*	
S	-	-2.50	-3.35	CARABIDS
d	7.00	-	ns	
a	4.52	ns	-	

STAPHYLINIDS

*measured as 100i/I where i = lower index value, I = higher index value for 1984 and 1985, for sites sampled in both years.

**measured as 100i/I where i = lower index value, I = higher index value for 1984+1985 (mean value) and 1984-85 (combined value) for sites sampled in both years.

***measured as variance of indices from mean for all samples in both years.

sample size beyond an initial number of about both taxa between 1984 and 1985 are less for a than for d, though not significantly different between S and a (Table 5.7a and d). In the case of the carabids, the value of S is less changeable than d, but for the staphylinids it is more so. The average change in index value for both taxa when sampling duration is increased from one to two years is less for a or d than for S, though not significantly different between the former two indices (Table 5.7b and d). The variation in species diversity between sites in both carabids and staphylinids is greatest as measured by S, and least using d (Table 5.7c). The discriminant ability of a lies between these two. Thus overall, a acts most consistently in fulfilling three of the requirements most useful in a diversity discriminant, changing relatively little between years or with increased sampling duration on the same site, but giving a relatively high level of separation of different sites.

When replicate samples exist, values for a 'common a', $\mathbf{a}$, can be calculated (Table 5.6) by the solution of maximum likelihood of

$$\sum_{i=1}^{z} S_i = \sum_{i=1}^{z} a \ln (1 + N_i / a)$$

where z = total number of samples

S_i = total species (in 'i'th

N_i = total individuals sample)

Standard errors are calculated from $\mathbf{a}$ using the individual sampling factors (X) to monitor variation due to population fluctuations on a site between years, and where

$$\mathrm{Var}(\mathbf{a}) = \mathbf{a} / -\ln (1 - X) \qquad \text{where} \quad X = 1-e^{-S_i / \mathbf{a}}$$

The **a** values, although only derived from a sample size of two, can nevertheless be regarded as giving a more accurate assessment of the proper diversity of a site than the *a* values of the individual samples from each year, considered separately or together, and so will henceforth be taken to represent the alpha diversity of the sites where applicable.

Perhaps the most revealing aspect of the Moor House **a** (or *a*) values, is the confirmation between the two beetle faunas as to the pattern of differences in environmental structure between sites. A strong positive correlation ($r = 0.71$, df = 14, $p < 0.01$) exists between the **a** values for carabids and staphylinids on different sites, supporting the proposition that 'the index of diversity does not measure some intrinsic character of the community, but is basically an expression of the diversity of the habitat in terms of its effect on the fauna' (Bullock 1971).

The effects of seasonal diversity in the carabid and staphylinid faunas on site A may be assessed using *a* values derived from monthly samples (Table 5.8). Monthly carabid numbers are too small to obtain reasonable *a* values, and so, bearing in mind the fact that carabid and staphylinid diversities are strongly correlated overall and thus may be considered to have basically similar ecologies, the data from both taxa have been combined to give a representative joint *a*. The results confirm Fisher's (1943) findings for macro-Lepidoptera that 'there is a very much greater difference between the *a* values for two different months than there is for the same month between years.' The fact that this seasonal cycle of diversity is so marked, and may well be differently skewed at different sites, re-emphasizes the need to use a minimum of a whole year's sampling in differentiating between the spatial effects of the environment.

For carabids and staphylinids on site A, in common with the findings of Taylor (1976) for macro-lepidopteran populations, if a theoretical lognormal distribution is superimposed upon the plots of numbers of species against numbers of individuals representing those species, the species frequency distributions tend to be systematically longer-tailed (in both directions) than expected for the logseries (Figure 5.12). One might expect therefore that such under-emphasis of the extremes of the distribution would lead to ***a*** being much less influenced by major changes in the abundance of the commonest species than other indices which do not involve an underlying mathematical model. A consideration of the contribution made by the most abundant carabid species, *Patrobus atrorufus* (43% of total carabids taken on site A), to the overall values of ***a***, *H*, *D* and *d* for carabids on site A (Table 5.9), reveals that ***a*** is indeed the least affected by the removal of the commonest species, followed closely by *H*, whereas *D* and *d* are radically influenced. Taylor (1976) found a similar ordering for the first three indices, in their relative bias towards the commonest species, for macro-lepidopteran samples.

To conclude, with regard to the Moor House data considered above, Williams' *a* is by far the most satisfactory index of alpha diversity. It is least influenced by changing values of species (*S*), total numbers of individuals, and contributions of the dominant and the rarest species, and provides a measure of the diversity of the different Moor House habitats and sites on which both carabid and staphylinid faunas agree. Consequently, in all subsequent analysis involving a consideration of species diversity, unless indicated otherwise, *a* (or ***a***) will be the index used.

Figure 5.12

Species:abundance curve for carabids and staphylinids where abundance is expressed as number of individuals/species. The theoretical curve has been superimposed. Data are from pitfall traps catches on limestone site A at Moor House in 1984-5.

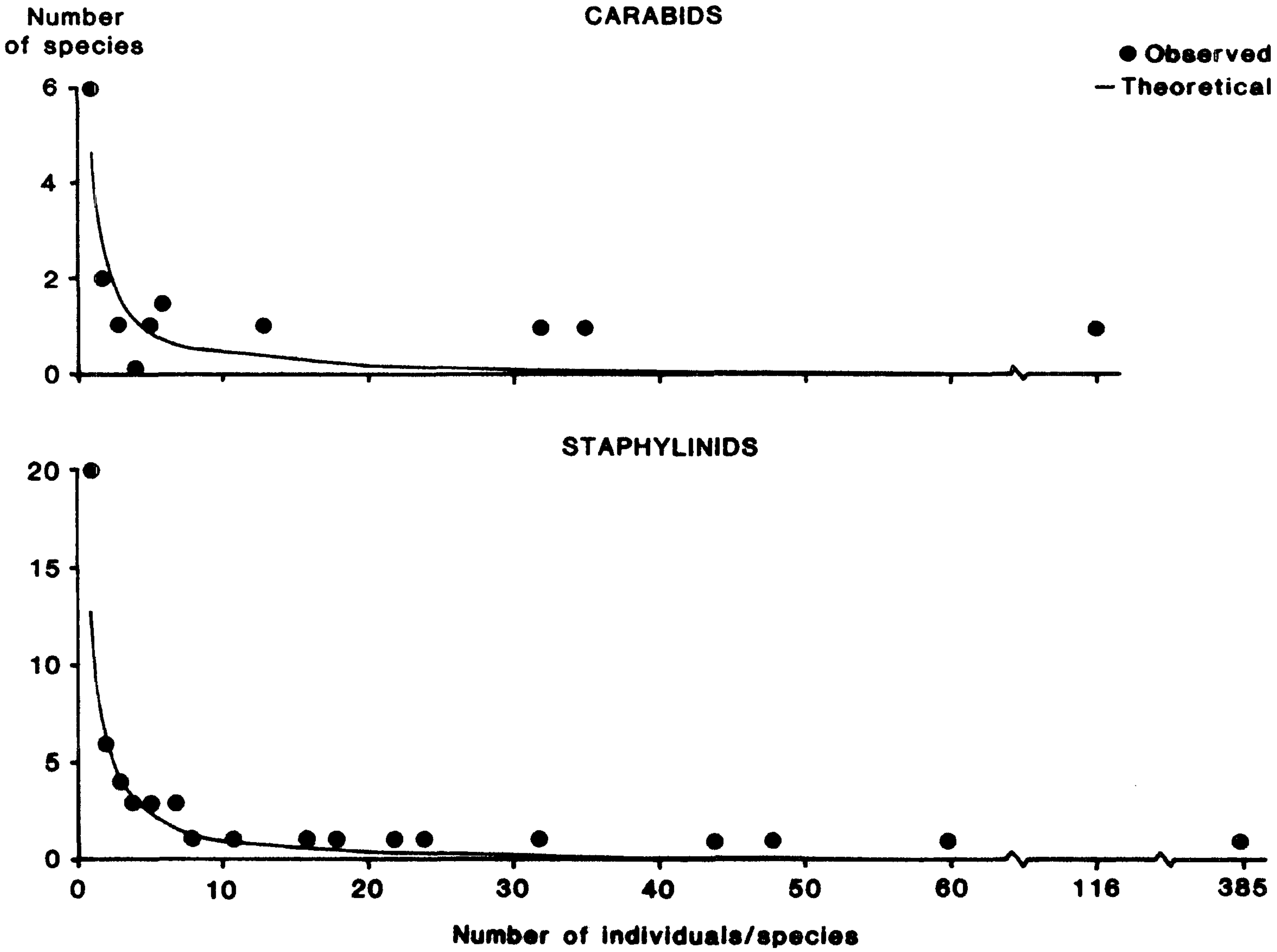


Table 5.8

a values for monthly pitfall trap catches from Site A.

	April	May	June	July	August	September	October
Staphylinids							
1985	4.0	8.0	4.0	3.0	2.5	6.0	8.0
1984	-	9.0	2.0	4.5	3.5	10.0	8.0
1983	-	-	2.0	-	3.0	6.0	-
Staphylinids + carabids							
1985	5.0	12.5	6.0	5.0	4.0	8.0	10.5
1984	-	13.0	4.0	7.0	4.5	8.0	12.0
1983		-	4.0	-	5.0	10.0	-

Table 5.9

The effect of removing the contribution of the dominant carabid species on the value of diversity indices a, H, D and d on site A.

	Value of index		Change as % of
Index	All species	P.atrorufus omitted	original value
a	3.10	3.50	12.9
H	1.78	2.03	14.0
D	4.32	5.68	31.5
d	0.46	0.26	-56.5

5:3 Beta diversity

5:3.1 Coefficient of Similarity.

The role of the indices considered in the previous section was to summarize and compare the species:abundance pattern in individual communities. The actual species composition of two different sites or habitats is compared by the use of an index which measures the mutual similarity (or dissimilarity) of their respective faunas. The simplest and most satisfactory index for this purpose is the 'coefficient of similarity' which, expressed in Sørensen's form, is defined thus:

$C = 2j / (a + b)$ where j = no. of species common to both samples

a = total species in sample a

b = total species in sample b

If applied as defined above, purely in terms of species numbers, such a coefficient gives equal weight to all species, and tends to over-emphasize the importance of rare species whose capture is heavily dependent on chance. Therefore, a modified form of the index has been used in this analysis, which takes abundance into consideration via the creation of 'pseudospecies' (Butterfield and Coulson 1983), one of which is added to the species total for a sample whenever the abundance of a species exceeds 29 (carabid) or five (staphylinid) individuals. (These cut-off levels are arbitrary, giving approximately one third of the Moor House species pseudospecies status on at least one site).

5:3.2 Sorting techniques

Sorting of the indices may be done by either classification or ordination. Classification basically involves grouping similar entities together in clusters. Ordination seeks to represent relationships between the entities as faithfully as possible in a low-dimensional space. Both techniques have been applied to the Moor House carabid and staphylinid data, using the multivariate statistical packages SPSS CLUSTAN and DECORANA respectively. The CLUSTAN program employs the average linkage method (Sneath and Sokal 1973) to place similar samples into groups. It then uses a hierarchical procedure to arrange these clusters into a dendrogram which indicates inter-group relationships. DECORANA (detrended correspondence analysis) is an improved eigenvector ordination technique based on an earlier method, reciprocal averaging, but correcting its main faults (Hill 1979, Hill and Gauch 1980). A two-dimensional graph is produced in which similar samples are near one another and dissimilar samples are far apart. An environmental interpretation of the sample arrangement may be imposed, arising from information external to the ordination itself.

5:4 The significance of habitat type for the fauna

5:4.1 Habitat-clusters

When the samples taken from the Moor House sites in 1984 and 1985 are clustered according to their similarities in both carabid and staphylinid composition, a distinctive pattern of site affinities emerges from each data set (Figure 5.13). Above a similarity coefficient value of 0.5, two samples will have over half their species (including pseudospecies) in common. This value may be set as the minimum level of similarity acceptable for the amalgamation of two samples or clusters. Imposing a base level of similarity of 0.5 upon each dendrogram separates the sites into several discrete clusters, with catches from the same sites consistently falling into the same cluster. The hierarchical pattern of clustering is remarkably similar for both taxa, producing the same four groups, which appear to be directly related to the nature of the habitat on which the sites are located, and may be labelled accordingly (Table 5.10). A similar segregation of sites according to habitat type is given by DECORANA (Figure 5.14). The significance of the spatial orientation of the catches from different sites between and within habitats on the plot, and the interpretation of its axes are considered in more detail in Chapter 8.

If the pattern of beta diversity shown above is indeed directly related to some fundamental difference in habitat structure between sites which is being reflected in their faunas, then some correlation should be present between these clusters and the *a* values of the sites which characterize them. The alpha diversities characterizing each habitat-cluster, and the average numbers and densities of carabid and staphylinid species composing its constituent sites are given in Table 5.11. Analyses of the significance of the differences between values are presented in Tables 5.12 and 5.13. The actual species compositions of different habitats, which must obviously account for much of the differences in beta (and alpha) diversity observed, are investigated in a later chapter.

5:4.2 The blanket peat fauna

The samples most dissimilar to all the rest are those deriving from the blanket peat (Figure 5.13), showing maximum levels of similarity with those

Figure 5.13

Clustering of the Moor House sites according to the similarity of their carabid and staphylinid faunas in 1984 and 1985. The dashed line indicates the level of similarity for inclusion within a cluster. Data are from sets of ten pitfall traps.

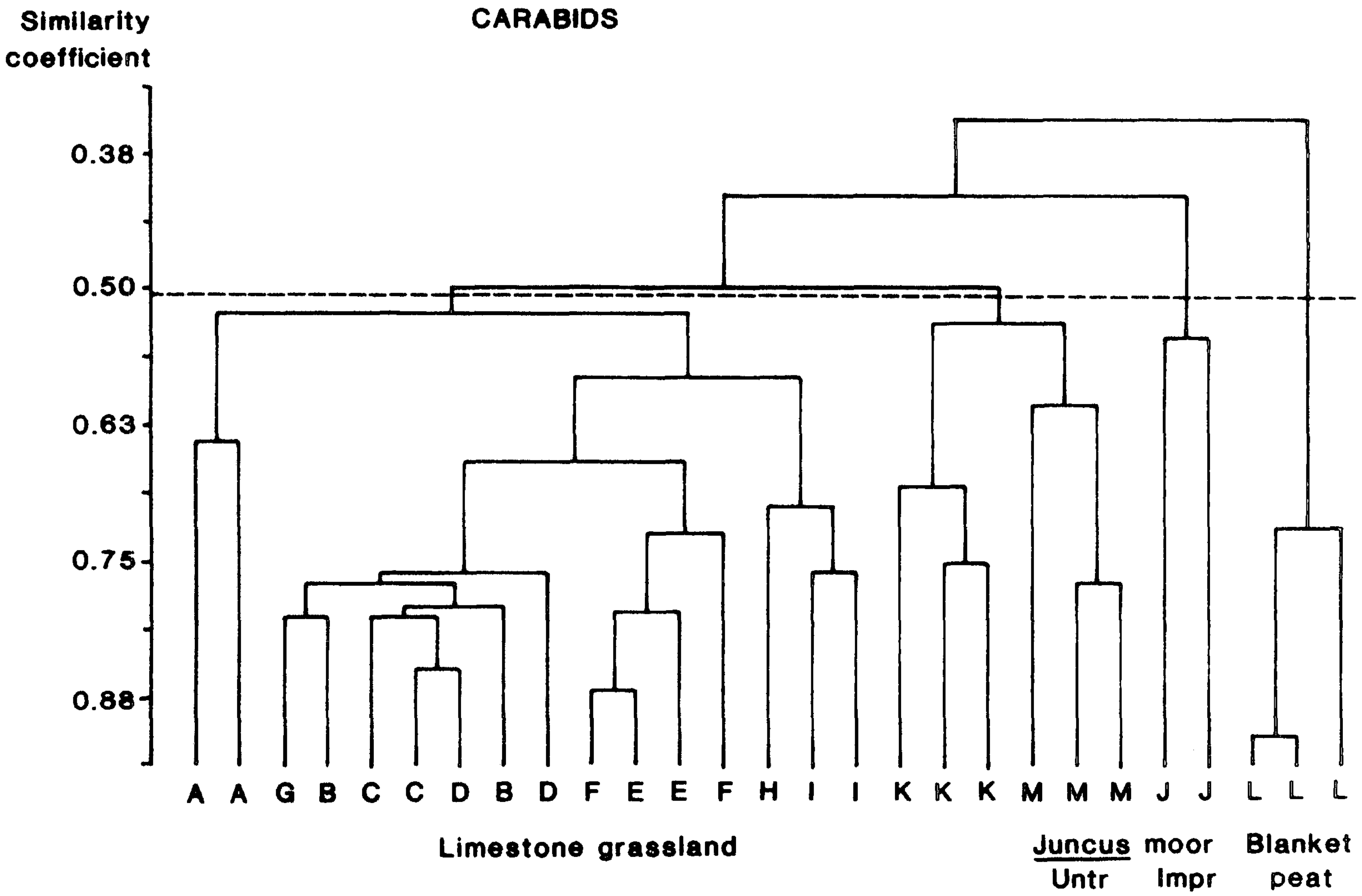


Figure 5.13 (cont.)

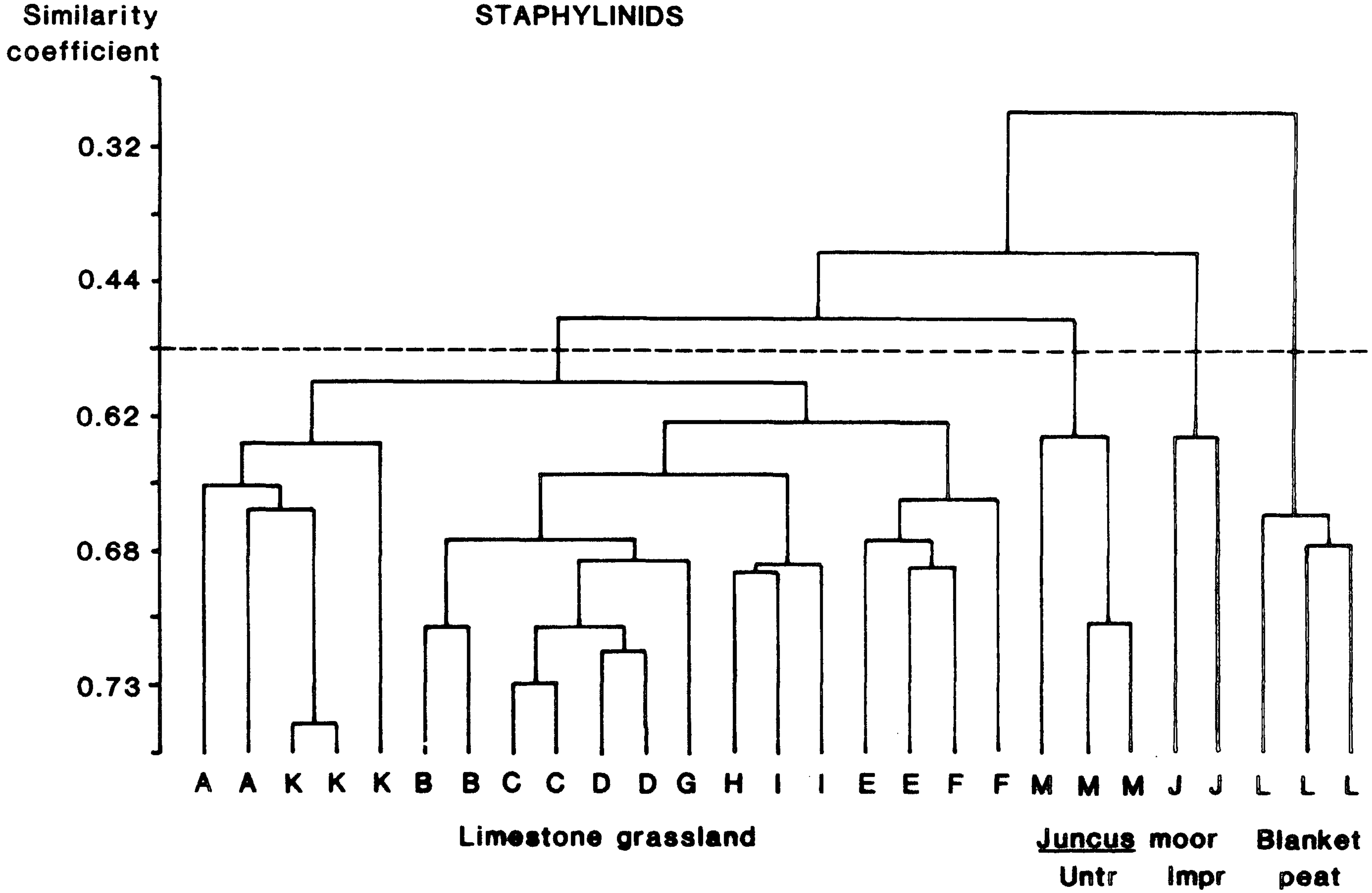


Table 5.10

Moor House habitat-clusters delimited by cluster analysis of carabid and staphylinid faunas (at a similarity level of 0.5).

Habitat-cluster	Sites	Number of samples
Blanket peat	L	3
Juncus moor (untreated)	M	3
Juncus moor (improved)	J	2
Limestone	A-K	19

Table 5.11

a values and average numbers of beetles in habitat-clusters at Moor House.

Habitat-cluster	Alpha		Species		Individuals	
	a	se	mean	se	mean	se
CARABIDS						
Blanket peat	2.3	0.3	6.0	0.5	30.7	5.1
Juncus moor (untreated)	4.7	0.6	11.3	0.8	54.0	13.6
Juncus moor (improved)	4.2	0.8	10.5	2.0	60.0	29.4
Limestone	3.6	0.0	13.3	0.4	157.6	18.4
STAPHYLINIDS						
Blanket peat	5.0	0.4	19.7	1.6	265.0	38.1
Juncus moor (untreated)	11.5	1.2	31.7	3.8	202.7	13.5
Juncus moor (improved)	12.2	1.9	38.0	1.6	309.0	138.0
Limestone	9.0	0.0	38.8	0.9	802.4	102.2

Figure 5.14

Ordination of the Moor House sites according to the similarity of their carabid and staphylinid faunas in 1984 and 1985. Data are from sets of ten pitfall traps.

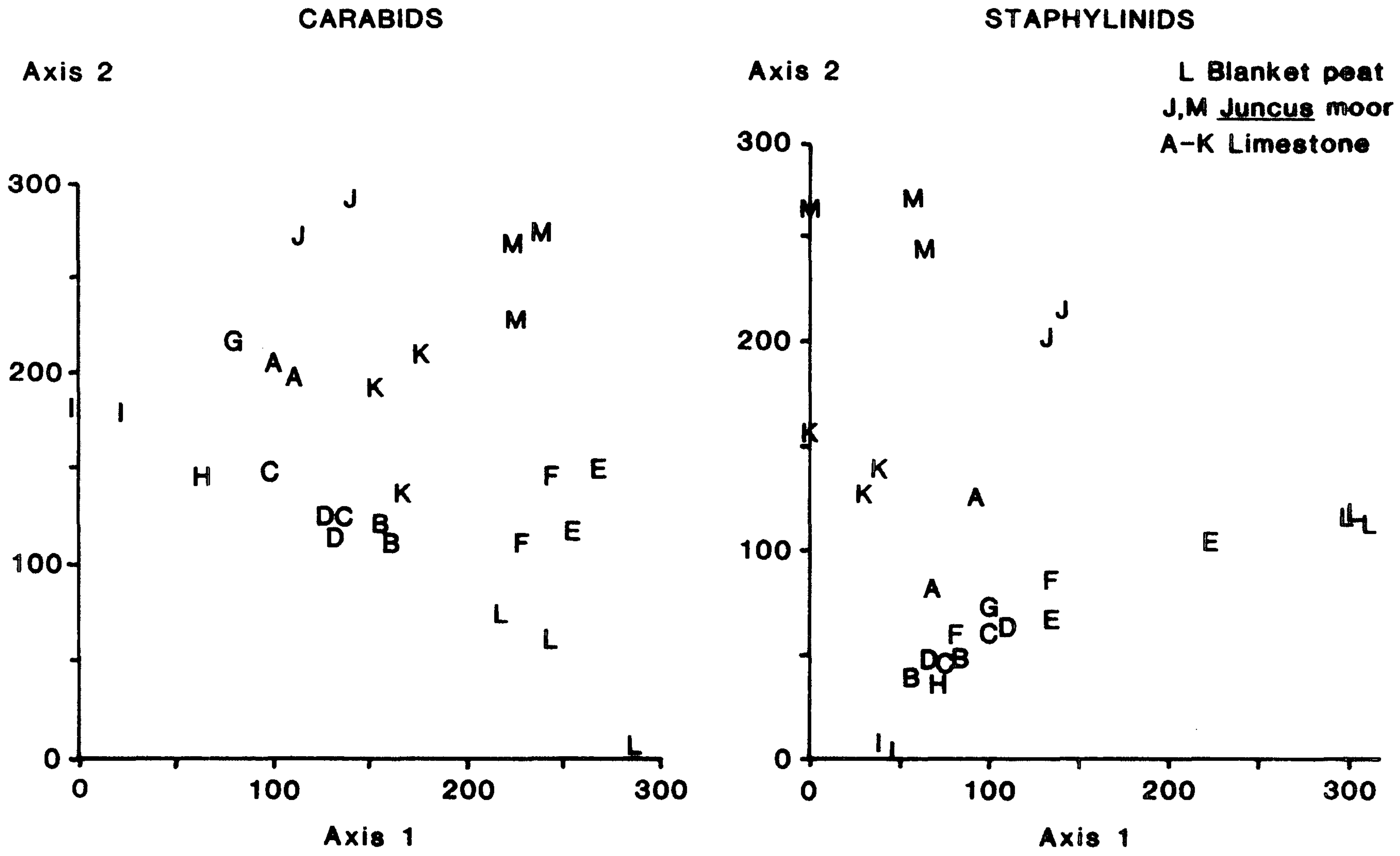


Table 5.12

Student's t-values for significant differences in numbers of species (upper value) and individuals (lower value) of carabids and staphylinids between habitat-clusters.

	Blanket peat	*Juncus* moor (untreated)	*Juncus* moor (improved)	Limestone		Characteristics of habitat
Blanket peat	- -	5.06 ns	ns 6.60	6.88 6.43	C A R A B I D S	Less carabid species than on untreated *Juncus* moor or limestone. Less staphylinid species than on improved *Juncus* moor or limestone.
Juncus moor (untreated)	ns ns		ns ns	7.90 4.22		Less carabid and staphylinid species and individuals than on limestone. More carabid species than on blanket peat.
Juncus moor (improved)	6.50 ns	ns ns		ns ns		More staphylinid species and carabid individuals than on blanket peat.
Limestone	7.90 4.73	2.59 5.66	ns ns	 -		More carabid and staphylinid species and individuals than on blanket peat or untreated *Juncus* moor.

STAPHYLINIDS

Table 5.13

Student's t-values for significant differences in *a* values of carabids and staphylinids between habitat-clusters.

	Blanket peat	*Juncus* moor (untreated)	*Juncus* moor (improved)	Limestone		Characteristics of habitat
Blanket peat	-	3.51	13.77	6.56	CARABIDS	Lower carabid and staphylinid diversities than on *Juncus* moor or limestone.
Juncus moor (untreated)	ns		ns	ns		
Juncus moor (improved)	4.02	ns	-	ns		Higher staphylinid diversities than on blanket peat.
Limestone	7.96	ns	ns	-		Higher carabid and staphylinid diversities than on blanket peat.

STAPHYLINIDS

from other sites of only 0.35 (carabids) and 0.30 (staphylinids). This habitat has a significantly lower faunal diversity than the limestone and improved *Juncus* moor (Table 5.13), with *a* values of only 2.3 (carabids) and 5.0 (staphylinids). Samples taken from the blanket peat average only half the number of species (6 carabids and 20 staphylinids) of those from the limestone, and the mean abundances of individuals (31 carabids and 265 staphylinids) are also significantly lower (Table 5.12).

5:4.3 The untreated *Juncus* moor fauna

The untreated *Juncus* moor possesses a carabid fauna which shows greater affinities to that on limestone than to that on its improved counterpart or on the blanket peat, but neither carabid or staphylinid faunas show very close similarities to any of the other habitats (Figure 5.13). *a* values for both carabids (4.7) and staphylinids (11.5) are double those from the blanket peat, but not significantly different to those from improved *Juncus* moor or limestone (Table 5.13). Mean numbers of species in samples taken from untreated *Juncus* moor (11 carabids and 32 staphylinids) are significantly lower than in those from limestone (Table 12), and average abundances of individuals are only a third of that on the latter habitat. Samples from the untreated *Juncus* moor possess significantly more carabid species than do those from the blanket peat.

5:4.4 The improved *Juncus* moor fauna

Samples taken from the improved *Juncus* moor show low levels of similarity in carabid or staphylinid faunas with those from all other habitats, including those from their adjacent untreated counterpart

(Figure 5.13). They possess twice as many staphylinid species and carabid individuals as do those from the blanket peat, and their **a** value is over double that of this latter habitat (Tables 5.11-13). Unlike the untreated Juncus moor, mean numbers of species (11 carabids and 38 staphylinids) and densities of individuals (60 carabids and 309 staphylinids) sampled from the improved Juncus moor, though lower, are not significantly different from those on the limestone overall, but (owing to the considerable within-site variation on these habitats) neither are they or their **a** values (carabid = 4.2, staphylinid = 12.2) significantly different from the untreated Juncus moor. It would appear that agricultural 'improvement' has resulted more in a change in species composition than in a marked rise in overall species numbers or densities.

5:4.5 The limestone fauna

All of the limestone sites (with the exception of Site K in the carabid dendrogram) cluster together, indicating the basic homogeneity of the limestone grassland and the distinctiveness of its fauna from that of surrounding habitats such as the Juncus moor and blanket peat (Figure 5.13). The diversity of the limestone grassland habitat in toto lies mid-way between that of the blanket peat and Juncus moor, with its **a** values of 3.6 (carabids) and 9.0 (staphylinids) being significantly higher than those from the blanket peat, and lower (though not significantly so) than those from the Juncus moor (Table 5.13). Mean numbers of species (13 carabids and 39 staphylinids) are twice, and of individuals (158 carabids and 802 staphylinids) over three times, that recorded from the blanket peat, and are also significantly higher than that observed on the untreated Juncus moor (Table 5.12). Despite the discreteness of the limestone habitat-cluster overall, there is nevertheless, evidence of considerable and apparently consistent variation between sites (Figure 5.13). This within-habitat heterogeneity is considered in Chapter 8.

CHAPTER 6 THE CATEGORIZATION AND PATTERN OF DISTRIBUTION OF SPECIES

6:1 Introduction

The blanket peat and limestone grassland habitats studied at Moor House and Tailbridge possessed distinctive carabid and staphylinid faunas overall (Chapter 5) but also had a number of species in common (Chapter 4). Many of those species which were common to pitfall trap catches on both limestone and blanket peat habitats on one study area, however, were taken on only one habitat type on the other. This suggests that many such species were typically resident on only one type of habitat, but in certain instances were found dispersing onto adjacent habitats.

Carabids have been shown to engage in two contrasting types of locomotory activity (Baars 1979): in a favourable environment 'random walk' predominates, where the beetle covers short distances in a continually changing direction within the habitat. Where adjacent habitat types are strongly contrasted and exhibit a well-defined interface, beetles are able to avoid crossing the boundary into a less favourable habitat, and any marked dispersal out of the preferred habitat represents a bout of 'directed movement' usually associated with breeding (Den Boer 1970, Rijnsdorp 1980), where long distances are covered in a more-or-less constant direction (Baars 1979). When the transition between habitat types is more gradual, beetles continually wander away from their preferred habitat in random walk until the increasingly unfavourable terrain encountered prompts a bout of rapid directed movement designed to bring the individual back into a more amenable locality.

It seems reasonable to expect that walking staphylinids may exhibit similar locomotory behaviour to carabids, and so in this chapter a system of categorization based upon the observed habitat preferences of different species is constructed with these behavioural characteristics in mind. It is used to distinguish between species resident and breeding on a habitat, and those deriving from elsewhere (Section 6:2). The ecological nature of the species composing each category, and the factors influencing their dispersal away from their normal habitat, are examined in Sections 6:3 and 6:4. Finally the effect of the interchange of species across the limestone:peat interface upon the species composition and diversity of these respective habitats is considered (Section 6:5).

6:2 The categorization of species

The blanket peat and limestone grassland habitats on the two study areas were strongly contrasted in nature, and exhibited a relatively sharp interface between them (Section 2:2). At Moor House, trapping of beetles on the former habitat occurred 400m from the nearest limestone outcrop, whilst at Tailbridge, catches were made up to 100m from the habitat boundary on both peat and limestone (Chapter 3). In view of this and the findings above, it seems likely that the great majority of the carabid (or flightless staphylinid) species common at such distances onto these habitats were resident and breeding there: only occasional individuals of the largest (or flying) species were likely to reach these sites from neighbouring habitats as a consequence of a bout of directed movement. The majority of species may therefore be satisfactorily categorized according to normal moorland habitat by comparing their relative abundances in pitfall trap catches on sites furthest from the limestone:peat interfaces on the study areas (Key 2). Species known to be of a nomadic lifestyle, and not necessarily associated with a particular moorland habitat (Hanski and Koskela 1977, Hammond pers. comm.) have been distinguished from amongst the other species beforehand (Key 1) and treated separately (Key 3).

Key 1.

A(B) Species able or unable to fly, exploiting resources more-or-less closely associated with a particular habitat. Settled Sp. (Key 2)

B(A) Species capable of flight, and exploiting transient resources not necessarily closely associated with a particular habitat. Nomadic Sp. (Key 3)

Key 2. (Settled species)

A(B) Species taken in pitfall trap catches.

1(2)Species present in over half of the catches made on blanket peat at Moor House in one year, with at least two individuals in one catch. Peat sp.

2(3)Species present in both catches made on blanket peat at Tailbridge, in numbers at least double those made on the two furthest limestone sites. Peat sp.

3(4)Species only present in catches made on blanket peat. Peat sp.

4(5)Species present in both catches made on the two furthest limestone sites at Tailbridge, in numbers at least double those made on the two blanket peat sites. Limestone sp.

5(6) Species present in at least half of the catches made on limestone at Moor House in one year, with at least two individuals in one catch. Limestone sp.

6(7) Species only present in catches made on limestone. Limestone sp.

7 Species not conforming to above criteria. Widespread sp.

B(A) Species present in window trap catches only. Vagrant Sp.

Key 3. (Nomadic species)

A(B) Species exploiting dung. Dung sp.

B(A) Species exploiting resources other than dung. Non-dung sp.

The species composition of each carabid and staphylinid category is given in Table 6.1, and its contribution to the fauna on limestone grassland and blanket peat habitats at Moor House and Tailbridge is summarized in Table 6.2. *Patrobus assimilis*, a typical Peat species at Tailbridge, has been placed in a class of its own with regard to Moor House, where it showed a distinct change in habitat preference with altitude. Similarly, *Notiophilus germinyi* acted as a Peat species at Tailbridge but as a Limestone species at Moor House, and has been classified accordingly. *Cychrus caraboides*, a large species taken only twice at Moor House, but on both limestone and blanket peat, has been classified as a Limestone species since it feeds on snails (Lindroth 1975) which are restricted to the limestone, and being large has comparatively high powers for dispersal.

Table 6.1

Carabid and staphylinid species categories at Moor House and Tailbridge.

CARABIDS
I.SETTLED
a)PEAT SPECIES (12)

i)Wet
Carabus glabratus
Agonum fuliginosum
Leistus rufescens
* Loricera pilicornis
Pterostichus diligens
P. nigrita
Patrobus assimilis

ii)Dry
Carabus problematicus
Dyschirius globosus
Pterostichus adstrictus
Calathus micropterus
Olisthopus rotundatus

b)LIMESTONE SPECIES (19)

Cychrus caraboides
Nebria gyllenhali
Notiophilus aestuans
N. aquaticus
N. germinyi
Clivina fossor
Patrobus atrorufus
Trechus micros
T. obtusus
Bembidion bruxellense
* B. guttula
Pterostichus madidus
P. melanarius
P. oblongopunctatus
P. strenuus
Calathus fuscipes
C. melanocephalus
Trichocellus cognatus
Bradycellus ruficollis

c)WIDESPREAD SPECIES (10)

Carabus nitens
C. violaceus
Nebria salina
Notiophilus biguttatus
* Trechus quadrstriatus
C. violaceus
Bembidion aeneum
Agonum muelleri
* Amara familiaris
A. lunicollis
A. ovata

d)VAGRANT SPECIES (2)

* Amara apricaria
* Bradycellus harpalinus

II.NOMADIC

None

STAPHYLINIDS
I.SETTLED
a)PEAT SPECIES (21)

Anthobium unicolor
Olophrum piceum
Arpedium brachypterum
Lesteva monticola
L. punctata
Stenus brunnipes
S. impressus
Euaesthetus laeviusculus
Lathrobium brunnipes
Othius punctulatus
Quedius boops
Q. molochinus
* Mycetoporus clavicornis
M. rufescens
Bolitobius inclinans
Tachinus elongatus
Myllaena brevicornis
* Boreophila islandica
Schistoglossa curtipennis
Atheta arctica
Oxypoda tirolensis

b)LIMESTONE SPECIES (48)

Olophrum assimile
* Acidota crenata
A. cruentata
Quedius curtipennis
Syntomium aneum
* Stenus canaliculatus
S. melanarius
S. nitidiusculus
Lathrobium fulvipenne
Othius angustus
O. myrmecolphilus
Gyrohypnus punctulatus
Xantholinus linearis
X. longventris
X. tricolor
* Philonthus laminatus
* P. varius
* Gabrius subnigritulus
* G. trossulus
Staphylinus aeneocephalus
Quedius boopoides
Q. fulvicollis
Q. nitipennis
Q. umbrinus
* Mycetoporus lepidus
* M. longulus
* Bryoporus rugipennis
Tachyporus atriceps
* T. chrysomelinus
* T. pusillus
* Tachinus corticinus
* T. signatus
* Cypha laeviuscula
* Schistoglossa gemina
* Aloconota gregaria
* Amischa analis
* A. cavifrons
* Liogluta nitidula
* Atheta elongatula
* A. fungi
* A. hybrida
* A. indubia
A. tibialis
Ocalea picata
Ocyusa hibernica
O. islandica
O. soror
* O. elongatula

Table 6.1 (cont.)

STAPHYLINIDS (cont.)
c)WIDESPREAD SPECIES (18)

* Lesteva longoelytrata
L. pubescens
* Anotylus rugosus
Stenus brevipennis
S. picipes
* S. pusillus
Lathrobium fovulum
Gyrohypnus angustatus
Xantholinus glabratus
Philonthus decorus
* Mycetoporus punctus
* Bolitobius cingulatus
Geostiba circellaris
Atheta exigua
* A. hypnorum
* A. palustris
* Philonthus cognatus
Schistoglossa curtipennis

d)VAGRANT SPECIES

* Anthophagus alpinus
* A. caraboides
* Stenus nanus
* Philonthus ebeninus
* Tachyporus hypnorum
* T. nitidulus
* Atheta debilis
* Aleunota rufotestacea
* Delephrum tectum

II.NOMADIC
a)DUNG SPECIES (36)

* Megarthrus depressus
* Carpelimus pusillus
* Omalium rivulare
* Platystethus arenarius
* Anotylus sculpturatus
* A. tetracarinatus
* Oxytelus laqueatus
* Philonthus fimetarius +
* P. marginatus +
* P. puella +
* P. rectangulus
* P. splendens +
* P. varians +
* Tachinus marginellus
* Autalia puncticollis +
* A. rivularis +
* Atheta atricolor
* A. nigripes +
* A. cauta +
* A. celata
* A. setigera +
* A. atramentatia +
* A. cadaverina
* A. excellens
* A. longicornis +
* A. cinnamoptera +
* A. fungicola
* A. macrocera +
* A. monticola
* A. parvula +
* A. sordidula +
* A. subsinuata
* Atheta trinotata
* Tinotus morion
* Aleochara bipustulata
* A. lanuginosa

b)NON-DUNG SPECIES (26)

* Omalium exiguum
* O. rugatum
O. laticolle
* Xylodromus concinnus
* Phyllodepa floralis
* Dropephylla grandiloqua
* D. vilis
* Coryphium angusticolle
* Philonthus discoideus
* P. nigriventris
* P. umbratilis
* Atheta aquatica
* A. sodalis
* A. diversa
* A. marcida
* A. nigricornis
* A. nigritula
* A. paracrassicornis
* A. procera
* A. triangulum
* A. xanthopus
* A. cribrata
* Oxypoda opaca
* O. induta
* O. spectabilis
* O. umbrata

* species taken in windowtraps

\+ specialist coprophages/predators

(Species totals in brackets)

Table 6.2

Contributions of each species category to pitfall trap catches on limestone and peat habitats.

CARABIDS

a)TAILBRIDGE	Distance onto habitat from interface (m)							
	Limestone grassland				*Juncus*/blanket peat			
	100	50	25	2	2	25	50	100
PEAT								
Species	3	3	4	8	9	10	9	11
Individuals	6	7	15	101	157	146	283	274
LIMESTONE								
Species	8	8	7	7	7	6	5	2
Individuals	291	133	92	135	85	24	21	9
WIDESPREAD								
Species	2	1	3	5	4	6	2	2
Individuals	5	24	13	16	17	74	74	28
TOTAL								
Species	13	12	14	20	20	22	17	15
Individuals	302	164	120	252	259	244	380	311
Alpha	2.8	3.0	4.1	5.1	5.1	5.9	3.7	3.3

Table 6.2 (cont.)

CARABIDS

b)MOOR HOUSE

	All Limestone outcrops (A-K)		Transect sites - metres from interface								All blanket peat sites (LX+LY)	
			Limestone (4)		Peat (2)		Peat (40)		Peat (400)			
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
PEAT												
Species	3.5	0.3	8.0	1.0	9.0	0.0	8.0	1.0	3.5	0.5	3.0	0.5
Individuals	34.3	10.2	167.5	73.5	135.0	59.0	49.5	4.5	7.5	0.5	20.7	5.2
_P_. _assimilis_												
Species	0.9	0.1	1.0	0.0	1.0	0.0	0.5	0.5	1.0	0.0	1.0	0.0
Individuals	26.6	11.8	5.0	2.0	2.5	2.5	4.0	1.0	4.5	1.5	2.3	0.7
LIMESTONE												
Species	4.5	0.3	4.0	0.0	1.5	0.5	2.0	0.0	0.5	0.5	0.3	0.3
Individuals	41.7	7.3	23.5	12.5	3.0	1.0	3.5	0.5	0.5	0.5	0.3	0.3
WIDESPREAD												
Species	2.1	0.2	2.5	0.5	2.0	0.0	1.5	0.5	0			
Individuals	9.7	1.7	23.5	3.5	8.0	4.0	3.0	0.0	0			
TOTAL												
Species	13.3	0.4	15.5	0.5	13.0	0.0	12.5	1.5	4.5	0.5	6.0	0.5
Individuals	157.6	18.4	219.5	66.5	148.5	64.5	60.0	4.0	12.5	0.5	30.7	5.1

Table 6.2 (cont.)

STAPHYLINIDS

a)TAILBRIDGE	Distance onto habitat from interface (m)							
	Limestone grassland				*Juncus*/blanket peat			
	100	50	25	2	2	25	50	100
PEAT								
Species	5	3	5	12	11	12	13	11
Individuals	10	10	10	32	62	102	182	112
LIMESTONE								
Species	21	18	19	22	16	10	9	7
Individuals	822	635	509	472	134	35	24	7
WIDESPREAD								
Species	1	2	1	4	6	5	5	2
Individuals	17	4	2	9	7	19	24	3
NOMADIC								
Species	3	5	6	10	7	-	4	1
Individuals	11	19	25	18	16	-	4	1
TOTAL								
Species	30	28	30	48	40	27	31	21
Individuals	860	664	545	531	219	156	234	123
Alpha	6.0	5.9	6.9	12.8	14.4	9.4	9.6	7.3

Table 6.2 (cont.)

STAPHYLINIDS

b)MOOR HOUSE

	All Limestone outcrops (A-K)		Transect sites - metres from interface								All blanket peat sites (LX+LY)	
			Limestone (4)		Peat (2)		Peat (40)		Peat (400)			
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
PEAT												
Species	8.9	0.5	12.0	1.0	12.0	0.0	13.0	2.0	16.0	0.0	15.0	1.2
Individuals	122.1	19.2	140.5	58.5	156.5	25.5	140.5	5.5	174.5	0.5	257.7	44.8
LIMESTONE												
Species	20.5	0.9	16.0	3.0	6.0	1.0	4.5	0.5	3.0	1.0	2.7	0.9
Individuals	649.8	101.2	141.0	79.0	29.0	13.0	5.5	0.5	3.5	0.5	4.0	0.0
WIDESPREAD												
Species	1.9	0.3	0.5	0.5	0.5	0.5	1.0	0.0	0.5	0.5	1.3	0.9
Individuals	2.8	0.6	0.5	0.5	0.5	0.5	1.5	0.5	0.5	0.5	3.0	2.1
NOMADIC												
Species	7.5	0.5	5.5	1.5	1.0	0.0	0.5	0.5	1.5	0.5	1.0	0.6
Individuals	27.6	3.8	7.5	1.5	1.0	0.0	0.5	0.5	1.5	0.5	1.0	0.6
TOTAL												
Species	38.8	0.9	34.0	5.0	19.5	1.5	19.0	2.0	21.0	1.0	19.7	1.6
Individuals	802.4	102.2	289.5	21.5	187.0	38.0	148.0	5.0	180.0	1.0	265.0	38.1

6:3 Settled species categories

6:3.1 Peat species

Twelve carabid and 21 staphylinid species recorded at Moor House and/or Tailbridge have been classified as Peat species (Table 6.1). Their restriction to the blanket peat on these areas appears to have been dictated by their need for a damp and shady environment. Sensitivity to the moistness or dryness of a habitat plays an important role in determining the distributions of many invertebrate species (Theile 1977, Coulson and Butterfield 1985). At low altitudes or more southerly latitudes where the prevailing climate is drier and more sunny, many of these Peat species are still present but are restricted to habitats such as forest, scrub and carr, where relatively damp and shady conditions prevail close to the ground (Den Boer 1970, Segers and Bosmans 1982, Walker 1985). They are largely absent from more open woodland, meadow and pasture in these regions, which do not provide such a suitable microclimate. At more northern latitudes or at higher altitudes, however, prevailing climatic conditions are sufficiently wet and cloudy that a suitably damp and shady environment occurs even on a relatively exposed habitat with a short plant cover such as blanket peat. All Peat species are characteristically present on this habitat elsewhere in northern England (Coulson and Butterfield 1979) and many have been recorded from blanket peat in western Ireland (Blackith and Speight 1974). Most of these species have also been taken at altitudes above 600m in Wales (Goodier 1968), and above 900m in Norway (Refseth 1980) even in the absence of a blanket peat cover.

6:3.2 Limestone species

Nineteen carabid and 48 staphylinid species comprise this class (Table 6.1). Although several Limestone species are apparently restricted to upland or northern habitats (Goodier, 1968, Refseth 1980, Butterfield and Coulson 1983, Hammond pers comm), most are common on grasslands at low altitude as well (Segers and Bosmans 1982, D'Hulster and Desender 1984, Walker 1985, Coombes and Sotherton 1986): they are typically present in hayfields or grazed pasture, but are seldom to be found in the more shady wooded habitats. They do not appear to exhibit a marked transition in habitat preference with altitude or latitude as the Peat species do, but are characteristic of grassland in all regions where they occur. Height of vegetation, rather than moisture, appears to be the most important factor in determining the distribution of these species.

6:3.3 Widespread species

Ten carabid and 18 staphylinid species form this category (Table 6.1), occurring on both limestone and peat habitats with no clear preference for either. Most species are frequent components of lowland communities in both woodlands and grasslands (Kasule 1968, Segers and Bosmans 1982, D'Hulster and Desender 1984, Walker 1985). A number of these species were only infrequently taken on the moor and are known to fly: they may not in fact have been resident on the moor at all but immigrants from outside (cf Chapter 7). Several of the staphylinid species have coprophilous tendencies (Hanski and Koskela 1977). Widespread species in general seem to be of a fairly eurytopic nature, often exploiting areas of marginal habitat, or able to exist in a variety of habitat types.

6:3.4 Vagrant species

Two carabid and nine staphylinid species recorded elsewhere as typical inhabitants of permanent habitat such as woodland (Refseth 1980) or pasture (Sotherton 1984) were taken only in window traps (Table 6.1). Some of these species (eg *Bradycellus harpalinus*, *Anthophagus alpinus*) have been taken in pitfalls on the study areas by other workers (Coulson and Butterfield 1979) and may simply inhabit the moor in very low densities, but most are more likely to have been vagrants from habitats further afield (cf Chapter 7).

6:4 Nomadic species categories

6:4.1 Dung species

All 36 Dung species recorded at Moor House and Tailbridge were staphylinids (Table 6.1) They are often abundant in mammalian dung (Hanski and Koskela 1977), either feeding on the dung itself (eg Oxytelines) or preying on other invertebrates such as fly larvae and nematodes inhabiting the dung (eg *Philonthus* spp. and Aleocharines). Some species are specialist predators adapted to exploit this microhabitat alone (Table 6.1), whereas others are more generalist and utilize other resources apart from dung (Hanski and Koskela 1977). Of all staphylinids taken in sheep dung at Tailbridge, 92% of species and 99% of individuals were of Dung species (Table 4.10).

6:4.2 Non-dung species

A total of 26 staphylinid species comprise this category (Table 6.1).

They are not typically inhabitants of dung (cf Hanski and Koskela 1977): only two individuals of *Atheta cribrata* were taken in sheep dung at Tailbridge (Table 4.10). Most species are scavengers in rotting vegetation (eg *Omalium* spp., *Carpelimus* spp., *Coryphium* spp.), or occur in blossoms or under bark (eg *Phyllodrepa* spp., *Dropephylla* spp.). Some species are markedly synanthropic (eg *Xylodromus* spp., *Omalium* spp., *Philonthus* spp.). The habitat requirements of many of these species are not met by moorland, and their anomalous occurrence there is considered in Chapter 7.

6:5 Faunal differences between study areas

6:5.1 Introduction

Some species of carabid and staphylinid were taken on one study area only: eleven carabid and 70 staphylinid species were caught only at Moor House, whilst eight carabid and eight staphylinid species were only taken at Tailbridge. The possible explanations for these differences are considered below.

6:5.2 Species of restricted geographical range

Species may have been restricted to only one study area by subtle but important environmental differences between the two regions. The most fundamental difference between the Moor House and Tailbridge sites was altitude (cf Chapter 2). Climatic conditions change with increasing elevation on the uplands in northern England, becoming generally cooler, cloudier and wetter (Heal and Smith 1978). Species' ranges are known to be differentially affected by such altitude-induced environmental changes (Mani

1968), and the presence of several fairly common species in catches from Moor House only can be attributed to this altitudinal change: the carabids *Carabus glabratus* and *Nebria rufescens*, and staphylinids *Olophrum assimile*, *Bryoporus rugipennis*, *Stenus brevipennis*, *Quedius boopoides*, *Oxypoda tirolensis* and *Ocyusa hibernica* are all characteristically northern or montane species (Goodier 1968, Refseth 1980, Hammond pers comm). Environmental conditions at Tailbridge (including increased competition from more lowland species) may have prevented the establishment of these species. Conversely, the absence from Moor House catches of the more lowland or southern carabids *Clivina fossor* and *Calathus fuscipes*, and staphylinids *Oxypoda islandica*, *Tachinus corticinus* and *Stenus pusillus*, which were taken frequently at Tailbridge, may be also have been related to the difference in altitude: the more rigorous climatic conditions on the former study area forbade the maintenance of stable populations of these species on the small patches of limestone present. The roles of altitude and extent of habitat in determining species composition are considered further in Chapter 8.

6:5.3 Rare species

Species may have been present in very low densities on both study areas, but were only detected by chance on one of them. Several species not taken on the study areas during the present investigation have been recorded there on previous occasions: the carabids *Dyschirius globosus* and *Olisthopus rotundatus*, and staphylinids *Amischa cavifrons* and *Philonthus cognatus*, all taken in low numbers at Tailbridge, have been similarly taken at Moor House or on the immediately adjacent moorland in other studies (Houston 1970, Butterfield and Coulson 1979, Butterfield pers. comm.). Conversely, the carabid *Pterostichus strenuus* has been taken at Tailbridge as well as at

Moor House in the past. Such species, particularly those which were flightless, were may well have been still in residence in 1984-6 but as small low-density populations which the present sampling programme failed to detect.

6:5.4 Vagrant species

Species taken occasionally on a study area may not have been typical moorland species but vagrants present there by chance. Such a possibility applies predominantly to species capable of flight, and is considered in detail in Chapter 7.

6:6 Dispersal across the habitat interface

6:6.1 Introduction

In this section, some of the most important factors influencing the nature and magnitude of dispersal of staphylinid and carabid species across the limestone:peat interface at Tailbridge and Moor House are considered. Data are derived from pitfall and window traps catches on sites along the transects on both study areas (Figures 3.1 and 3.2).

6:6.2 Staphylinids: the influence of flight

Two-thirds of all staphylinid species taken on the study areas were capable of flight (Section 4:3). Such flying species had a potentially higher dispersal range than those which could only walk, and the magnitude of their dispersal away from their preferred habitat may be expected to differ from that of their flightless counterparts. It is this aspect which is now considered.

Of the 48 Limestone species taken on the two study areas, 46% showed flight activity (Table 6.1). Both flightless and flying species were present in pitfall catches on peat, but their proportionate abundance on such a habitat and pattern of distribution across the habitat interface were very different (Figure 6.1): flightless species showed a far steeper decay curve of abundance with distance onto the peat than flying species. At Tailbridge the proportion of total individuals taken further than 2m onto the peat, relative to that from the limestone itself, was ten times higher for flying than nonflying Limestone species ($X^2 = 46.6$, df = 1, $p < 0.001$; Table 6.3). A similar (but not significant) trend was present in the Moor House data (Figure 6.2 and Table 6.3). Numbers of individuals of Limestone species actually taken in flight over the peat at Moor House were nearly two-thirds those similarly taken over the adjacent limestone (Table 6.3), while at Tailbridge window trap catches of these species were not significantly different between the habitats. Clearly, flying Limestone species are not necessarily remaining closely associated with their preferred habitat once airborne, but are considerably dispersed over the moor in general. The proportion of this group actually taken on the peat surface (as opposed to on the limestone) is significantly lower than that taken in flight over this habitat at Moor House ($X^2 = 8.98$, df = 1, $p < 0.01$): individuals of flying species present on the peat itself merely represent a chance fallout from the aerial fauna above, and not a large-scale overground dispersal of individuals from limestone onto peat.

Only two of the 20 Peat species taken at Moor House and Tailbridge showed any flight activity (Table 6.1), but again at Tailbridge their pattern of abundance in pitfall traps across the limestone:peat interface

Figure 6.1

Distribution:abundance patterns of individuals of staphylinid Limestone, Peat and Nomadic species along the transect at Tailbridge in 1986, comparing flightless and flying species. Total catches from sets of ten pitfall traps and individual window traps are shown, and standard errors for means of window trap catches are indicated. The X axis is not drawn to scale. The position of the interface is arrowed.

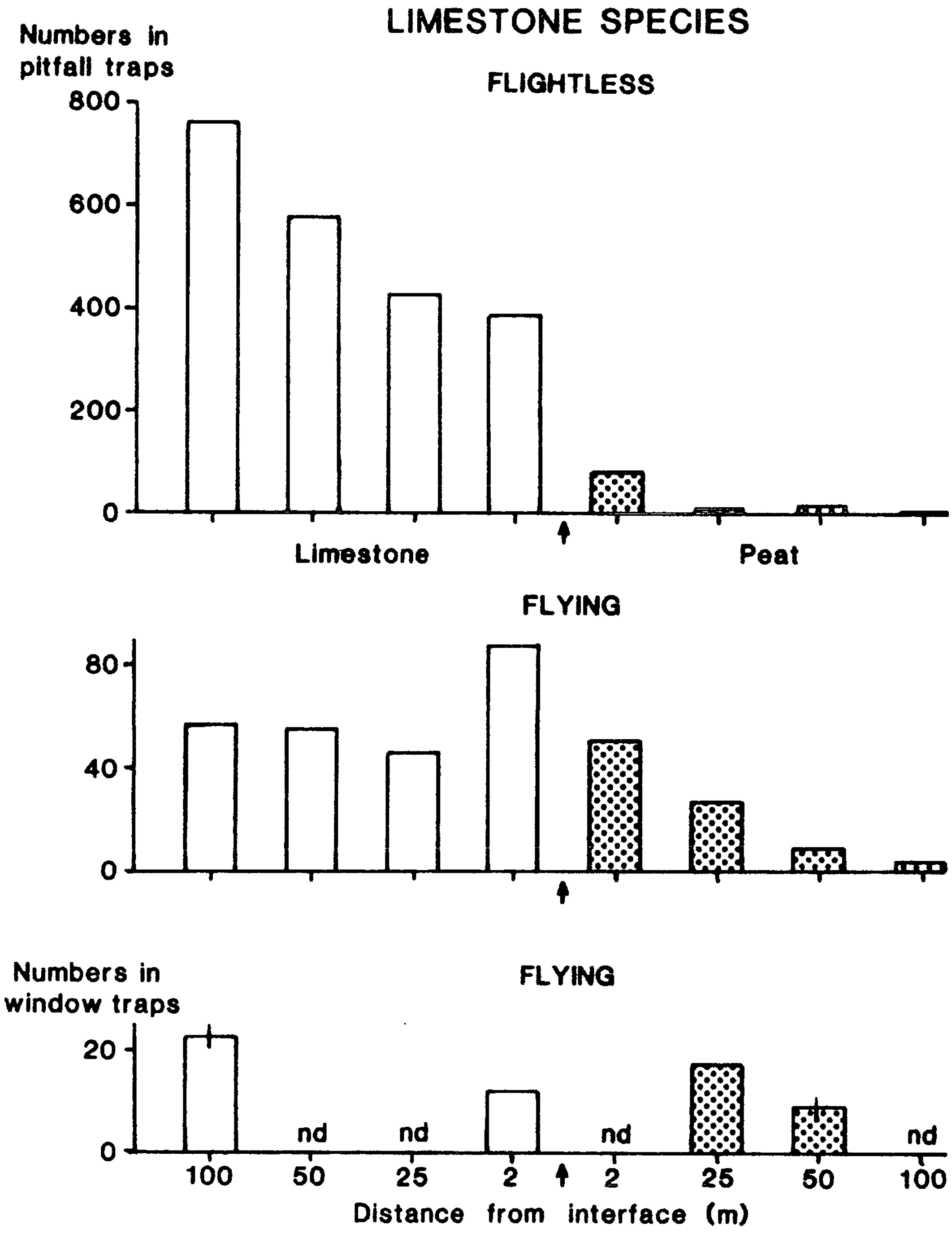


Figure 6.1 (cont.)

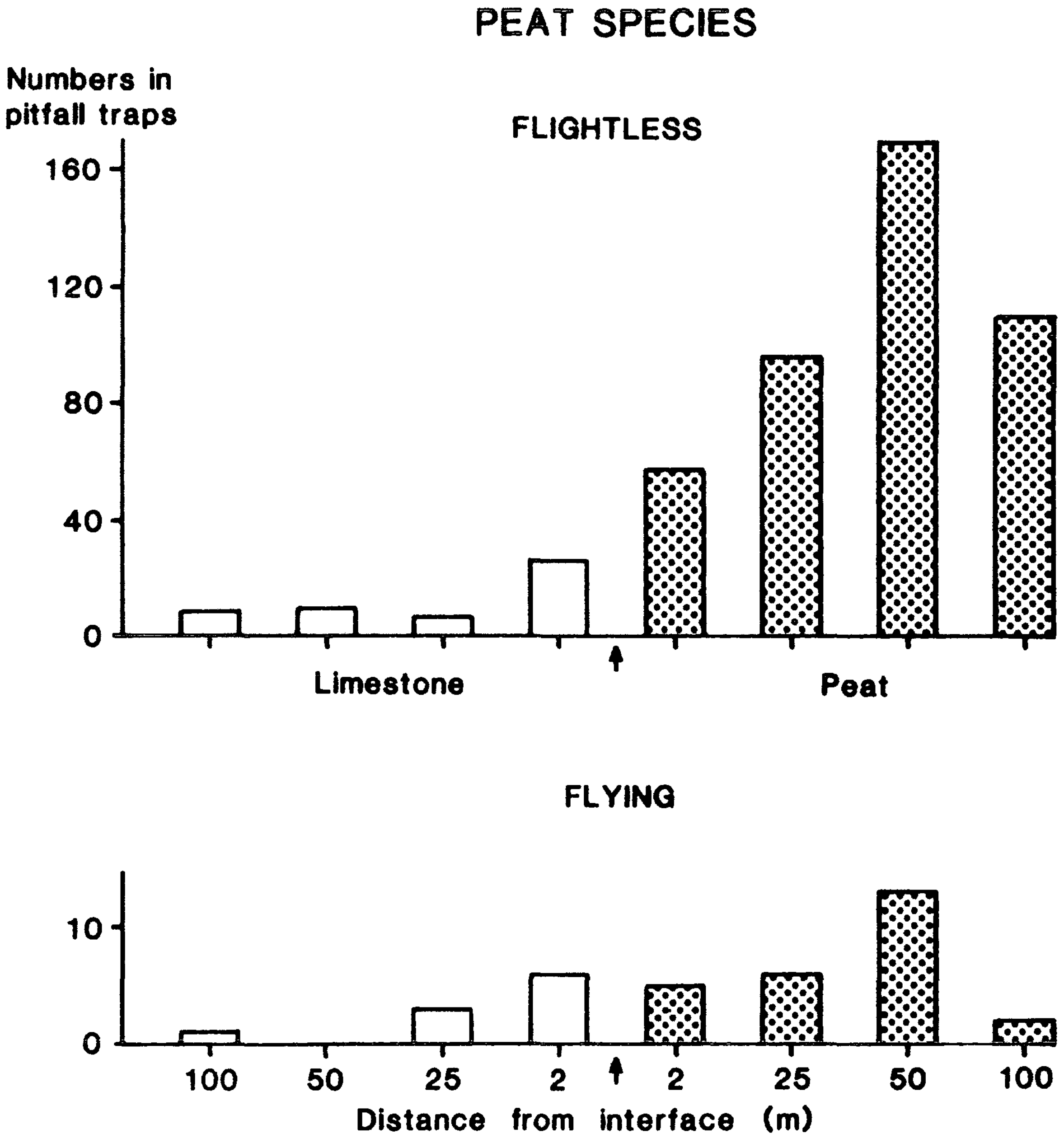


Figure 6.1 (cont.)

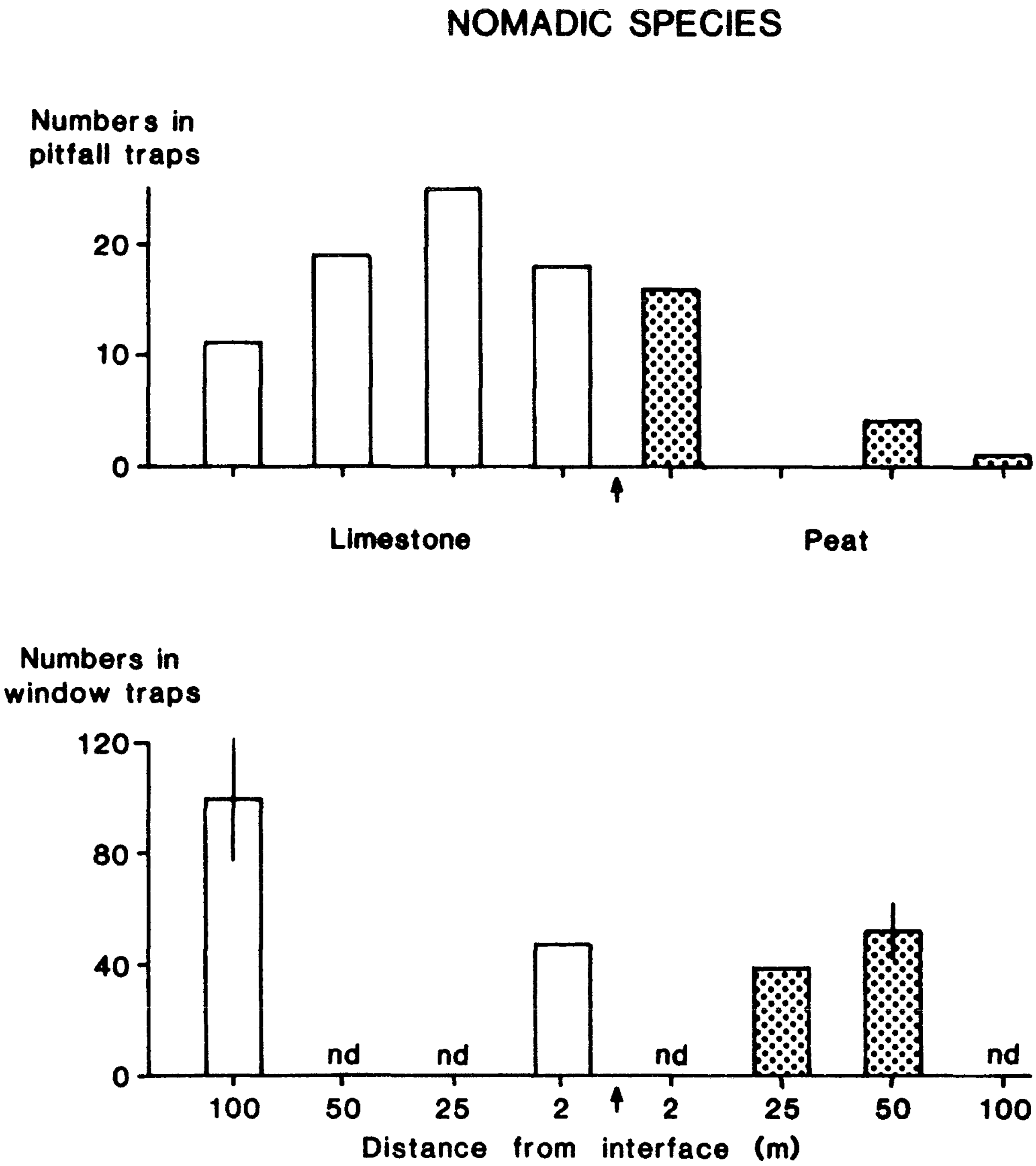


Figure 6.2

Distribution:abundance patterns of individuals of staphylinid Limestone, Peat and Nomadic species along the transect at Moor House in 1985, comparing flightless and flying species. Total catches from sets of twenty pitfall traps and individual window traps are shown, and standard errors for means of window trap catches are indicated. The X axis is not drawn to scale. The position of the interface is arrowed.

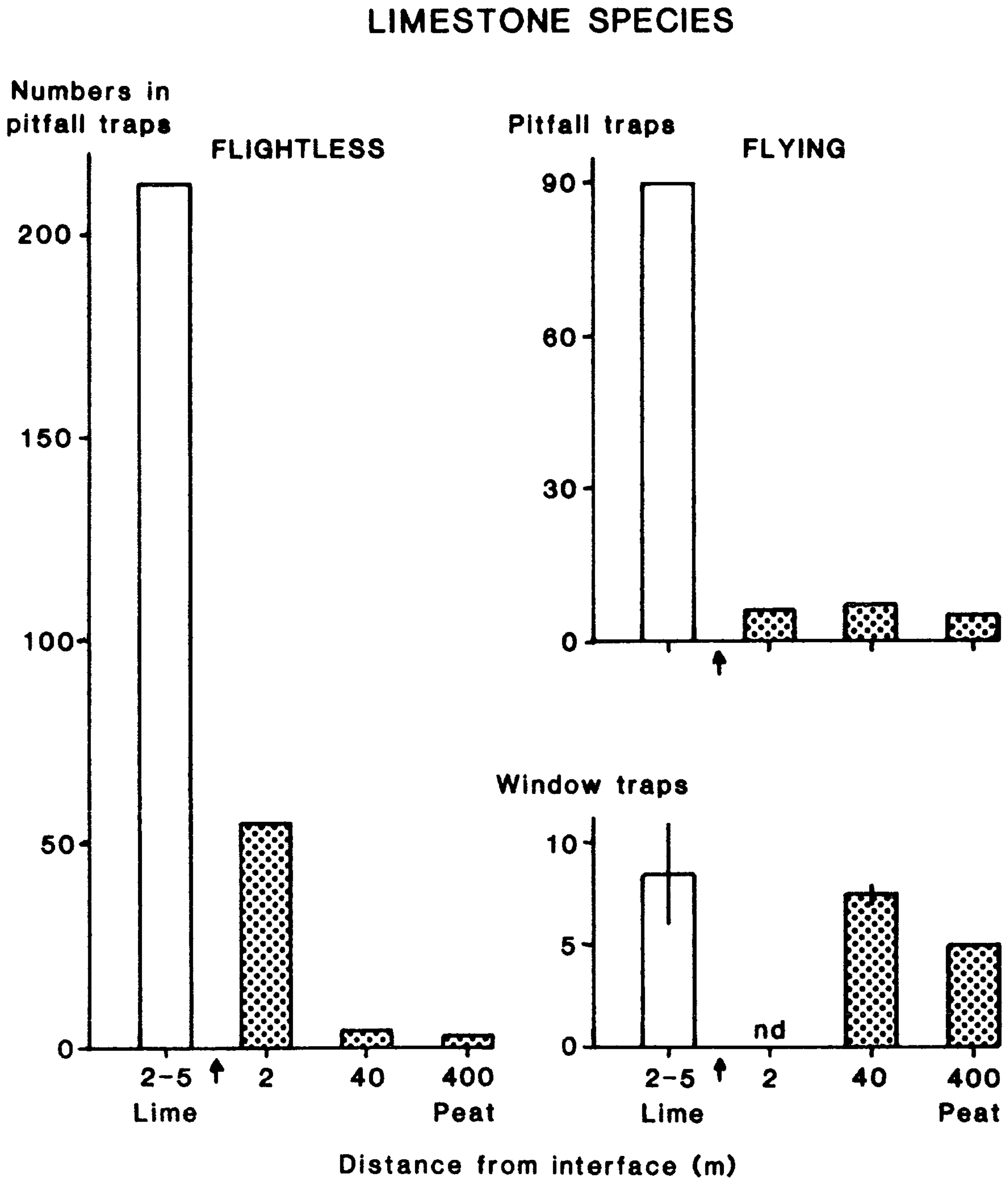


Figure 6.2 (cont.)

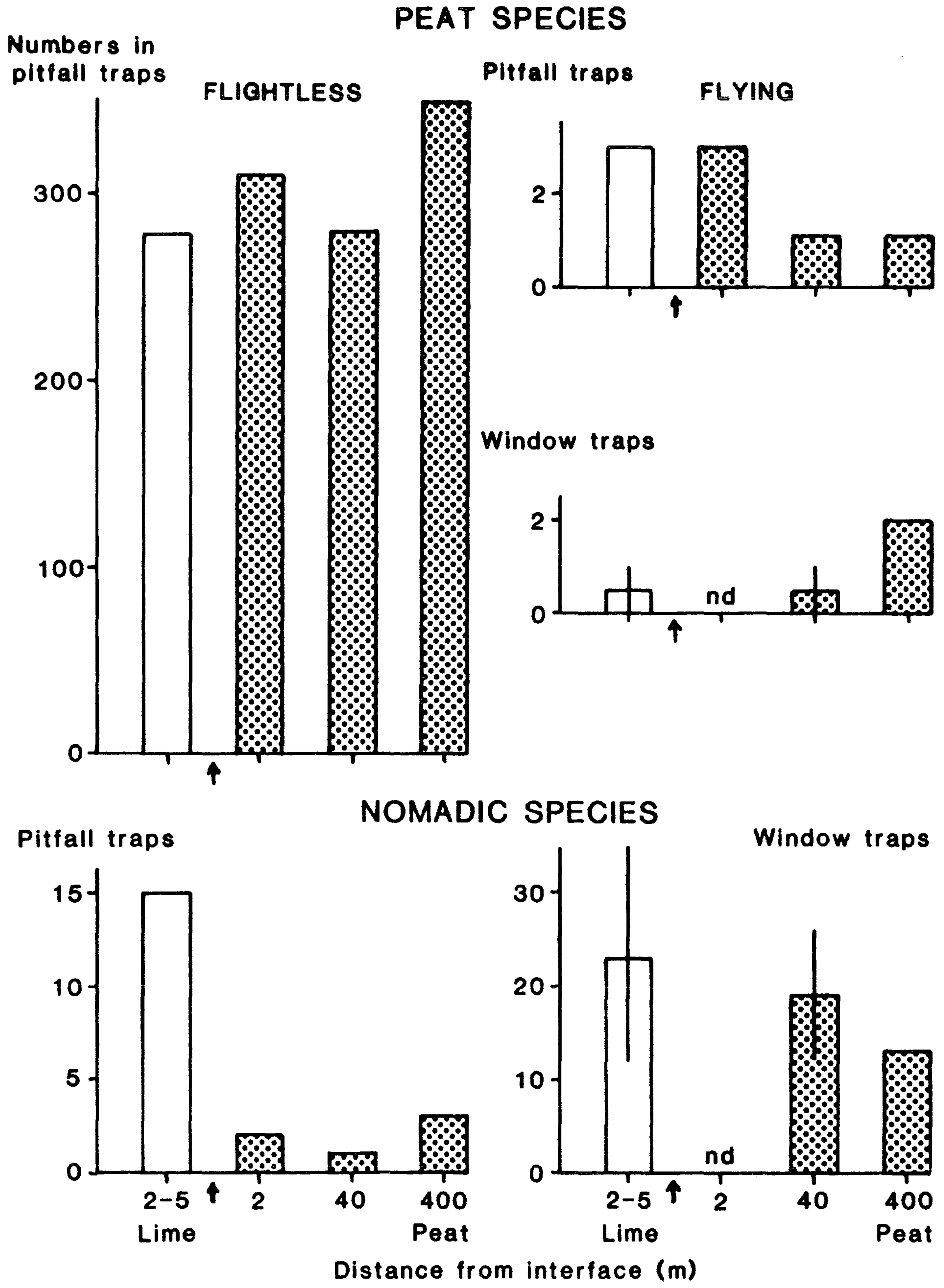


Table 6.3

Numbers of individuals of Limestone staphylinid species. Significance levels given by **: $p < 0.01$, ***: $p < 0.001$.

a)Tailbridge

Mean numbers of individuals of

	FLIGHTLESS SPECIES			FLYING SPECIES					
Habitat	Pitfall traps			Pitfall traps			Window traps		
	n	mean	se	n	mean	se	n	mean	se
Limestone +	3	548	83	3	61.8	9.1	2	19.0	3.8
Peat	4	9.8	5.9	4	22.8	10.6	3	11.7	2.9
% on peat		1.6	***		27.0	**		43.4	

b)Moor House

Mean numbers of individuals of

	FLIGHTLESS SPECIES			FLYING SPECIES					
Habitat	Pitfall traps			Pitfall traps			Window traps		
	n	mean	se	n	mean	se	n	mean	se
Limestone	2	106	47	2	50.0	27.0	2	8.5	0.5
Peat	4	1.8	0.5	4	3.0	0.7	3	6.3	0.7
% on peat		1.7			5.7	**		42.6	

differed from that of flightless species (Figure 6.1 and Table 6.4): the proportional abundance of flying species taken on limestone more than 2m from the interface, relative to that on peat, was twice as great as for flightless species. In a comparable manner to flying Limestone species, flying Peat species were able to disperse further from their preferred habitat, the peat, than their flightless counterparts. No Peat species were taken in flight at Tailbridge, but at Moor House a few individuals were taken in window traps on both peat and limestone (Figure 6.2 and Table 6.4). On the latter study area, both flying and nonflying Peat species were equally as abundant in catches from the limestone outcrops as from the peat. However, even for such small areas of limestone, the data indicate the importance of flight in determining the relative abundances of Peat species present: numbers of individuals of flightless species taken on the larger outcrop (Site F) were only 41% of those caught on the smaller one (Site E), but all individuals of flying species taken on limestone were from the larger site: the increased distance from peat:limestone interface to pitfall trap at this site, which was so influential in the capture of flightless beetles, was negligible in the case of flying individuals.

Nomadic species taken on the study areas exhibited a pattern of distribution and abundance very similar to that of flying Limestone species (Figures 6.1 and 6.2; Table 6.5): the majority of individuals caught in pitfall traps were on limestone, but specimens were also taken sporadically on peat. Although average numbers of individuals taken on the peat itself were only about a tenth of those from the limestone, the difference in their relative abundance between habitat types was far less marked in window trap catches (Table 6.5): average numbers taken in window traps on peat were significantly less than on limestone, but were still proportionately significantly greater than those taken by pitfall on the peat surface. The

Table 6.4

Numbers of individuals of Peat staphylinid species.

a) Tailbridge

Habitat	Mean numbers of individuals of					
	FLIGHTLESS SPECIES			FLYING SPECIES		
	Pitfall traps			Pitfall traps		
	n	mean	se	n	mean	se
Peat +	3	108	23	3	6.5	2.7
Limestone	4	8.7	0.9	4	1.3	0.9
% on limestone		7.5			16.7	

b) Moor House

Habitat	Mean numbers of individuals of								
	FLIGHTLESS SPECIES			FLYING SPECIES					
	Pitfall traps			Pitfall traps			Window traps		
	n	mean	se	n	mean	se	n	mean	se
Peat +	2	157	10	2	0.5	0.3	2	1.0	0.6
Limestone	4	139	60	4	1.5	1.5	3	0.5	0.5
% on limestone		46.7			75.0			33.3	

+ excluding site 2m from interface

Table 6.5

Numbers of individuals of Nomadic staphylinid species. Significance level given by *: $p < 0.05$.

a)Tailbridge

Habitat	Mean numbers of individuals						
	Pitfall traps				Window trap		
	n	mean	se		n	mean	se
Limestone	4	18.3	2.8		4	81.7	22.2
Peat	4	1.7	1.2		4	47.0	7.5
% on peat		8.4		*		36.5	

b)Moor House

Habitat	Mean numbers of individuals						
	Pitfall traps				Window trap		
	n	mean	se		n	mean	se
Limestone	2	7.5	1.5		2	11.5	0.5
Peat	4	1.0	0.4		3	7.3	0.3
% on peat		11.8		*		38.8	

majority (78%) of Nomadic species taken on both Moor House and Tailbridge transects were coprophilous (Dung species). The ratio for sheep dung abundance on limestone and blanket peat habitats at Moor House has been calculated as 6.6:1 (White 1960). Individuals of Nomadic species taken on the peat were almost exclusively coprophilous: only one specimen of a Non-dung Nomadic species occurred in pitfall traps more than 2m onto peat. Thus the occasional coprophilous staphylinids taken on the peat may have been actively exploiting the low densities of dung present, rather than merely vagrants from a chance aerial 'fall-out' over the habitat.

The selective effect of flight on the dispersal of individuals did not merely operate at an inter-specific level however: the Peat species, _Mycetoporus clavicornis_ is wing dimorphic and was present on the study areas in both brachypterous and macropterous forms. The latter form could fly (nb. no other wing dimorphic species taken showed evidence of flight, whether or not macropterous individuals were present). Although blanket peat was the preferred habitat of _M. clavicornis_, it was also occasionally taken in pitfall traps on limestone, and in window traps on both habitats (Table 6.6). Those taken on the limestone sward itself showed a significantly higher frequency of macroptery (56%) than those taken on the peat (20%). Thus even within a single species, wing condition was differentially affecting the dispersal of individuals, with flying individuals achieving greater distances away from the peat than their nonflying counterparts. Such a phenomenon is well known to influence the rates of colonization of new polder by carabid species in the Netherlands (Den Boer _et al_. 1971, 1977).

6:6.3 Carabids and staphylinids: the influence of body size

The occurrence of individuals of flightless species far onto an adjacent atypical habitat must have entailed a sustained bout of directed movement overground (Section 6:1). The distance attained by such dispersal will be limited by the size of the beetle: larger species with longer legs can cover greater distances than their smaller counterparts (cf Baars 1979). The staphylinid data from Moor House and Tailbridge confirm this: of all flightless Limestone species 5-12mm in length, 60% were represented in catches 25m or more onto the peat, whereas only 18% of species 1-4mm in size were present (Table 6.7). This significant difference between size categories indicates that only the larger species were able to achieve any substantial dispersal away from their original habitat. Carabid species on the other hand, being relatively longer-legged than staphylinids and generally considerably larger (rarely less than 5mm in length), exhibited no such well-defined size restrictions on dispersal over this distance: 88% of all Limestone carabid species occurred on peat at least 25m from the limestone at Tailbridge: most species were capable of dispersing at least this far from their normal habitat. Similarly, body size was not an important factor in determining the successful dispersal of flying Limestone species of staphylinid over such distances: amongst those species which had alighted and been taken on peat 25m or more from the limestone, both large (5-12mm) and small (1-4mm) species were equally well represented (Table 6.7).

6:6.4 Carabids: the influence of moisture conditions

The restriction of Peat species of carabid to the blanket peat on the

Table 6.6

Wing condition and distribution of "*Mycetoporus clavicornis*'.

	Individuals in pitfalls on		
	Limestone		Peat
Total individuals	16		15
No. macropterous	9		3
% macropterous	56	*	20

* significant difference: $p < 0.05$

Table 6.7

Body size and dispersal of Limestone staphylinid species.

		% total species in size class		
	n	1-4mm		5-12mm
Flying	22	46		57
Flightless	26	18	*	60

* significant difference: $p < 0.05$

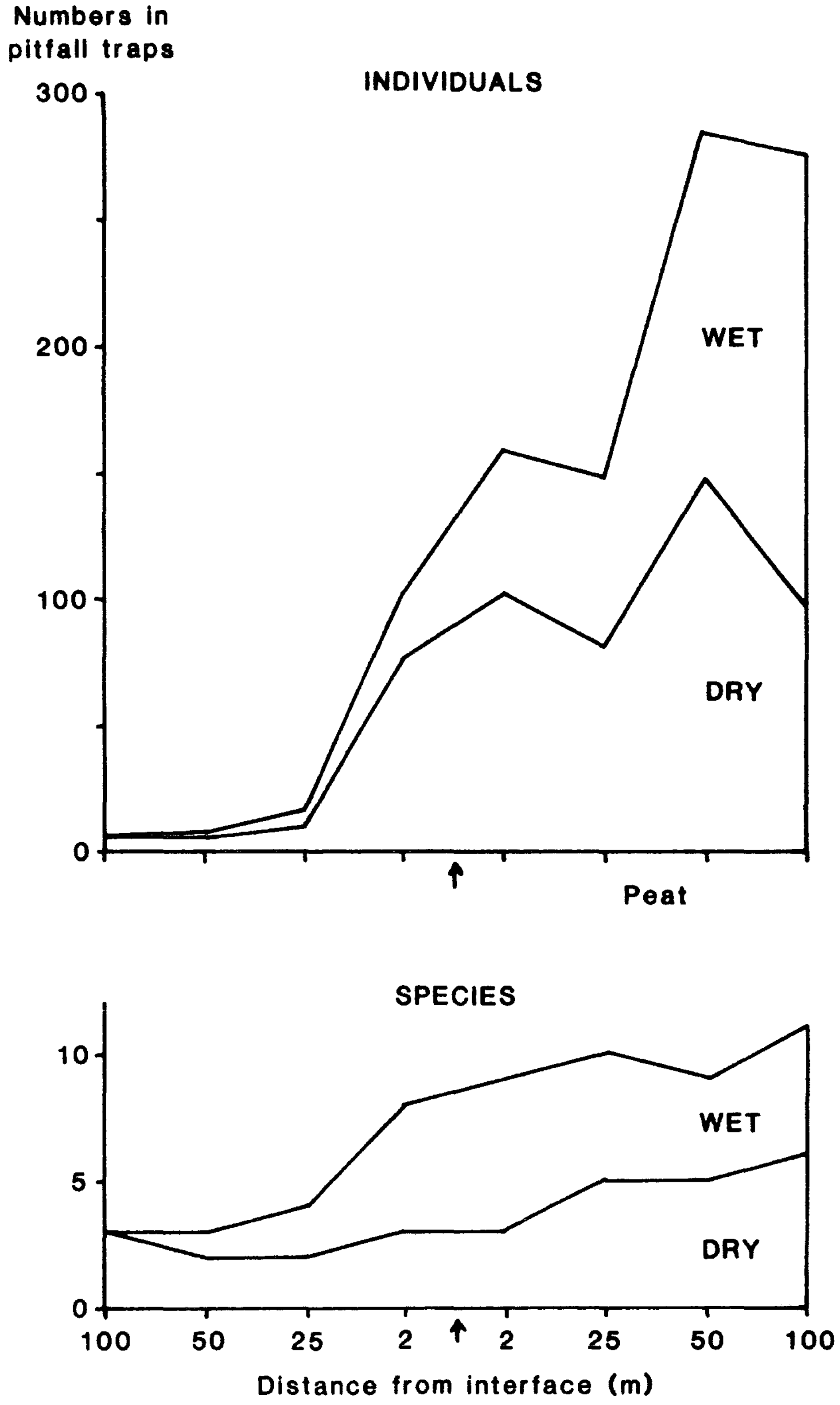
moor appeared to be linked with a need for specific moisture and shade conditions (cf Section 6:3.1). These requirements are often dictated by the immature rather than adult stages (Lindroth 1949, Houston 1970, Theile 1977). Within the Peat species category a further sub-division can be made according to the degree of hygrophily and consequent level of stenotopy exhibited by individual species with regard to the blanket peat: in a comprehensive analysis of the carabid communities on peat and upland grasslands in northern England, Butterfield and Coulson (1983) recognized five species as forming a distinct assemblage (Association B) characteristic of deep wet blanket peat habitats (Peat Community III). With one exception, this assemblage always contributed less than 10% to the annual catch on any grassland or shallow dry heath-like moorland between 200m-450m (Peat Community I). A further two species, although occurring too infrequently and locally to be included in this group, comprised 44% of the catch over two years on a site which possessed attributes of altitude, rainfall, peat depth and vegetation type very similar to those of Peat Community III. Houston (1970) recorded all of these species as breeding on wet habitats on the Moor House Reserve, with most of them producing summer larvae which were active during the season when the threat of inundation was lowest. These seven Wet species (Table 6.1) may be considered the carabids most representative of the blanket peat 'proper'. The remaining five Peat species did not form a discrete association in the analysis of Butterfield and Coulson (1983), but occurred on a wide variety of habitats. They were most characteristic of the relatively dry heath-like moor (Community I) or on sites where areas of *Juncus squarrosus* abutted an area of deeper wetter blanket bog (three sites from Community III). These Dry species (Table 6.1) exhibited a variety of life history strategies at Moor House (Houston 1970), but the majority were recorded as breeding on both wet and non-wet sites.

In the present study Wet and Dry Peat species showed a marked difference in their degree of dispersal away from the blanket peat (Figure 6.3). At 400m onto the blanket peat at Moor House, Wet species comprised 93% of all individuals of Peat species taken in pitfalls: Dry species formed only a minor component. At only 100m onto the peat at Tailbridge, however, Wet species constituted only 65% of total individuals taken: Dry species formed a third of the catch. This trend was continued across the peat-limestone transect, with the contribution of Wet species to the total individuals of Peat species declining significantly with increasing distance from the deep blanket peat ($r = 0.99$, $df = 6$, $p < 0.001$), until on the furthest limestone site they were absent from pitfall trap catches altogether (Figure 6.3): these Wet species did not appear to wander more than 100m from the blanket peat.

The Dry Peat species were taken in greatest abundance on the Juncus moor and on the blanket peat site adjacent to this habitat, but were also present on all of the limestone sites (Figure 6.3). Of the six individuals of Dry species taken 100m onto the limestone, five were of Carabus problematicus and Pterostichus adstrictus: the two largest (24 and 12mm respectively) and hence potentially most mobile Peat species. These species were also present on grassland sites in the moorland survey of Butterfield and Coulson (1983) where they formed up to 10% of the annual catch. The sixth specimen was of Notiophilus germinyi, a species which has already been noted as having a complex set of habitat preferences over the altitudinal range in question (Section 6:2). The only other Dry Peat species making a notable contribution to the fauna on the limestone more than 2m from the habitat interface was Dyschirius globosus, a small (3mm) burrowing species which was also taken on several grassland and dry peat sites in the moorland survey. Although its normal habitat is Sphagnum and marshy places, Houston

Figure 6.3

Distribution:abundance patterns of carabid Wet and Dry Peat species and individuals along the transect at Tailbridge in 1986. Total catches from sets of ten pitfall traps are shown. The X axis is not drawn to scale. The position of the interface is arrowed.



(1970) suggests that the burrowing lifestyle of D. globosus enables it to avoid the drier conditions encountered on the former habitats.

Although Peat species were only encountered on the limestone grassland 50m or more from the peat at Tailbridge as occasional individuals, presumably engaged in directed movement (cf Section 6:2), the situation changed closer to the habitat interface: on the limestone 2m from the interface at Tailbridge, Peat species represented 40% of all carabid species and individuals taken in pitfalls. Their abundance on the immediately adjacent limestone habitat must have resulted from bouts of random walk carrying individuals away from the peat habitat to a distance at which directed movement was triggered to transport them back (cf Baars 1979). Only a quarter of these individuals were of Wet Peat species: for such species the contrast between the blanket peat and limestone grassland was marked, and inhibited much random walk away from the blanket peat. The Dry species, forming three-quarters of the total individuals taken, appear to have been acting as peat 'edge' species, exploiting the shallower Juncus moor habitat and grassland:peat interface, but not forming a significant component of either grassland or deep blanket peat faunas 'proper' in the absence of any marginal dry peat habitat. Data from the Moor House transect show a similar pattern of distribution and abundance for Wet and Dry Peat species (Table 6.2): 40m or more onto the blanket peat, Dry species comprised only half the proportion of individuals of Peat species taken in pitfall traps that they did at 2m onto the peat and on the limestone itself: a significant difference ($X^2 = 58$, df = 1, $p < 0.001$).

Further consequences of the difference in stenotopy between Wet and Dry Peat species are revealed in their relative abundances on the Moor House limestone outcrops in 1984 and 1985: during the relatively warm, dry field season of the former year, numbers of individuals of Wet Peat species taken in pitfall traps were fewer, and formed a significantly lower proportion of the total Peat species catch on a given outcrop than in the cooler and wetter season of 1985 (paired $t = 2.3$, $df = 10$, $p < 0.05$). Numbers of individuals of Wet species taken on the same blanket peat site in 1984 (17) and 1985 (14), however, were not markedly different. The hotter and drier conditions in 1984 had their greatest impact on the shallow mineral soils and marginal peat, and least on the deep, moisture-retaining blanket bog. A greater disparity in moisture conditions between limestone and blanket bog resulted, and consequently, in 1984 fewer Wet Peat species ventured across the interface onto the dry limestone outcrops although overall numbers on blanket peat remained constant between years. Numbers of the more adaptable Dry species taken on either habitat also did not change significantly between years.

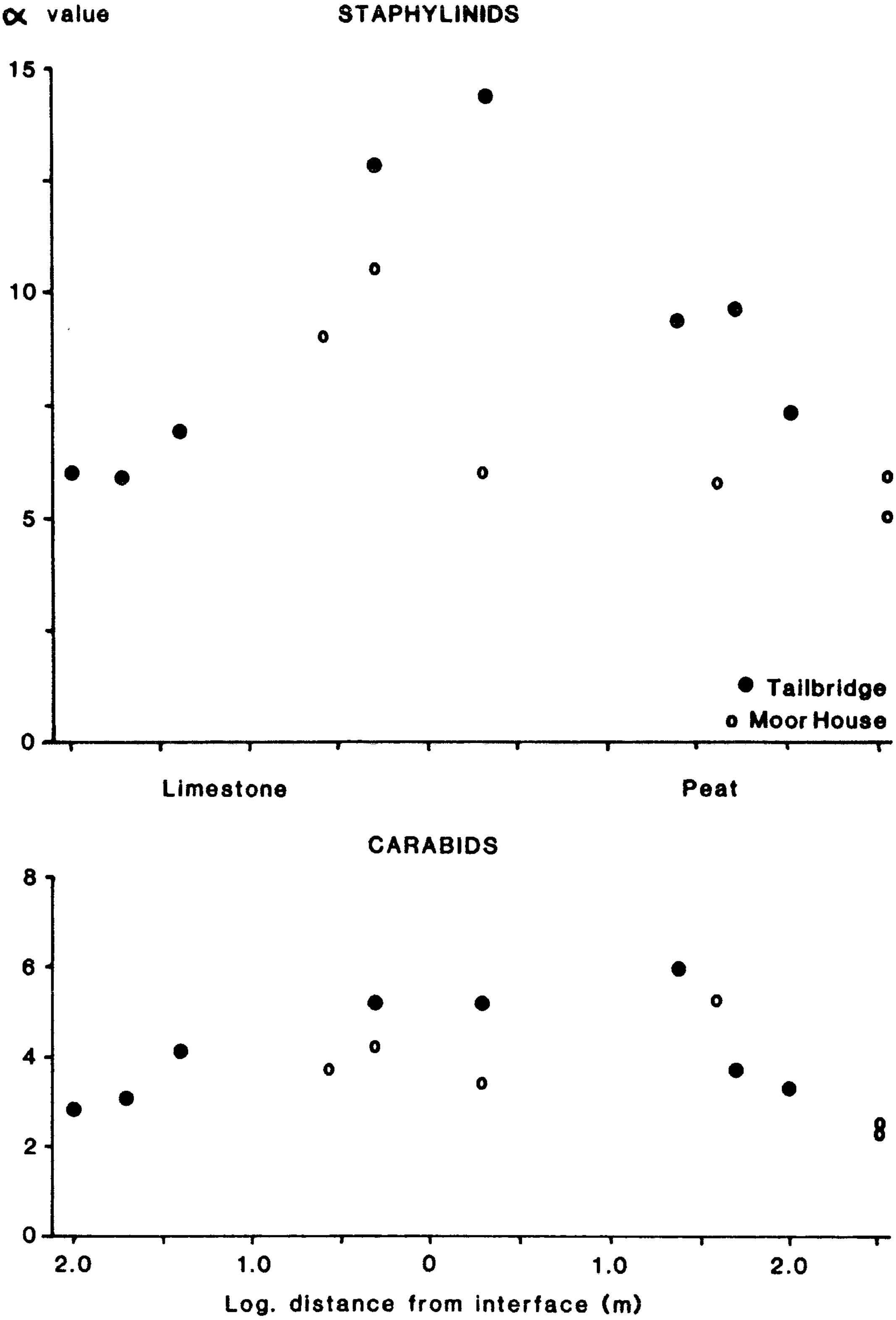
6:7 The species composition and diversity of the faunas

In the previous section the extent of, and the factors affecting, the dispersal of species across the interface between limestone grassland and blanket peat were examined. In this section the effect of such interchange of beetles across a habitat boundary upon the overall diversity and species composition of the respective habitats is considered.

The alpha diversity values ($\underline{a}$) for carabids and staphylinids derived from pitfall catches across the limestone:peat interfaces at Tailbridge and Moor House are depicted in Figure 6.4. Although carabid $\underline{a}$ values were invariably lower than those for staphylinids, those of both taxa exhibited the same distinctive pattern on both study areas: $\underline{a}$ values were relatively low at distances greater than 50m onto either limestone grassland or blanket peat, but rose considerably with decreasing distance from the habitat

Figure 6.4

Pattern of a diversity for carabids and staphylinids along the transects at Tailbridge and Moor House. Data are from pitfall trap catches only.



boundary, becoming double the previous values close to the interface itself. The relatively high a values for catches from the limestone outcrops at Moor House (cf Section 5:4) are seen to fit nicely into the overall pattern when their radii (and hence approximate distances from interface to traps) are taken into account: they corresponded most closely in diversity to the Tailbridge limestone sites 2m and 25m from the interface, and not to those 50m or more onto this habitat, where overall diversities were little higher than those at a similar distance onto the blanket peat.

This pattern of species diversity equates closely with the changing species composition of catches along the transects. The numbers of species from each species category, and the percentage contribution of each category to the total individuals taken on a site, are depicted in Figures 6.5 and 6.6. Total numbers of individuals in each category in a catch are given in Table 6.2. At a distance of 400m onto the peat at Moor House, the contribution of non-Peat species to the local fauna was minimal: the great majority of all carabid and staphylinid species and individuals taken were of Peat species, and the occasional vagrants recorded were mostly either particularly large carabids or flying staphylinids - both categories which possessed relatively high powers of dispersal (cf Section 6:6). Total numbers of species and individuals were low, and a values correspondingly small. At sites closer to the habitat interface, the influence of invading species from the adjacent habitat became greater, with the presence of vagrant individuals of atypical species causing species numbers to rise but without any marked change in total numbers of individuals: even at 100m from the habitat boundary at Tailbridge, Peat species formed about a fifth of the carabid and staphylinid species taken on the limestone, although their percentage contribution to the total individuals caught was negligible. Conversely, Limestone species comprised 13% (carabids) and 33%

Figure 6.5

Pattern of species richness for carabids and staphylinids along the transects at Tailbridge and Moor House. Data are from pitfall trap catches only.

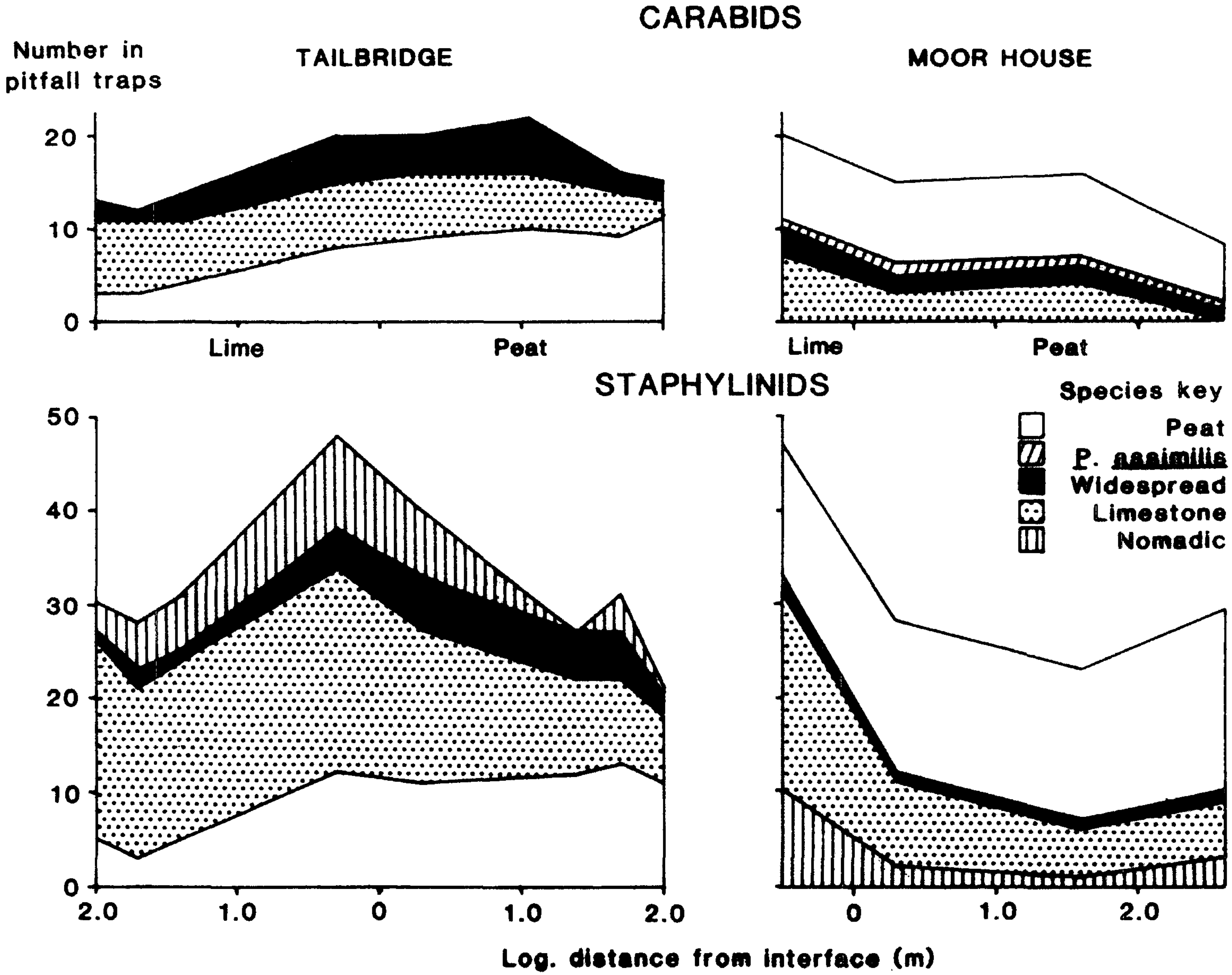
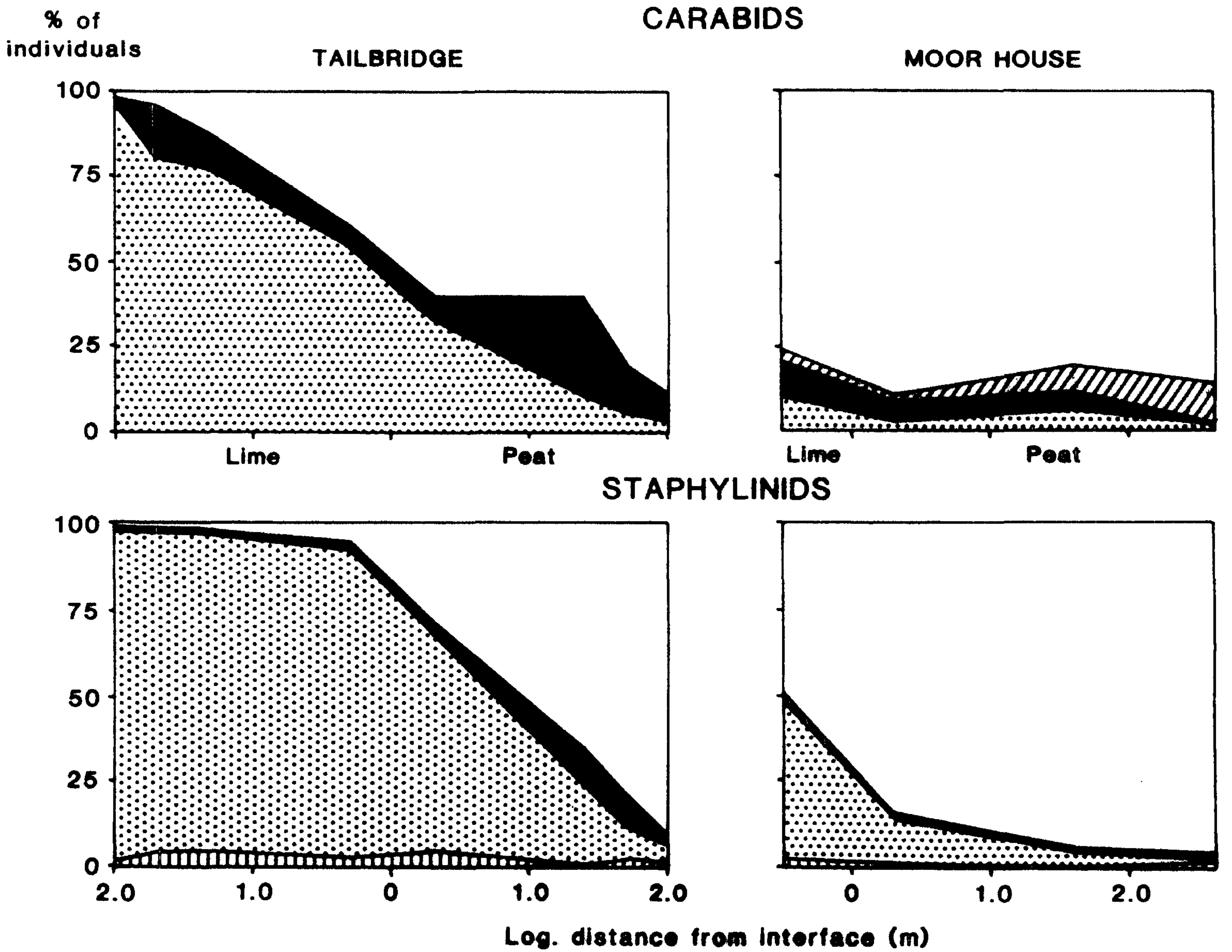


Figure 6.6

Species composition of carabid and staphylinid faunas along the transects at Tailbridge and Moor House . Data are from pitfall trap catches only (for totals see Table 6:1)



(staphylinids) of species taken 100m onto the peat, but less than a tenth of the total individuals. In association with this interchange across the interface, *a* values of the faunas at these sites were increased (Figure 6.5).

At distances of 25m or less from the habitat interface, the influx of species from the adjacent habitat was considerable (Figures 6.5 and 6.6): Limestone species comprised only a third to a half of the carabid and staphylinid species taken on the limestone grassland at 2m from the interface at Tailbridge, although they still formed upto 88% of the total individuals caught there. The converse situation prevailed at 2m onto the peat. Besides the intrusion onto these sites of species from the adjacent habitat, there was also a substantial Widespread species component largely concentrated along the interface itself, which contributed to the already augmented numbers of species present. The resultant *a* values recorded for these sites were twice those on the same habitat at 50-100m from the interface (Figure 6.5). The contribution of Peat species to the local limestone grassland fauna was most prominent in the catches on limestone outcrops along the transect at Moor House: here they constituted up to half of the total carabid and staphylinid species and three-quarters of the total individuals. This greatly augmented contribution of Peat species is simply explained: the Moor House traps, being positioned centrally on the limestone grassland, were subject to an influx of Peat species from all directions, whereas at Tailbridge the influx was unidirectional. The impact of Peat species on catches from the former sites was therefore greater than in traps at an equivalent distance onto the limestone at Tailbridge.

Although overall *a* values for carabid and staphylinid faunas were greatly increased immediately either side of the habitat interface, those for individual Limestone and Peat species categories did not alter significantly between habitats (Figure 6.7 and Table 6.8) despite their considerable change in abundance across the interface (cf Figure 6.5 and Table 6.2). Such a situation is to be expected if the species component on the atypical habitat was merely a subset of that on the normal habitat, and confirms earlier conclusions that Williams' *a* provides a robust measure of the species diversity within a particular community.

Figure 6.7

Pattern of a diversity for carabid and staphylinid Limestone and Peat species along the transects at Tailbridge and Moor House (data from both study areas combined). Data are from pitfall trap catches only.

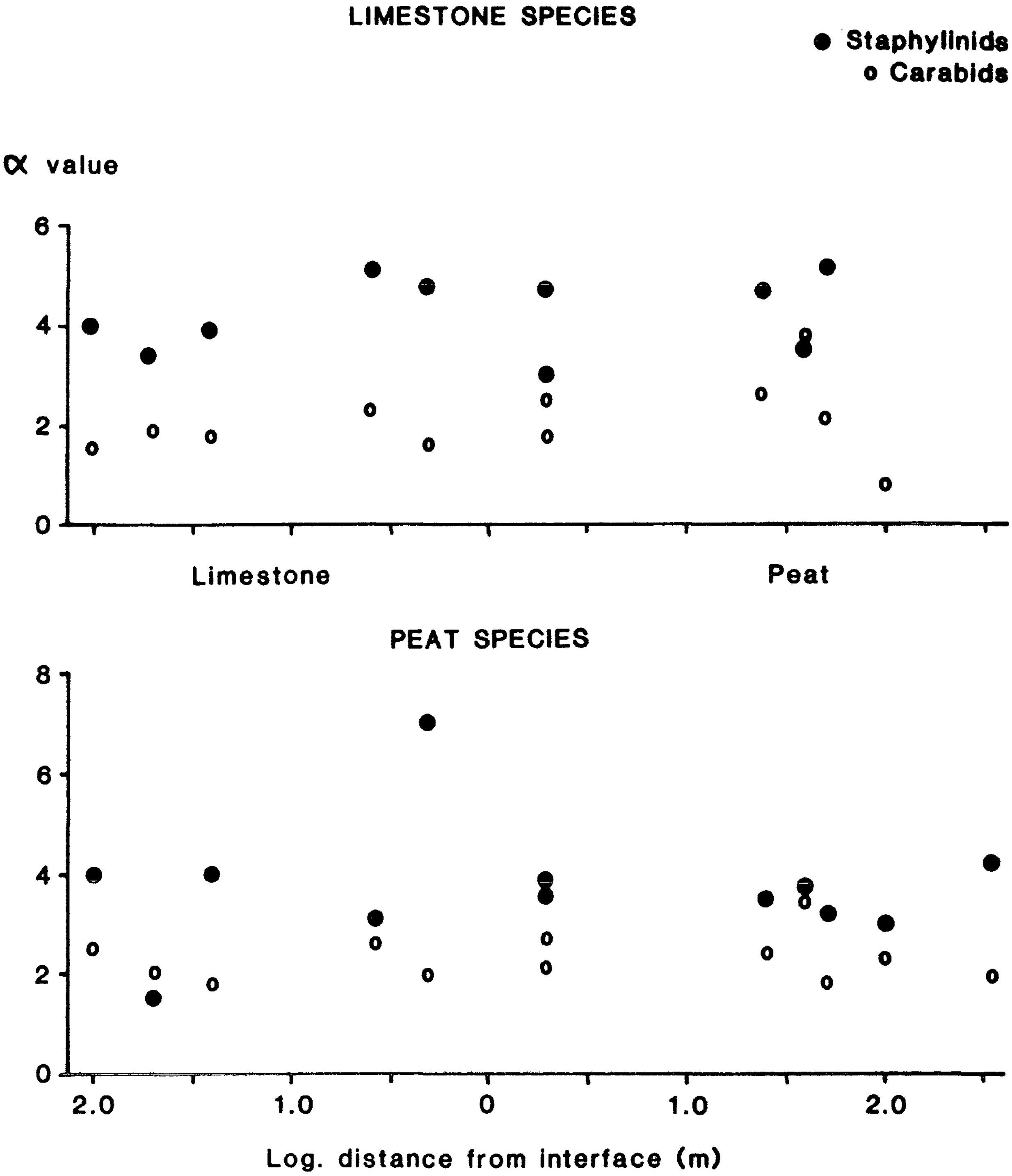


Table 6.8

_a_ values of Peat and Limestone species on peat and limestone habitats at Tailbridge.

Species category	Limestone			Peat		
	n	mean _a_	se	n	mean _a_	se
CARABIDS						
Peat	4	2.2	0.2	4	2.4	0.2
Limestone	4	1.8	0.1	4	2.4	0.4
STAPHYLINIDS						
Peat	4	3.9	0.9	4	3.6	0.2
Limestone	4	4.2	0.5	4	4.2	0.9

CHAPTER 7 THE AERIAL FAUNA AT MOOR HOUSE

7:1 Introduction

The window traps in operation at Moor House during 1984-5 continuously sampled from the air 0.5-1.0m above ground level, on both limestone and peat habitats (Chapter 3). A few carabids and a considerable number of staphylinids were taken in these traps (Section 4:3). Besides these two groups, many other insect taxa (and spiders) were taken (Table 7.1). In the first part of this chapter, the nature of flight activity on the Reserve in all of these groups is examined, In the second part, the origin of the aerial fauna is investigated.

7:2 Flight activity within the invertebrate fauna

7:2.1 Introduction

Flight is a fundamental characteristic of the majority of higher insects. At Moor House the three large orders Diptera, Coleoptera and Homoptera (flies, beetles and bugs), were all well represented in window trap catches, and have each been considered separately. Other insect orders, mainly Lepidoptera and Hymenoptera, were less abundant and have been grouped into one heterogeneous assemblage; Other Insects. Small airborne spiders (Araenida) were also taken in the window traps, and hence have been included in the analysis (Tables 7.1 and 7.2). Possible bias in the catching efficiency of window traps for different taxa demands some caution in the interpretation of the composition of samples from the traps (cf Section 3:2), but an overview of the aerial fauna in general helps to place

Table 7.1

Mean abundances of invertebrates taken in window traps at Moor House and Durham during 1984 and 1985.

Average numbers of individuals per window trap

		Total specimens		Coleoptera		Homoptera		Diptera		Other Insects		Araenae	
	n	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
MOOR HOUSE													
Limestone													
1984	5	1468	331	284	22.1	80.2	19.7	922	329	163	48.9	19.6	4.1
1985	4	1068	159	208	35.2	11.0	1.5	802	170	35.0	8.1	12.0	4.5
Juncus moor													
1985	1	2547		306		5		2052		54		125	
Blanket peat													
1984	3	1278	350	66.3	9.6	98.0	41.0	955	291	146	42.9	13.0	6.0
1985	4	620	40.9	46.5	9.4	23.5	1.7	506	36.4	22.5	6.8	20.0	7.3
DURHAM													
Field station													
1984	1	1652		734		188		584		107		44	
1985	1	2004		831		148		930		95		0	

Table 7.2

Percentage abundances of invertebrates taken in window traps at Moor House and Durham during 1984 and 1985.

			Percentage of total individuals in window traps				
	n	Mean no. of specimens	Coleoptera	Homoptera	Diptera	Other Insects	Araenae
MOOR HOUSE							
Limestone							
1984	5	1468	19.4	5.5	62.8	11.1	1.3
1985	4	1068	21.0	1.1	73.2	3.3	1.2
Juncus moor							
1985	1	2547	12.0	0.2	80.8	2.1	4.9
Blanket peat							
1984	3	1278	5.2	7.7	74.7	11.4	1.0
1985	4	620	8.0	3.8	81.7	3.4	3.1
DURHAM							
Field station							
1984	1	1657	44.4	11.3	35.3	6.4	2.6
1985	1	2004	41.5	7.4	46.4	4.7	0.0

the subsequent more detailed analysis of carabid and staphylinid flight activity in context.

7:2.2 The overall aerial fauna

a) Differences between years

The mean number of invertebrates taken per window trap was higher in 1984 than in 1985 on both limestone grassland (1468 and 1068 respectively) and blanket peat (1278 and 620), though not significantly so. Much of the variance about these mean values was caused by fluctuations in the abundance of Diptera, which always formed the bulk (60-80%) of the catch in a window trap (Table 7.1). Both Homoptera and Other Insects were significantly more abundant in catches in 1984 than in the following year: numbers of Homoptera taken in 1984 (mean = 86.9) were five times those taken in 1985 (mean = 15.9, t = 3.87, df = 7, $p < 0.01$), whilst the Other Insects showed a decline of equal magnitude between 1984 (mean = 157) and 1985 (mean = 31.6, t = 3.39, df = 7, $p < 0.05$). Numbers of Coleoptera and Araenida were not significantly different between years.

The between-year differences are reflected in the percentage contributions made by each category to the total catch in each year (Table 7.2): the relative importance of Homoptera and Other Insects in window trap catches was greater in 1984 (6.2% and 11% respectively) than in 1985 (1.5% and 3.1%). Window trap data from Durham field station showed the same trend: numbers of Homoptera and Other Insects taken were higher in 1984 than in 1985. These changes in the aerial fauna between years may simply reflect differences in the overall population densities of the taxa concerned, with a constant proportion of individuals flying in each year (cf

Section 7:2.4). Alternatively, overall population sizes may have remained constant, but levels of flight activity within them altered between years according to prevailing weather conditions (cf Section 7:3).

b) Seasonal distribution of flying insects

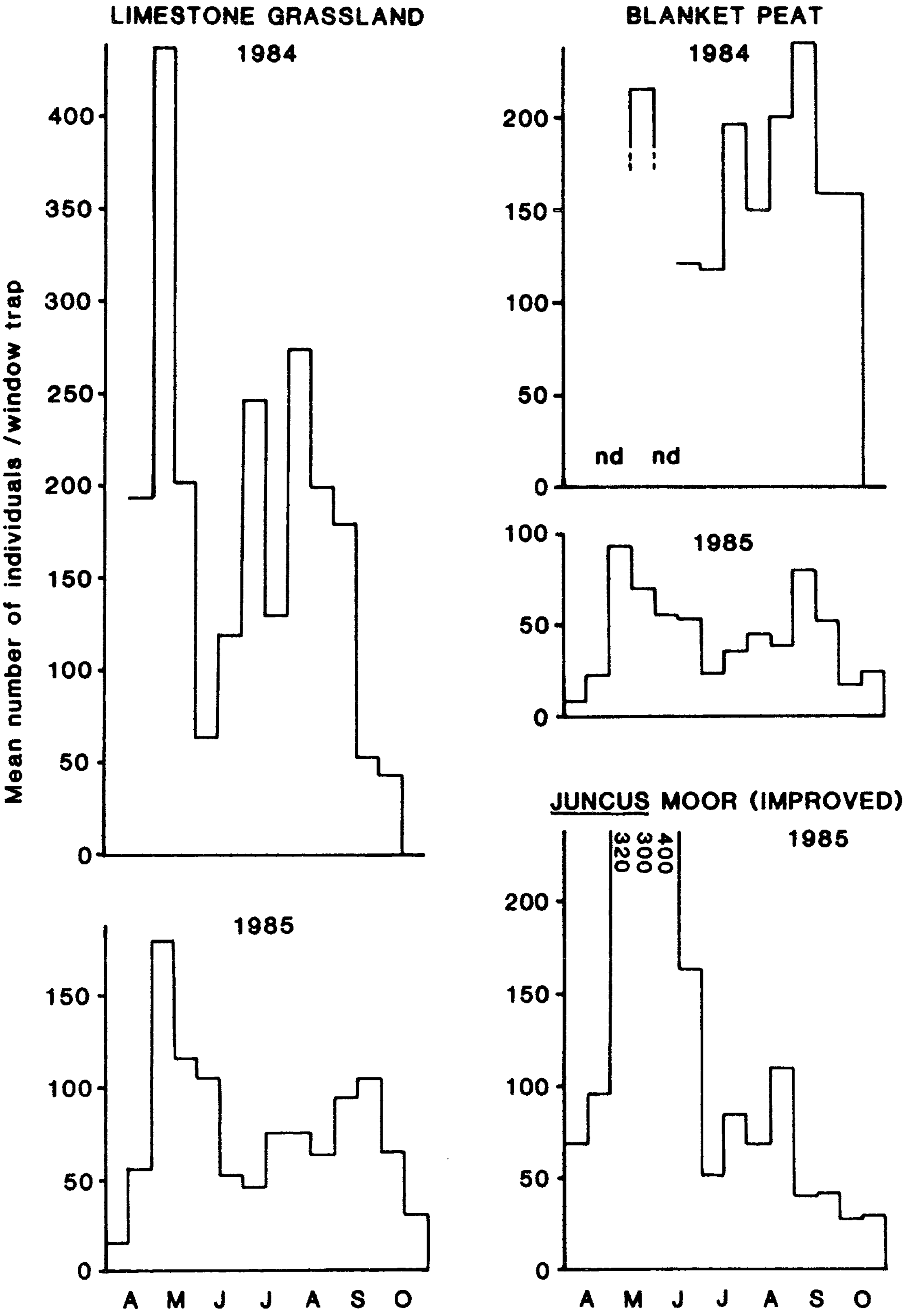
Abundances of insects taken in window traps at fortnightly intervals during the 1984 and 1985 field seasons showed a distinctive seasonal pattern (Figure 7.1): total numbers of flying individuals peaked in late spring/early summer, fell in midsummer, and then rose to a second peak of abundance in late summmer/early autumn. This pattern was characteristic of the aerial faunas sampled over all habitat types in both years.

c) Differences between habitat types

Mean abundances of total flying insects (and spiders) were higher in limestone grassland traps than in those from blanket peat in both years (Table 7.1), though not significantly so. Diptera, Other Insects and Araenida showed no consistent differences in abundance between these habitats: Diptera formed about three-quarters of the samples in each case, whilst the contributions of the other two groups combined generally represented less than a tenth of the total catch. The greater abundance of total specimens in the grassland traps was due to the presence of significantly greater numbers of Coleoptera: beetles were nearly five times as abundant in these window traps (mean = 250) as in those on blanket peat (mean = 55): they accounted for approximately 19% of the fauna taken in the former traps, but only 6% of that in the latter traps. Homoptera, though always a minor component of window trap catches, were significantly less

Figure 7.1

Seasonal pattern of abundance of airborne insects (and spiders) at Moor House in 1984 and 1985. Window trap data for blanket peat in 1984 are incomplete.



abundant in limestone grassland catches (1984 mean = 80.2, 1985 mean = 11.0) than in blanket peat ones (1984 mean = 98.0, 1985 mean = 23.5, $t = 5.54$, $df = 6$, $p < 0.01$). The aerial sample from the improved Juncus moor contained over twice as many specimens (2547) as the average limestone grassland trap in the same year (mean = 1068), and four times as many as the average blanket peat trap (mean = 620). The great majority (81%) of these individuals were Diptera. Coleoptera, although 50% more abundant than on the average limestone site in 1984(mean = 208), represented only 12% of the total sample. The window trap catches from Durham field station, although possessing total numbers of specimens comparable to those from Moor House (Table 7.1), had a much lower fly component (41%) which was compensated for by a much larger proportion of beetles (42%). Absolute numbers of bugs and Other insects caught were substantially higher than at Moor House, though their percentage contributions were still small (9.6% and 5.6% respectively). The differences in proportional representation of taxa in the Durham and Moor House traps can be directly equated with the altitudinal change between the study areas: Coulson and Whittaker (1978) have reviewed these changes in faunal composition between lowland and upland habitats.

7:2.3 Carabids

Twelve carabids were taken in window traps at Moor House during 1984 and 1985 (Table 4.6). Two of these were single individuals of species also caught by pitfall trap on the Reserve during the same period. The other ten individuals were of three species absent from pitfall trap catches in the two years of sampling. Flight activity by carabids at Moor House was clearly very low.

7:2.4 Staphylinids

Two-thirds of the 145 species of staphylinid taken at Moor House during 1984 and 1985 were captured in window traps, indicating a high capacity for flight within this taxon on the Reserve (cf Section 4:3). Flight activity was not restricted to a certain time of year, but occurred throughout the field season, from April to October (Figure 7.2). Peaks of abundance in window trap catches occurred in late spring/early summer, and also in late summer/early autumn, but even outside these periods, substantial numbers of species were flying.

Forty Settled species were taken by window trap, representing 41% of the total species recorded for this category on the Reserve (Table 7.3). Average numbers of species and individuals of these flying Settled species taken per trap were not significantly different between years, either on the ground or in the air. Overall, window trap catches accounted for 21% of all individuals of these species taken at Moor House (Table 7.3). The seasonal pattern of abundance of flying Settled species in pitfall and window trap catches in 1985 is shown in Figure 7.3. The majority of individuals were taken early in the season, with a peak of abundance both on the ground and in the air in May. After this time, numbers progessively declined throughout the season, and average abundances in pitfalls during July-September (mean = 27.5) were significantly lower than in April-June (mean = 72.3; $t = 2.77$, $df = 12$, $p < 0.05$). Similarly, numbers in window traps in the former period (mean = 4.2) were significantly greater than in the latter (mean = 27.3; $t = 3.14$, $df = 10$, $p < 0.05$). A significant difference also existed in pitfall:window trap catch ratios, with higher values in July-September (mean = 0.90) than in April-June (mean = 0.73; $t = 2.62$, $df = 11$, $p < 0.05$), indicating a real decline in flight activity

Figure 7.2

Seasonal pattern of abundance of total airborne staphylinid species and individuals at Moor House in 1984 and 1985. Numbers in window traps represent seasonal catch of all traps combined.

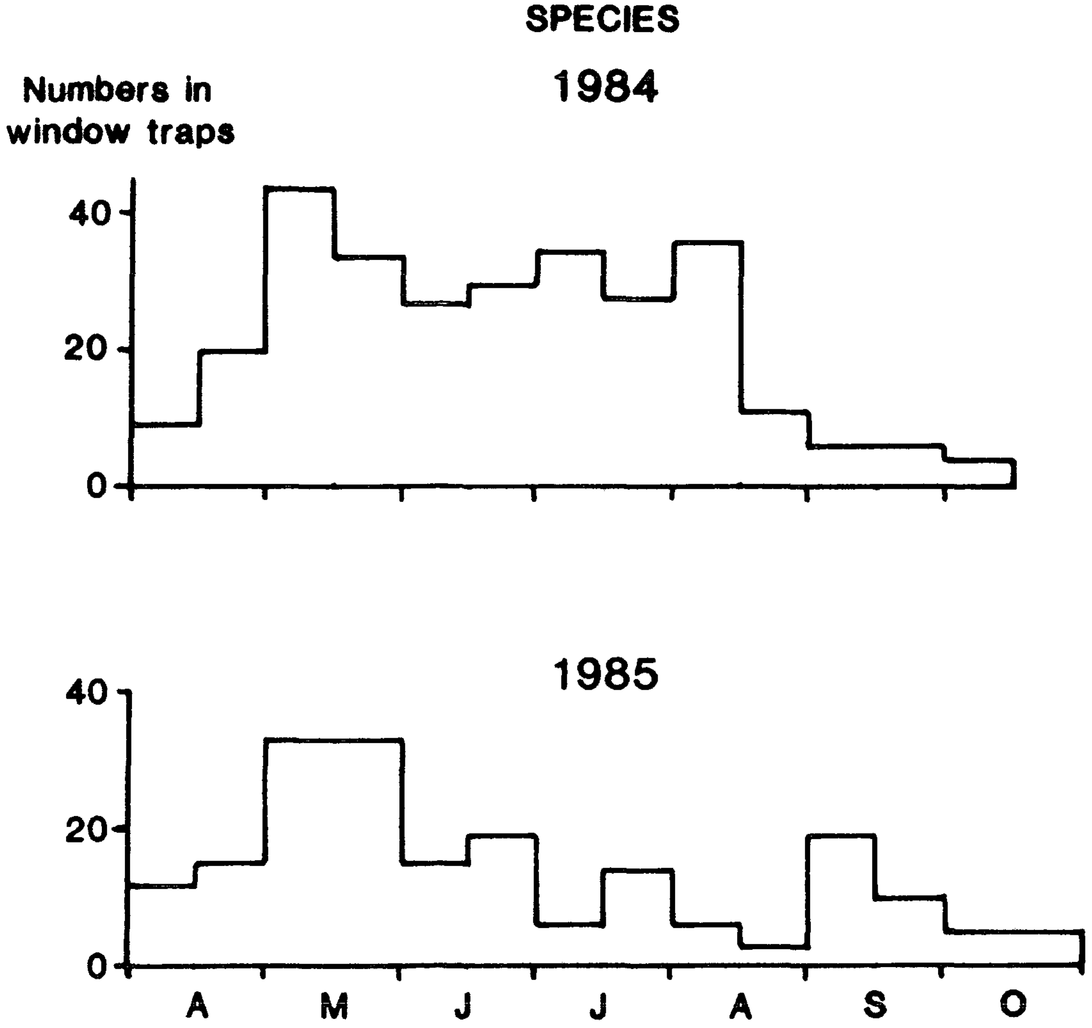


Figure 7.2 (cont.)

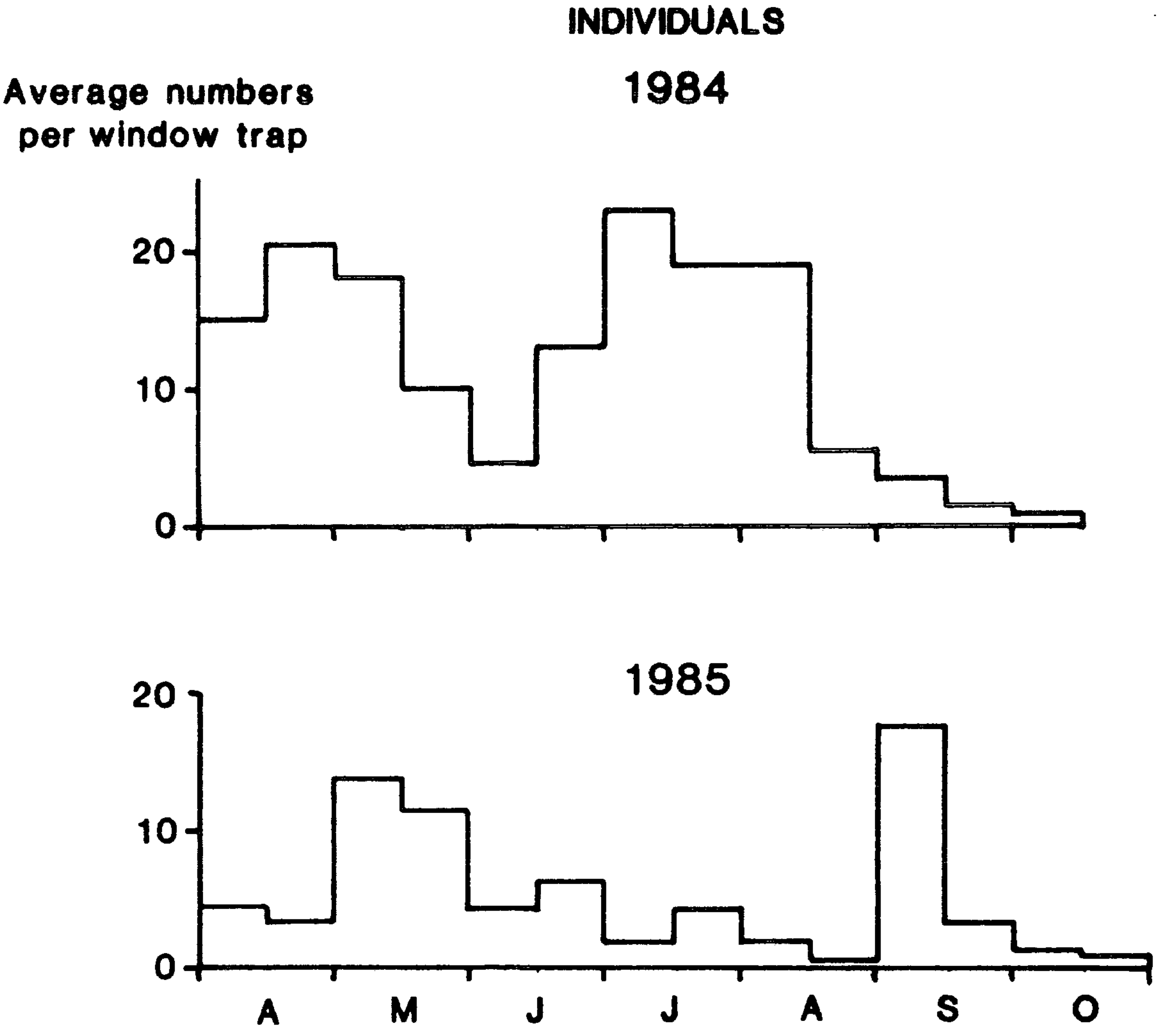


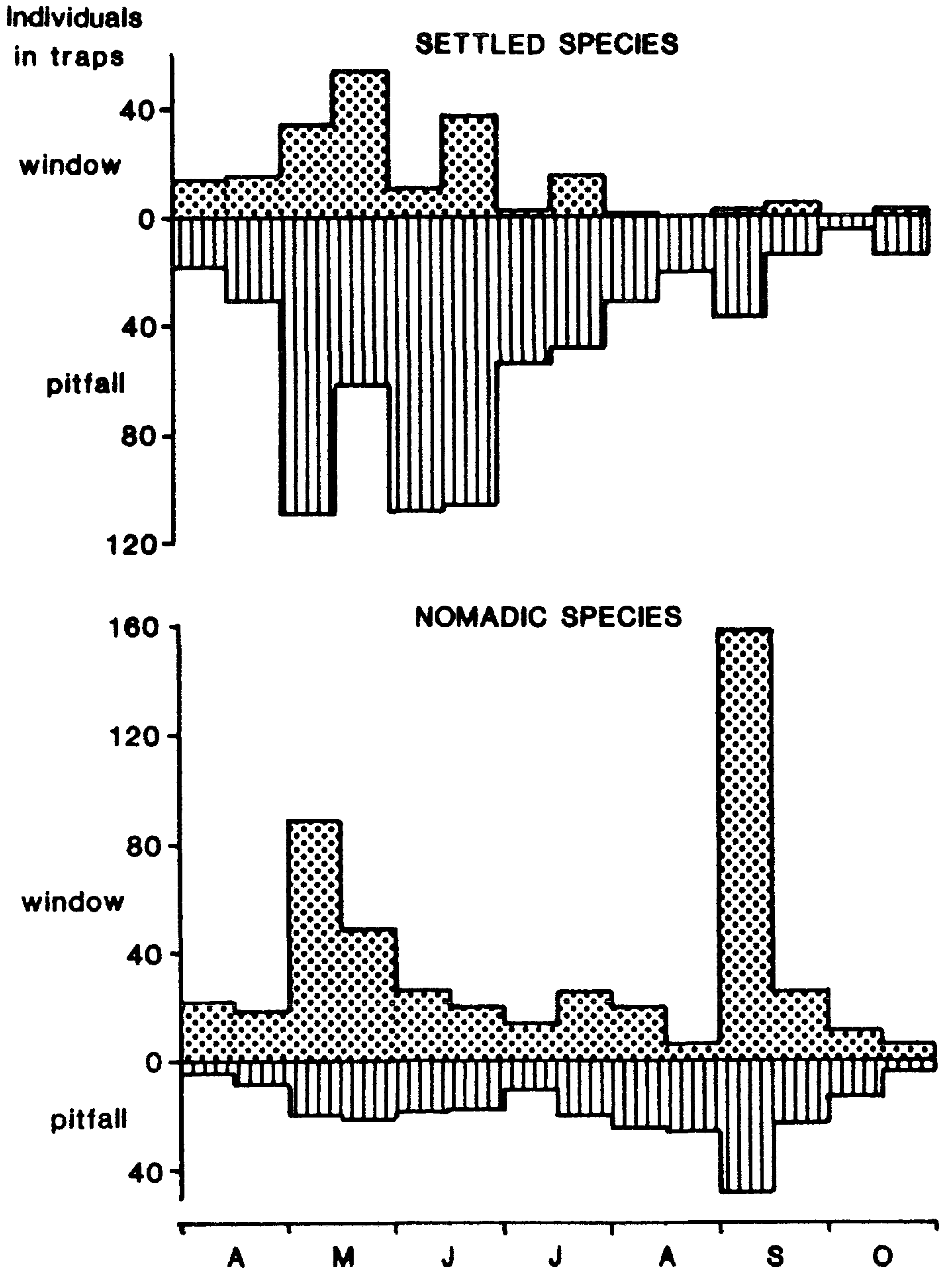
Table 7.3

Flight activity in staphylinids at Moor House.

Species category	No. of species flying	% total species in category	% individuals flying (of flying species)
SETTLED (total)	41	47.1	20.8
Peat	2	10.0	5.6
Widespread	9	37.5	44.2
Limestone	23	52.3	19.8
Vagrant	7	100	100
NOMADIC (total)	59	98.3	70.5

Figure 7.3

Seasonal pattern of abundance of individuals of flying staphylinid species in window and pitfall trap catches at Moor House in 1985, comparing Settled and Nomadic species. Numbers in traps represent seasonal catch of all traps combined.



of these species in addition to their overall fall in abundance in catches in late summer and autumn. Many of the flying Settled species at Moor House appeared to be univoltine, breeding relatively early in the season (Figure 7.4), and their peak of flight activity accompanied the general increase in activity and/or abundance on the ground at this time (evident in the augmented pitfall trap catches).

The contribution of these flying species to the total species within different categories of Settled species varied considerably (Table 7.3): they represented only 10% of Peat, but 52% of Limestone species. The proportion of Widespread species capable of flight gave an intermediate value of 38%, while by definition, all Rare species flew. Moreover, the level of flight activity exhibited by the flying species within each category differed markedly according to the associated habitat type: only 6% of all individuals of flying Peat species taken were captured in window traps, compared to 20% of those of Limestone species (Table 7.3). The implications of this differential level of flight activity between species resident on the blanket peat and on the limestone outcrops at Moor House are considered in detail in Chapter 9.

A total of 60 Nomadic species was taken at Moor House during 1984 and 1985. Their seasonal pattern of abundance in window and pitfall trap catches during 1985 is given in Figure 7.3. They were active on the Reserve throughout the season, peaking in numbers in May and September. There was no significant difference in the numbers of individuals taken in the first and second halves of the field season. Relative to the Settled species, Nomadic species exhibited very high levels of flight activity (Table 7.3): 98% of these latter species were actually taken in flight on the Reserve, and only a single individual of one species, *Omalium laticolle*, was taken by pitfall trap alone. Moreover, 71% of all individuals of Nomadic species

Figure 7.4

Seasonal pattern of abundance of four common flying staphylinid species in window and pitfall trap catches at Moor House in 1985. comparing Settled and Nomadic species. Numbers in traps represent seasonal catch of all traps combined.

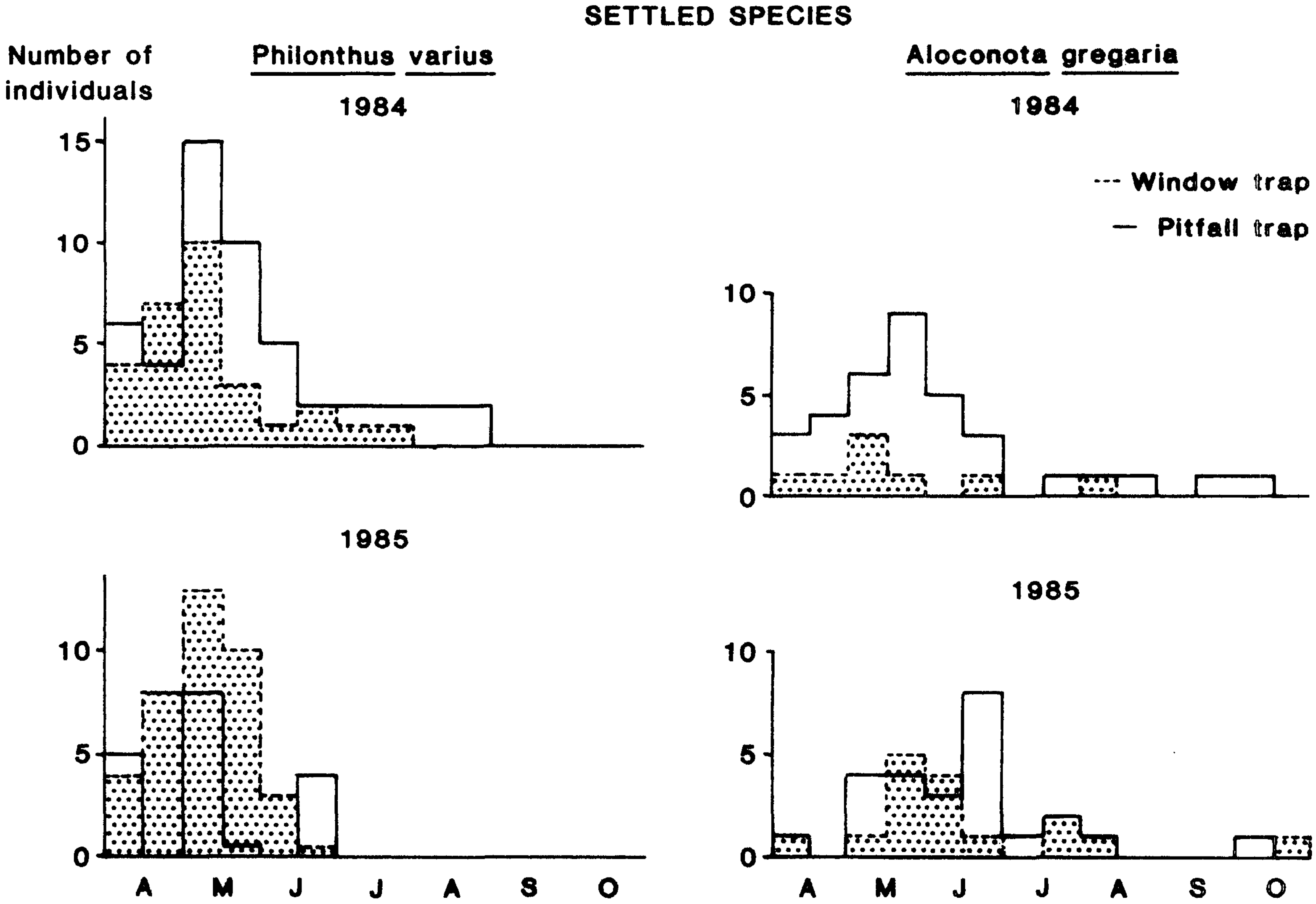
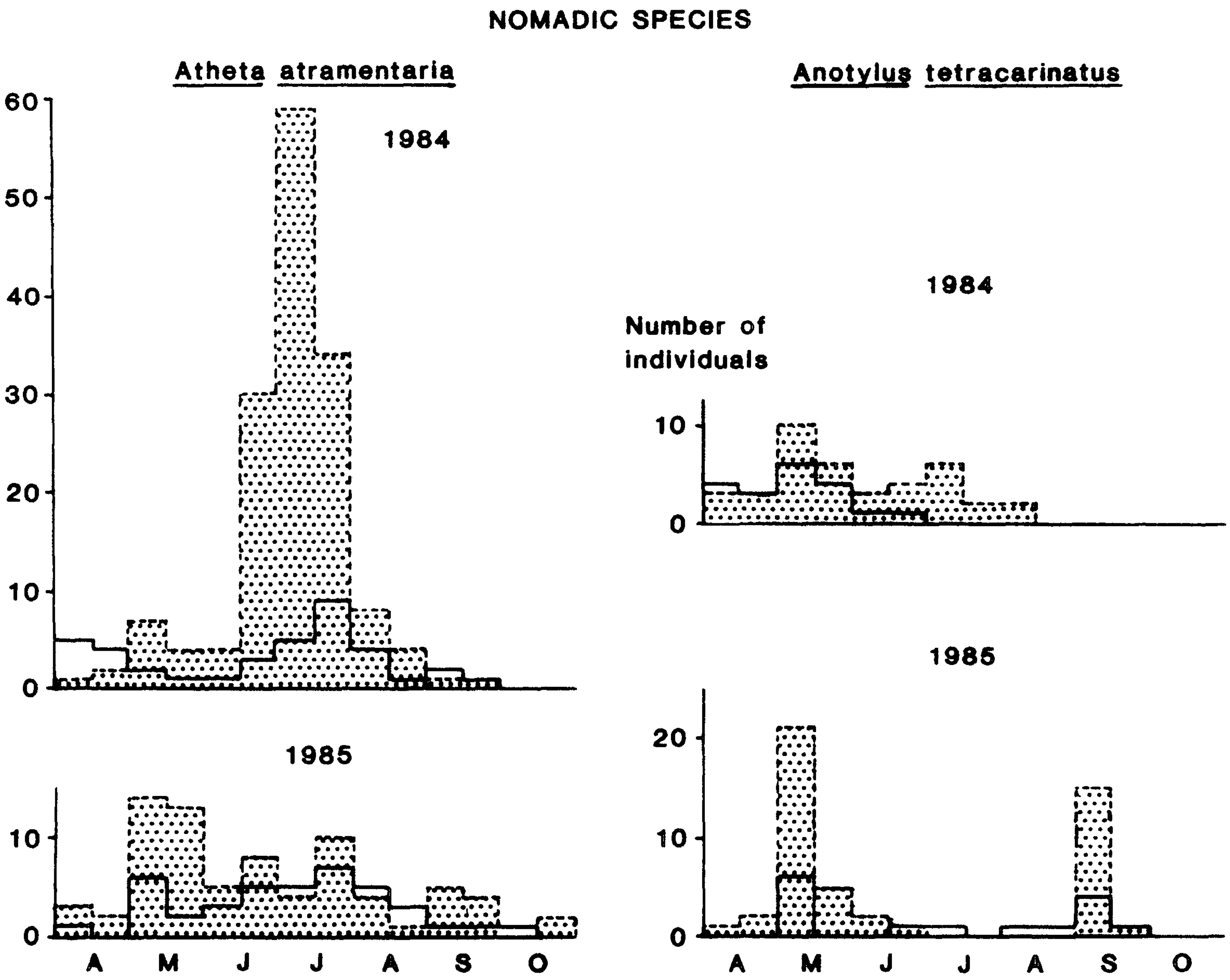


Figure 7.4 (cont.)



taken at Moor House were caught in window traps, in contrast to only 21% of those of Settled species (Table 7.3).

The seasonal peaks in abundance of individuals of Nomadic species were much more marked in window than in pitfall trap catches. These periodic high levels of flight activity by Nomadic species may be related in part to specific stages in the life-cycle of the species concerned: besides the differing contributions of univoltine species breeding or emerging at a specific time of year, many species appeared to be bi- or multivoltine, exhibiting several peaks of flight activity in a season (Figure 7.4; also Koskela 1979). However, the continuous high levels of flight activity throughout the season can be attributed more directly to the ecology of these species and the nature of the resources that they exploit: the transient occurrence of commodities such as dung demands that species dependent upon them must disperse regularly and effectively as current resources are exhausted and new ones must be sought. Thus for the continued existence of small nomadic staphylinids flight is essential. The continuous presence of sheep on the Reserve during the field season ensured a near constant supply of dung throughout this period, and hence high levels of flight activity were sustained by the coprophiles.

7:3 The origin of the aerial fauna

7:3.1 Introduction

Species capable of flight possess considerable potential for long-range dispersal (Johnson 1969). Their occurrence over (or on) a particular habitat does not necessarily mean that they originated there. The possible sources of origin of species within the aerial fauna at Moor House are threefold;

a)The habitat over which the species was flying;

b)A different habitat within the same locality;

c)A habitat outside the Reserve.

In the following sections these three possibilities are considered in more detail.

7:3.2 The immediate habitat

Window trap data for Diptera, Coleoptera and Homoptera collected from limestone grassland site A and blanket peat site L in 1984 and 1985 are compared with similar data from pitfall traps operating on these sites in 1978 (after Coulson and Butterfield 1979) in Table 7.4. The proportions of total Coleoptera and Homoptera taken from the air over each habitat type closely reflect the relative abundances of these two taxa caught on the ground below (Table 7.4): over three-quarters of all beetles sampled occurred on or above the limestone grassland, whilst three-quarters of all bugs caught were associated with the blanket peat. The proportions of Diptera in each category do not correspond so closely: nearly three-quarters of the total Diptera taken in pitfalls, but only a third of those sampled by window traps, were from the blanket peat. Fly populations fluctuated markedly from year to year (see Table 7.1) and hence may have been very different in 1978 and 1984/5. However, the discrepancy may also be explained by the brachypterous condition of certain fly species only abundant on the blanket peat: tipulids such as Molophilus ater and Tipula subnodicornis (female), which featured prominently in pitfall catches from the blanket peat (Coulson and Butterfield 1979), cannot fly and hence are absent from the window trap samples. When tipulid numbers are excluded from

Table 7.4

Percentages of Coleoptera, Homoptera and Diptera taken on limestone and blanket peat in pitfall and window traps.

	% of total class on habitat		
	Coleoptera	Homoptera	Diptera
PITFALL TRAPS 1978			
Limestone	75.5	27.7	27.5
Blanket peat	24.5	72.3	72.5
Total Individuals	665	155	564
WINDOW TRAP 1984			
Limestone	81.0	28.7	67.5
Blanket peat	19.0	71.3	32.5
Total Individuals	432	247	3500
WINDOW TRAP 1985			
Limestone	82.0	31.7	58.9
Blanket peat	18.0	68.3	41.1
Total Individuals	200	41	1334

the pitfall trap data, the percentage of flies in pitfall catches from the limestone grassland relative to those on the blanket peat increases to 41%: a value which corresponds closely to those for the window traps on this limestone site (33% and 41%, for 1984 and 1985 respectively). These data suggest that the numbers of insects present in the air largely reflected the abundances of their populations on the ground immediately below.

7:3.3 Local moorland

Although the basic pattern of seasonal abundance of flying invertebrates (Figure 7.1) corresponds quite closely to that for invertebrates taken in water traps at Moor House by Nelson (1971), the marked difference in abundance patterns for fauna on limestone and peat displayed by catches from the latter traps was not evident in the window trap data: the same basic pattern of seasonal abundance characterized the aerial faunas over all habitat types considered (Figure 7.1). Such a situation would not be expected if the total aerial component was derived directly from invertebrate populations on the habitat beneath. Moreover, the overall beta diversity value (Sørensen's Index) between limestone and blanket peat habitats for flying staphylinid species taken in window traps (0.55) was over twice that for the same species in pitfall traps (0.27). Although only two Peat species of staphylinid were taken in flight (Table 7.3), an average of 14.4 (± 1.2) species of staphylinid was taken in window traps on the blanket peat (Table 4.8). Eleven of these species taken on the peat were Limestone species resident on the outcrops nearby. These data indicate that although the majority of flying individuals may have stayed closely associated with their preferred habitat, there was also a component which actively flew or was blown into other localities where it mixed with the local airborne fauna.

7:3.4 Regions beyond the Reserve

i) Staphylinids and carabids

Although the majority of atypical species captured in flight over a habitat were still probably of local origin, dispersing from an area of favourable habitat nearby, there is evidence that many flying individuals taken at Moor House did not originate there, but represented an immigrant component from outside the Reserve. During 1984-5 winged individuals of four carabid and 85 staphylinid species previously unrecorded at Moor House were caught on the Reserve. All of these species were each represented by only a few individuals, mostly in in window trap catches, and many have specific habitat requirements which moorland is unlikely to meet (Table 7.5) and must therefore have originated in other regions. Extensive Pennine moorland borders the Reserve to the north, south and east: non-moorland immigrants are unlikely to have entered from these directions. On the other side of the escarpment marking the Reserve's western boundary lies the Eden valley. This extensive lowland region represents the most likely source of atypical immigrant species. Most of the staphylinid species involved were relatively small (2-5mm), but even the larger flying staphylinids (eg <u>Philonthus</u> spp.) and carabids were likely to have been influenced by the comparatively strong winds (4-7m/s) which characterized much of the field season (Section 2:3). The significant positive correlation between the proportion of staphylinids taken in the west-facing sectors of window traps and the percentage of westerly winds (Figure 7.5) provides evidence that their direction of flight was largely determined by the prevailing wind.

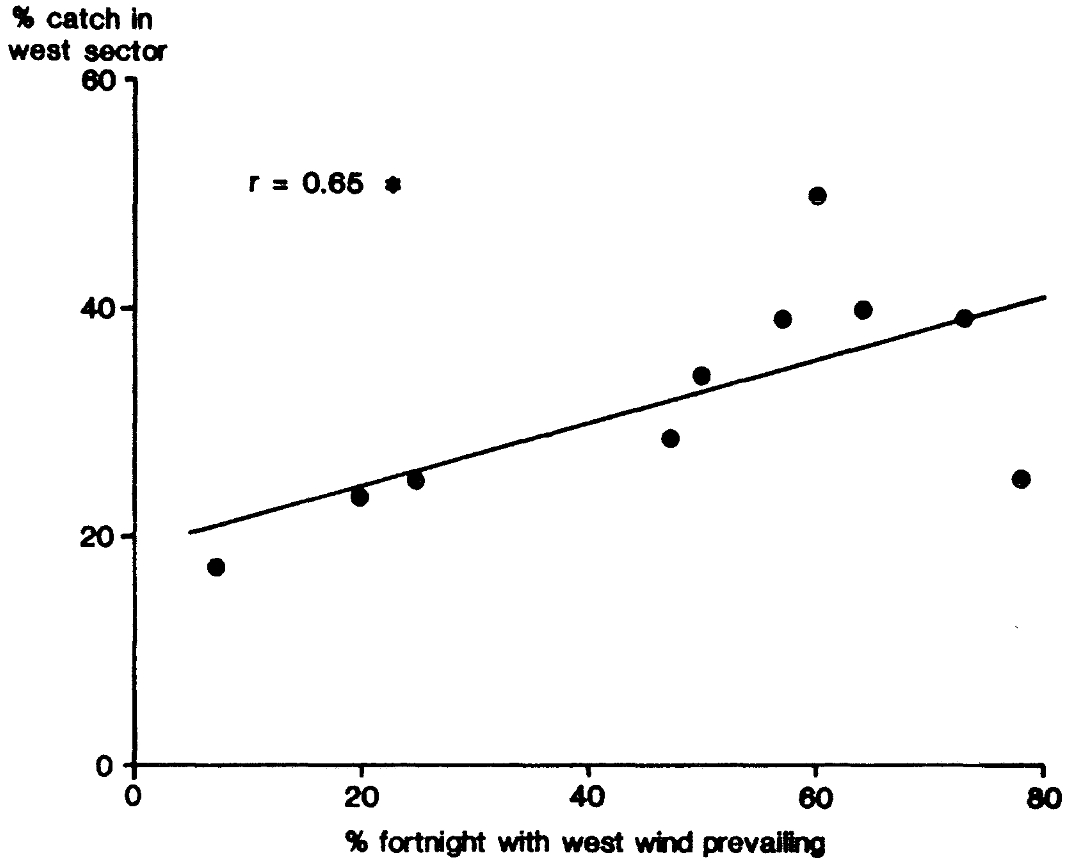
Table 7.5

Anomalous species of carabid and staphylinid taken at Moor House in 1984-5.

	Numbers taken	Typical habitat/ecology
CARABIDS		
Amara apricaria	1	Synanthropic
A. ovata	2	Dry gravelly ground
STAPHYLINIDS		
Dropephylla vilis	1	Under bark
D. grandiloqua	5	"
Phyllodrepa floralis	1	"
Xylodromus concinnus	4	Synanthropic
Omalium caesium	1	"
Philonthus umbratilis	2	"
P. discoideus	2	"

Figure 7.5

Proportion of total staphylinids caught in west-facing sectors of window traps per fortnight in relation to the prevalence of westerly winds. Significance level given by *: $p < 0.05$.



Settled species of staphylinid recorded at Moor House were either resident on the moor and maintaining viable populations from one year to the next, or vagrants originating elsewhere. The relative contributions of these two components to the aerial fauna over the Reserve in a season will have been largely determined by prevailing weather conditions. Flight activity by resident species was at its peak during the first half of the field seasons of 1984 and 1985 (cf Section 7:2.4), when average daily hours of sunshine were reasonably high and climatic conditions most conducive to staphylinid flight (Koskela 1979). Between April-June numbers taken in window traps exhibited no significant correlation with distance from the Pennine escarpment (Figure 7.6), and maximum numbers occurred in the south- and east-facing sectors of these traps in 1984 (Figure 7.7). Species each contributing less than 1% to the total staphylinids taken in window traps in 1984 (Uncommon species) comprised only 30% of the individuals of Settled species taken in flight during these months: immigration of vagrant individuals from the Eden valley was at a minimum. Similarly, numbers of individuals of Nomadic species taken in window traps showed no significant trend with distance from the western escarpment or with orientation of window trap sector (Figures 7.6 and 7.7).

In the second half of the season conditions were less conducive to flight: daily hours of sunshine decreased, and a strong westerly wind prevailed for most of the time (Section 2:3). The proportion of resident Settled species in flight declined but the influence of vagrant species brought in from the west increased: individuals of Settled species taken during July-September showed a significant negative correlation with distance from the Pennine escarpment (Figure 7.6), decreasing by 14% with every 100m increase in distance. Total numbers taken in the west-facing sectors of the window traps were significantly higher than in the

Figure 7.6

Seasonal abundance of staphylinid individuals in window trap catches at Moor House in 1984 and 1985 in relation to distance of trap from the western escarpment, comparing Settled and Nomadic species. Significance levels given by **: $p < 0.01$, ***: $p < 0.001$.

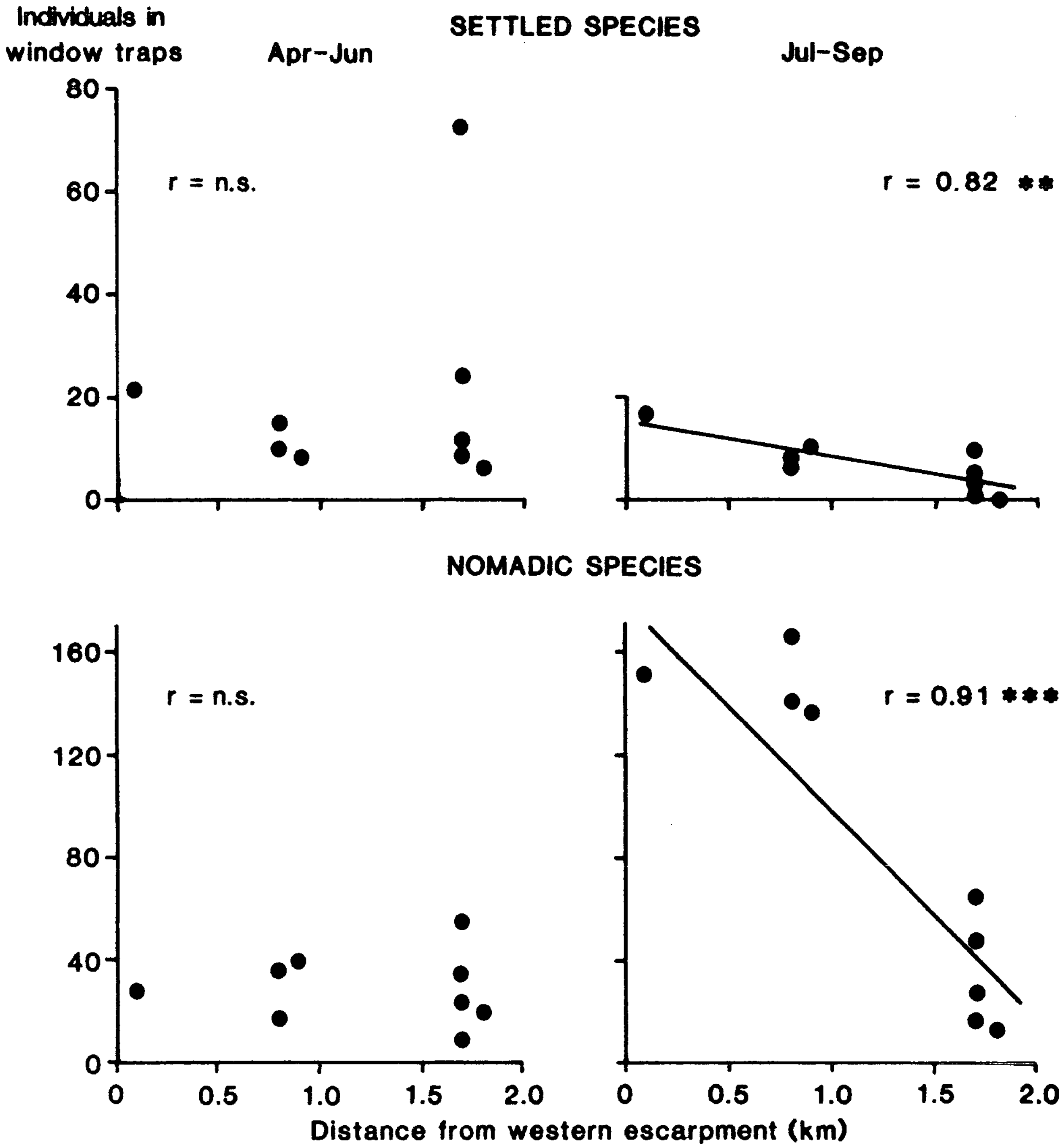
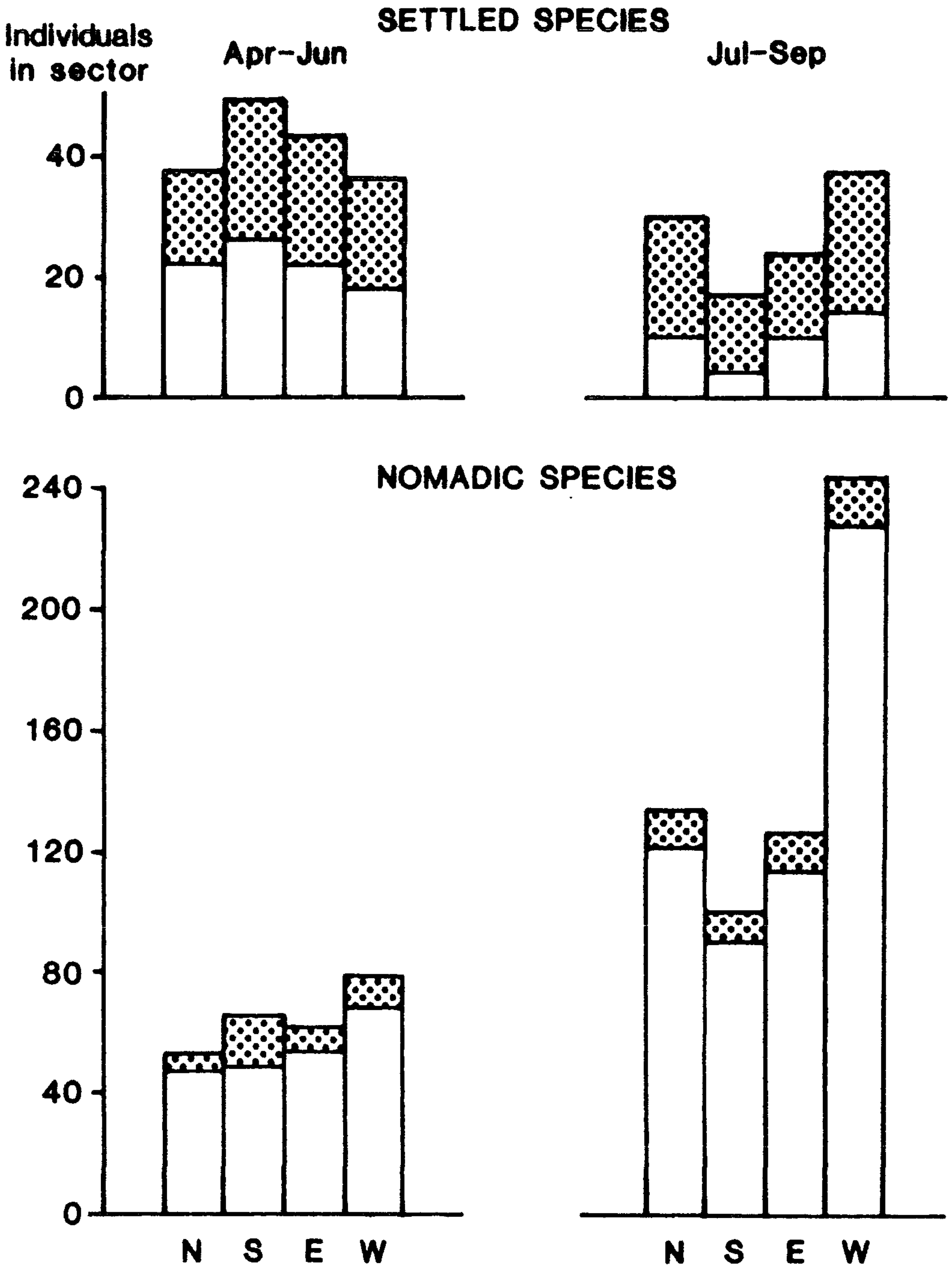


Figure 7.7

Seasonal abundance of staphylinid individuals in window trap catches at Moor House in 1984 in relation to orientation of window trap sectors, comparing Settled and Nomadic species. Numbers in traps represent seasonal catch of all traps combined. Stippled areas indicate proportion of Uncommon species (species each comprising less than 1% of total catch).



east-facing sectors during these months in 1984 (Wilcoxon T = 7, n = 12, $p < 0.01$), and Uncommon species comprised 60% of the total Settled species individuals taken (Figure 7.7). Similarly there was a significant negative correlation between numbers of individuals of Nomadic species taken in window traps and distance from the western escarpment (Figure 7.6): numbers of individuals decreased by 18% with every 100m increase in distance. Total numbers of individuals of Nomadic species taken in west-facing sectors of window traps at this time were over twice those from other sectors (Figure 7.7), with numbers of Common species (those comprising more than 1% of the total staphylinid catch) being significantly more abundant in the west- than in the east-facing sectors (Wilcoxon T = 4.5, n = 11, $p < 0.01$). Nomadic species do not have spatially stable populations, and are typically far more active fliers (and for longer in the season) than Settled species (Section 7:2). Consequently, their pattern of distribution was more greatly influenced by the seasonal change in air patterns than was that of Settled species, resulting in a much higher level of immigration from the west (as evidenced by the considerable number of individuals in the west-facing sector of the window traps). Of the eleven individuals of Non-dung Nomadic species which almost certainly did not originate on the Reserve, <u>Dropephylla grandiloqua</u>, <u>Xylodromus concinnus</u>, <u>Philonthus discoideus</u> and <u>Philonthus umbratilis</u> (cf Table 7.5), ten were taken during July-September. Only one <u>Philonthus</u>, a genus of relatively large and powerful fliers, was taken before this time .

Besides direction of the prevailing wind, overall seasonal conditions in the region also significantly influenced the level of input of aerial plankton onto the Reserve. In 1984, average temperatures and daily hours of sunshine at Moor House were higher, and precipitation levels were lower during July-September than in 1985 (Table 7.6). In the latter year, numbers of individuals of both Settled and Nomadic species were only about a third of those taken in 1984 during these months (Figure 7.8): a significant between-year difference. In particular, numbers of individuals of Non-dung Nomadic species (many almost certainly vagrants on the moor) were significantly lower in this year than in 1984 in both window traps (means = 2.7 and 10.3 respectively; $t = 3.67$, $df = 8$, $p = < 0.01$) and pitfall traps (means = 2.8 and 9.0 respectively; $t = 2.85$, $df = 12$, $p = < 0.05$). It is probable that the more amenable climatic conditions on the Reserve in 1984 were also characteristic of the region as a whole, and that the increased numbers of airborne staphylinids taken in window traps in this year resulted directly from increased flight activity in the Eden valley, and a correspondingly higher density of aerial plankton being carried into the Reserve.

Average numbers of Nomadic species and individuals taken on the ground and in the air at Tailbridge in 1986 were significantly lower than at Moor House in the previous two years (Table 7.7). Although this may be attributed in part to wetter cloudier weather conditions in 1986 (relative to 1984 and 1985) and an associated decrease in general levels of flight activity, there is another explanation: Tailbridge is a relatively sheltered plateau of moorland, lying to the south of Moor House and the Eden valley and immediately surrounded on all sides by stretches of moor and fell. It was not directly exposed to strong prevailing winds carrying material up from the Eden valley in the dramatic way that Moor House was, and hence may have experienced a lower input and subsequent fallout of aerial plankton

ii) Aphids: additional evidence

Besides staphylinids and carabids, many aphid species were also taken

Figure 7.8

Seasonal abundance of staphylinid individuals in window trap catches at Moor House in 1984 and 1985 compared. Significance level given by *: $p < 0.05$.

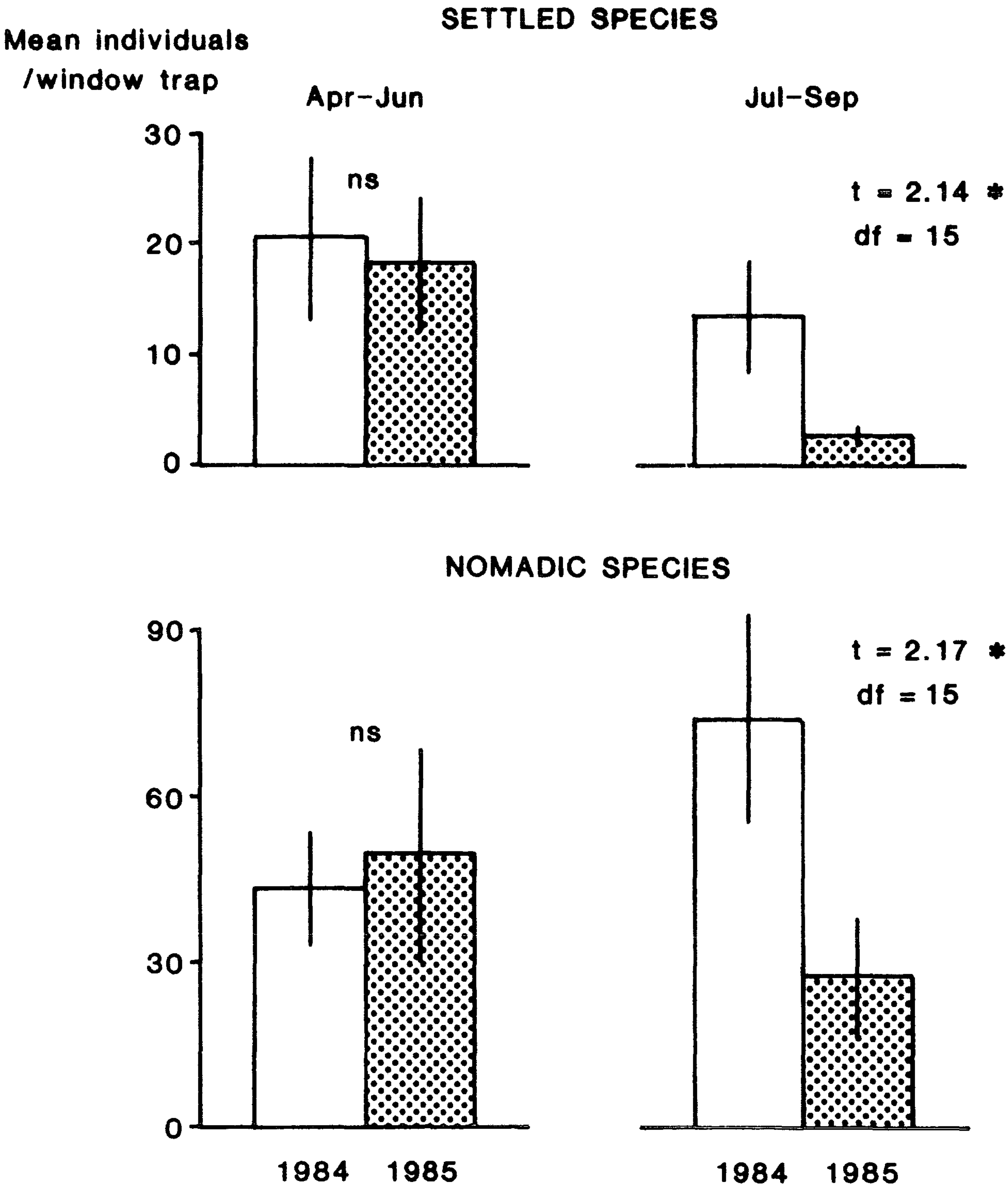


Table 7.6

Climatic differences between years at Moor House.

	Fortnightly averages (July-September)						Significant
	1984			1985			difference
	n	mean	se	n	mean	se	($p < 0.05$)
Sunshine (hr/day)	6	8.1	0.6	6	3.5	1.0	*
Temperature (°C)	6	10.7	1.0	6	9.4	0.4	
Rainfall (mm)	6	4.9	2.6	6	2.6	0.2	*

Table 7.7

Comparative abundance of Nomadic species at Tailbridge and Moor House.

	Average numbers taken						Significant
	TAILBRIDGE			MOOR HOUSE			difference
	n	mean	se	n	mean	se	($p < 0.05$)
PITFALL TRAP							
Species	8	4.5	1.2	27	6.9	0.6	
Individuals	8	11.8	3.3	27	27.0	5.2	*
WINDOW TRAP							
Species	(6)	8.5	0.9	(17)	14.9	1.6	*
Individuals	(6)	63.5	13.0	(17)	73.5	16.4	*

in very low numbers in window and pitfall traps (Table 7.8). Their anomalous occurrence on a habitat where they have not previously been recorded as breeding residents (cf Nelson 1971, Coulson and Whittaker 1978) provides even stronger support in favour of a general input of aerial plankton onto the Moor House Reserve.

The Aphidae constitute one of the largest and most widespread of plant bug groups, and many species exhibit specific associations with their host plants (Ris Lambers 1953). They often occur in considerable abundance as pests on crop plants grown extensively in the lowlands (eg Hughes 1963). Dispersing alate adults are frequently carried to considerable heights by turbulent air currents and become randomly distributed in a manner comparable with that of oceanic plankton. Since these individuals are unable to direct their flight in windspeeds exceeding about 0.7m/s, they move with the wind (Taylor 1958). They may be carried considerable distances in the upper air before ultimately entering the boundary layer close to the ground, when they alight indiscriminately on the local vegetation.

A total of 36 aphid species was identified from material in pitfall and window trap catches in 1984 (Tables 7.8 and 7.9). Of these, only four occurred in appreciable numbers, collectively comprising 85% of all individuals, and 94% of all apterae/nymphs taken. The other 32 species were represented by averages of only 2.2 and 1.7 individuals/species in pitfall and window trap catches respectively. Eight of the latter species (ten individuals) were represented by apterae/nymphs. Many have specific host plants which do not occur on the eastern slopes of the Reserve (cf Eddy *et al*. 1969), but are typical components of a more lowland flora (eg *Drepanosiphum platanoidis*: *Acer* species; *Acyrthrosiphon malvae*: *Fragaria* species; *Tuberculoides annulatus*: *Quercus* species). Their high diversity in

Table 7.8

Aphid species taken in traps at Moor House during 1984. Unbracketed figures refer to alatae, and bracketed figures to apterae or nymphs. A * denotes a tentative identification.

Species	Total numbers taken	
	Pitfall traps	Window trap
Rhopalosiphoninus staphylae	48 (90)	71
Sitobion avenae	81 (34)	26 (1)
Rhopalosiphum padi	46 (24)	55
Metopolophium dirhodum	49 (27)	6 (2)
Drepanosiphum platanoidis	16	7
Rhopalosiphum insertum	4	6
Brachycaudus helichrysi	7	1
Metopolophium festucae	5	1
Sitobion fragariae	3	1
Thecabius affinis	3	3
* *Thecabius* sp.	(2)	-
Acyrthosiphon pisum	2	2
Acyrthosiphon malvae	2	1
Acyrthosiphon sp.	(1)	-
Hayhirstia atriplicis	1	5
Myzus persicae	2	1
Dactynotus sp.	-	1
Dactynotus sp.	(1)	-
Jacksonia papillata	2	-
* *Dysaphis* sp.	(2)	-
Loxodonta africaria	(1)	-
	Pitfall traps	Window traps
Myzus ascalonicus	1	-
* *Mysus* sp.	(1)	-
Cavariella aegopodii	1	-
Macrosyphum rosae	1	-
Cinara sp.	1	
Kallistaphis betulicola	1	-
Hyadaphis foeniculi	1	-
* *Aphis solani*	(1)	-
Capitophorus sp.	(1)	-
* *Metopopophium cerasi*	(1)	-
Macrosiphum euphorbiae	-	2
Pemphigus sp.	-	2
Eulachrus brevipilosus	-	1
Anoecia corni	-	1
Brachycolus stellariae	-	1
Cavariella pastinacea	-	1
Tuberculoides annulatus	-	1
Metopolophium fasciatum	-	1
Hypermyzella rhinanthi	-	1
TOTAL SPECIES	27	24
TOTAL INDIVIDUALS	459	201

Table 7.9

Numbers of alate aphids (with numbers of apterae/nymphs in brackets) taken at Moor House during 1984.

i)Pitfall traps	Location of pitfall traps												
	Limestone grassland										*Juncus* moor		Blanket peat
	A	B	C	D	E	F	G	H	I	K	J	M	L
IDENTIFIED SPECIES													
(= total species)													
No. species	7	8	4	6	6	6	10	9	11	3	8	5	2
No. individuals	25	16	18	22	41	18	31	32	73	11	40	39	93
COMMON SPECIES													
Rhopalosiphoninus staphylae	6	-	2(2)	1(1)	14(4)	4	3	3	-	-	3(3)		12(80)
Sitobion avenae	7	(2)	4	1(4)	12	3(4)	4(5)	13	22(1)	3	5(7)	5(11)	1
Rhopalosiphum padi	7	8	2(1)	2	1	1	1	5(1)	11	2	5(10)	2(12)	-
Metopolophium dirhodum	2	1	3(3)	5(5)	2(6)	1(1)	3(6)	(2)	23	6(1)	1(1)	2(4)	-
RARE SPECIES													
No. species	3	5	3	2	2	2	6	5	8	-	4	2	-
No. individuals	3	5	3	3	2	4	9	8	16	-	6	2	-

Table 7.9 (cont.)

ii) Window traps	Location of window trap							
	Limestone grassland					Blanket peat		
	a	b	c	f	i	l	d	g
Total no. of individuals	86	58	52	43	205	52	31	49
IDENTIFIED SPECIES								
No. of species	11	4	6	4	14	2	4	7
No. of individuals	24	15	14	14	66	43	10	15
COMMON SPECIES								
Rhopalosiphoninus staphylae	7	6	2	10	1	40	2	3
Sitobion avenae	7	2	3	2(1)	9	-	1	2
Rhopalosiphum padi	2	6	6	1	29	3	3	5
Metopolophium dirhodum	1	-	-	-	5(2)	-	-	
RARE SPECIES								
No. of species	7	1	3	1	10	3	3	4
No. of individuals	7	1	3	1	20	4	4	5

catches from both ground (William's *a* =16.4) and air (*a* =14.0) suggests an aerial planktonic rather than a local moorland origin. Both numbers of species and individuals taken in pitfall traps were significantly negatively correlated with distance from the Pennine escarpment (Figure 7.9), and greatest abundances occurred in the west-facing sectors of the window traps (Table 7.10). Their seasonal pattern of occurrence on the Reserve coincided with the predominance of westerly winds over this region in summer and autumn (Figure 7.10). The evidence suggests that these rarer aphid species were vagrants carried over from the Eden valley by the prevailing winds: as the aerial plankton was carried over the escarpment into the wetter cooler region beyond, a 'fallout' of individuals occurred.

Abundances in pitfall traps of three of the four most common aphid species taken at Moor House, *Sitobion venae*, *Rhopalosiphum padi* and *Metopolophium dirhodum*, also showed a significant negative correlation with distance from the western escarpment (Figure 7.11), and over half (51%) of the individuals taken by window trap occurred in west-facing sectors (Table 7.10): these species too appear to have entered the Reserve in aerial plankton from the west. However, both *S. avenae* and *R. padi* were also represented by a number of apterate adults and nymphs in catches on *Juncus squarrosus* moor (Table 7.9), suggesting the existence of a number of small breeding colonies on these low-lying areas. *Graminaceae* are amongst the main host plants of these species, and were plentiful on the reseeded moorland and enclosed ungrazed grassland where such wingless forms were most abundant. It may be that the colonies themselves were initiated by vagrant individuals from the west, early in the season. Substantial numbers of *M. dirhodum* apterae and nymphs were taken, but as a random scatter of individuals across the moor, suggesting a planktonic, not local, origin. The percentage contribution of these three commoner aphid species, together

Figure 7.9

Numbers of rare aphid species and individuals in window trap catches at Moor House in 1984 in relation to distance of trap from the western escarpment. Significance levels given by **: $p < 0.01$.

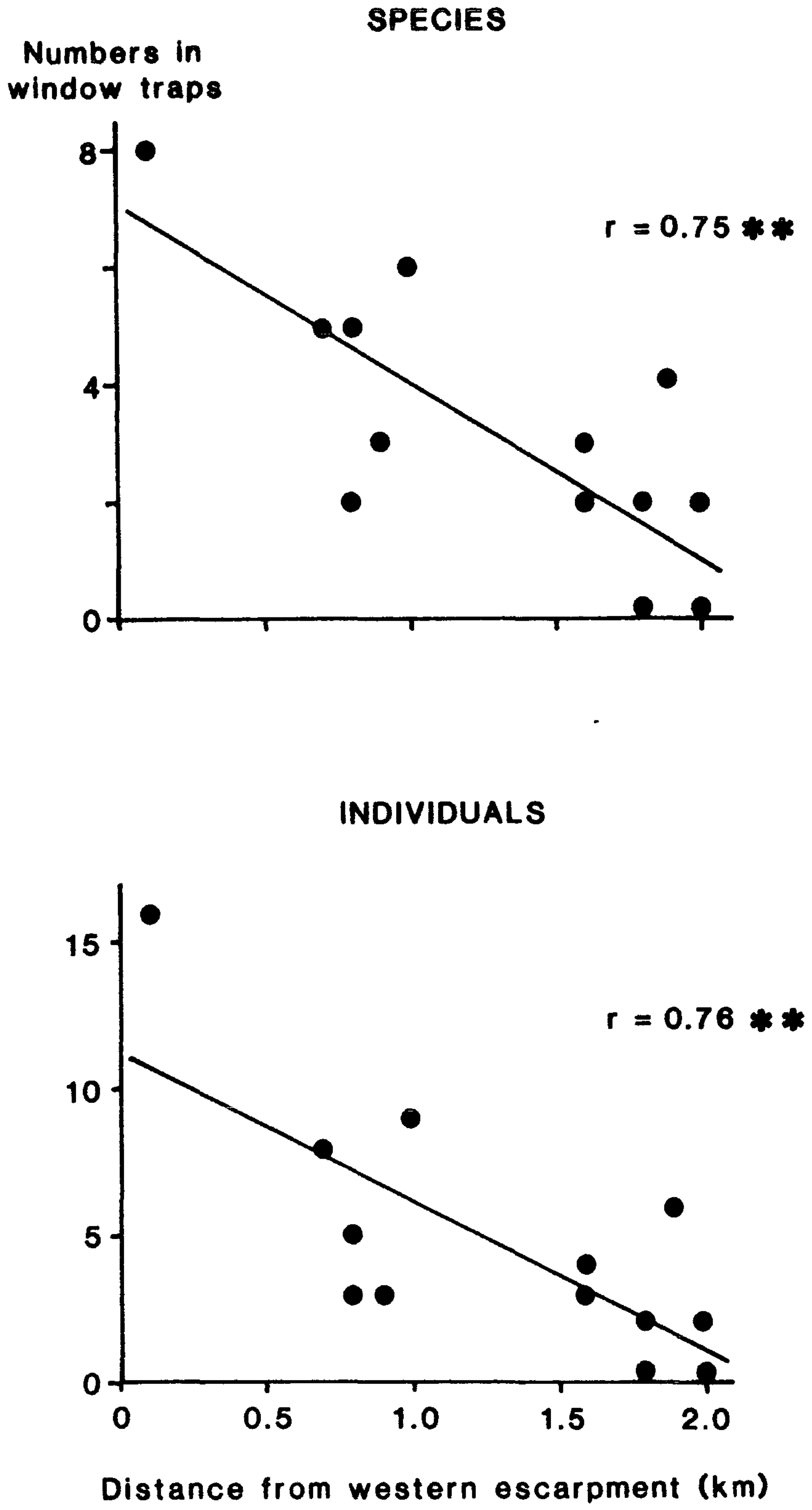


Table 7.10

Abundances of aphids taken in different sectors of window traps.

(data from all traps combined)

	Number of aphids* in sector			
	North	South	East	West
TOTAL SPECIES				
No. individuals	137	96	142	231
Mean aphids/trap (8 traps)	17.1	12.0	17.8	28.9
(±standard error)	±2.7	±2.2	±3.8	±12.5
IDENTIFIED SPECIES				
No. of species	6	10	6	19
No. of individuals	35	35	34	95
COMMON SPECIES				
Rhopalosiphoninus staphylae	24	11	18	18
Sitobion avenae	2	6	2	16
Rhopalosiphum padi	6	9	11	29
Metopolophium dirhodum	-	-	1	5
RARE SPECIES				
Total species	3	7	2	15
Total individuals	3	9	2	27
% OF TOTAL CATCH				
No. of insects	2623	2545	2649	3206
No. of aphids**	11	24	16	77
% aphids	0.42	0.94	0.06	2.40

*excluding specimens of uncertain derivation (bags displaced by sheep)

**excluding *Rhopalosiphoninus staphylae*

Figure 7.10

Seasonal pattern of abundance of individuals of rare aphid species in window trap catches at Moor House in 1984, in relation to the prevalence of westerly winds.

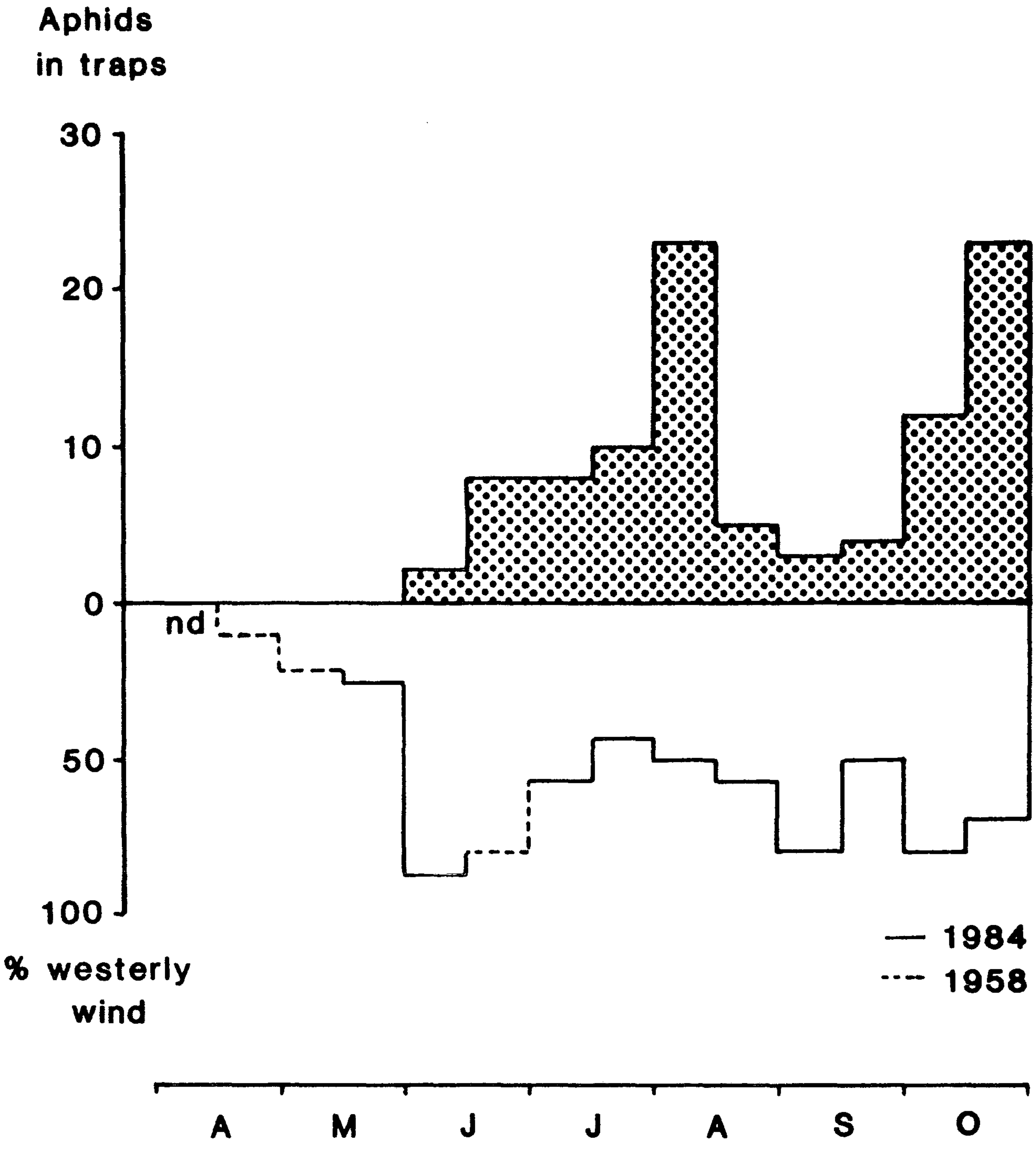
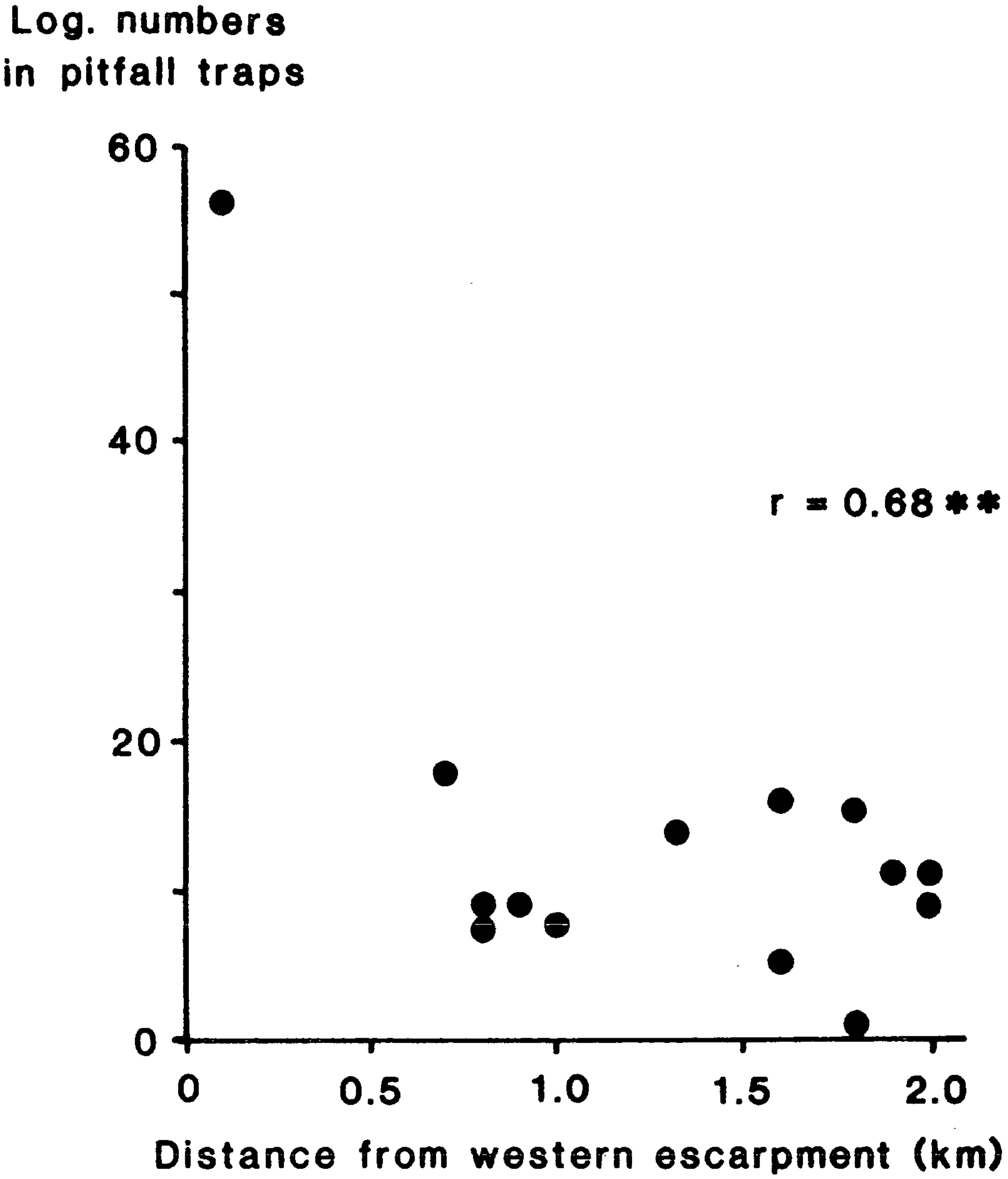


Figure 7.11

Numbers of Rhopalosiphum padi, Sitobion avenae and Metopolophium dirhodum in pitfall trap catches at Moor House in 1984 in relation to distance of trap from the western escarpment. Significance level given by **: $p < 0.01$.

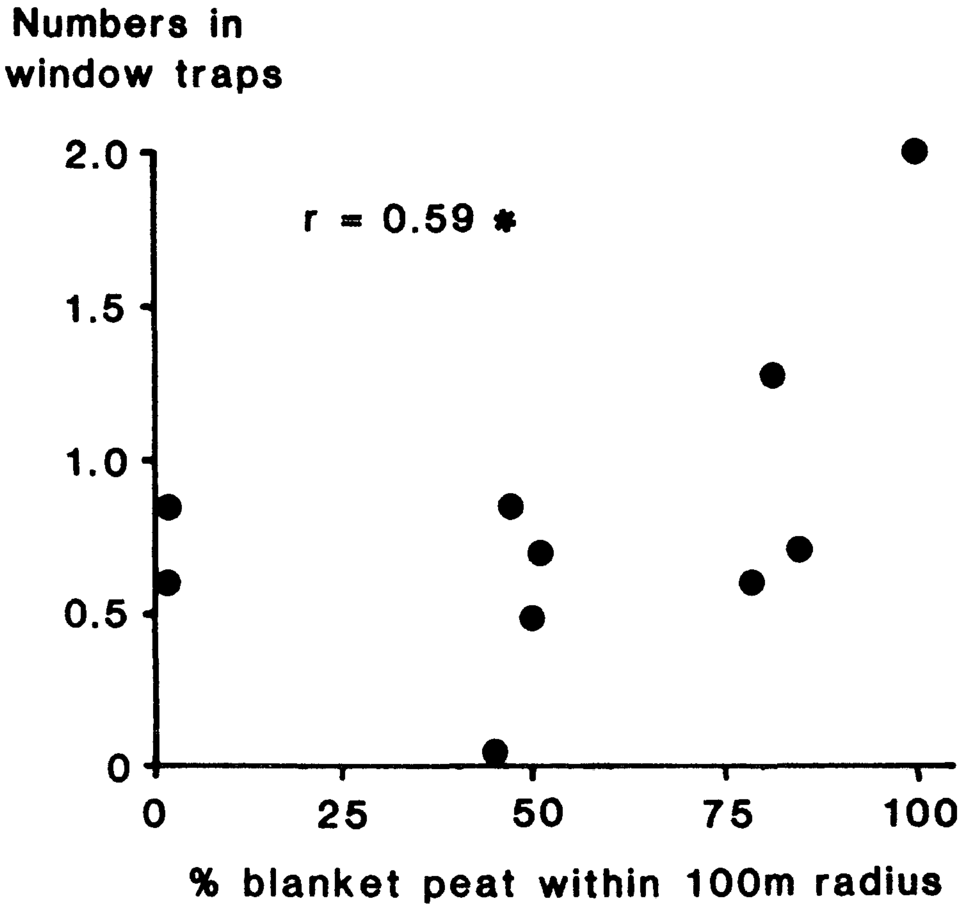


with the other rarer species, to the total insects taken in window traps was ten times as high in catches only 100m from the western escarpment (7.0%) as in those at a distance of 700m or more (mean=0.7%), and was over three times higher in the west-facing (2.4%) than in the other (mean = 0.75%) sectors of the traps (Table 7.10), indicating that only small planktonic forms such as aphids were being carried in from the west, and not the aerial fauna in general. In parallel with the staphylinids, aphids were significantly more abundant in window traps in 1984 (mean =130 ± 16) than in 1985 (mean =9 ± 1; t =3.77, df =15, $p < 0.01$).

Only Rhodosiphoninus staphylae, the most frequently taken aphid species at Moor House, showed evidence of being a breeding moorland resident. Its apterae and nymphs accounted for over half of such stages taken in pitfall traps, and none were present in window trap catches (Table 7.9). No significant relationship existed between numbers of alatae taken and distance from the Pennine escarpment (Table 7.9), and numbers taken in west-facing sectors of the window traps were no higher than in other sectors (Table 7.10). Numbers of specimens taken in pitfall traps, however, were significantly positively correlated with the percentage of blanket peat in the vicinity of the traps (Figure 7.12). Numbers of alatae taken in window traps exhibited a similar pattern of distribution: they showed a significant positive correlation with total numbers of R. staphylae taken in pitfall traps on the same site ($r = 0.97$, df = 4, $p < 0.05$). Breeding populations of this species appeared to be closely associated with the Callunetum-Eriophoretum, but its actual host plant remains a mystery: none of the host plants recorded for this species (Staphylea, Antheridium, Crocus, Vincia, Hedera, Humulus, Cardamine hirsuta) are known to occur on this habitat (Eddy et al. 1969).

Figure 7.12

Numbers of *Roposiphoninus staphylae* in window trap catches at Moor House in 1984 in relation to proportion of blanket peat comprising vegetation within 100m radius of trap. Significance level given by *: $p < 0.05$.



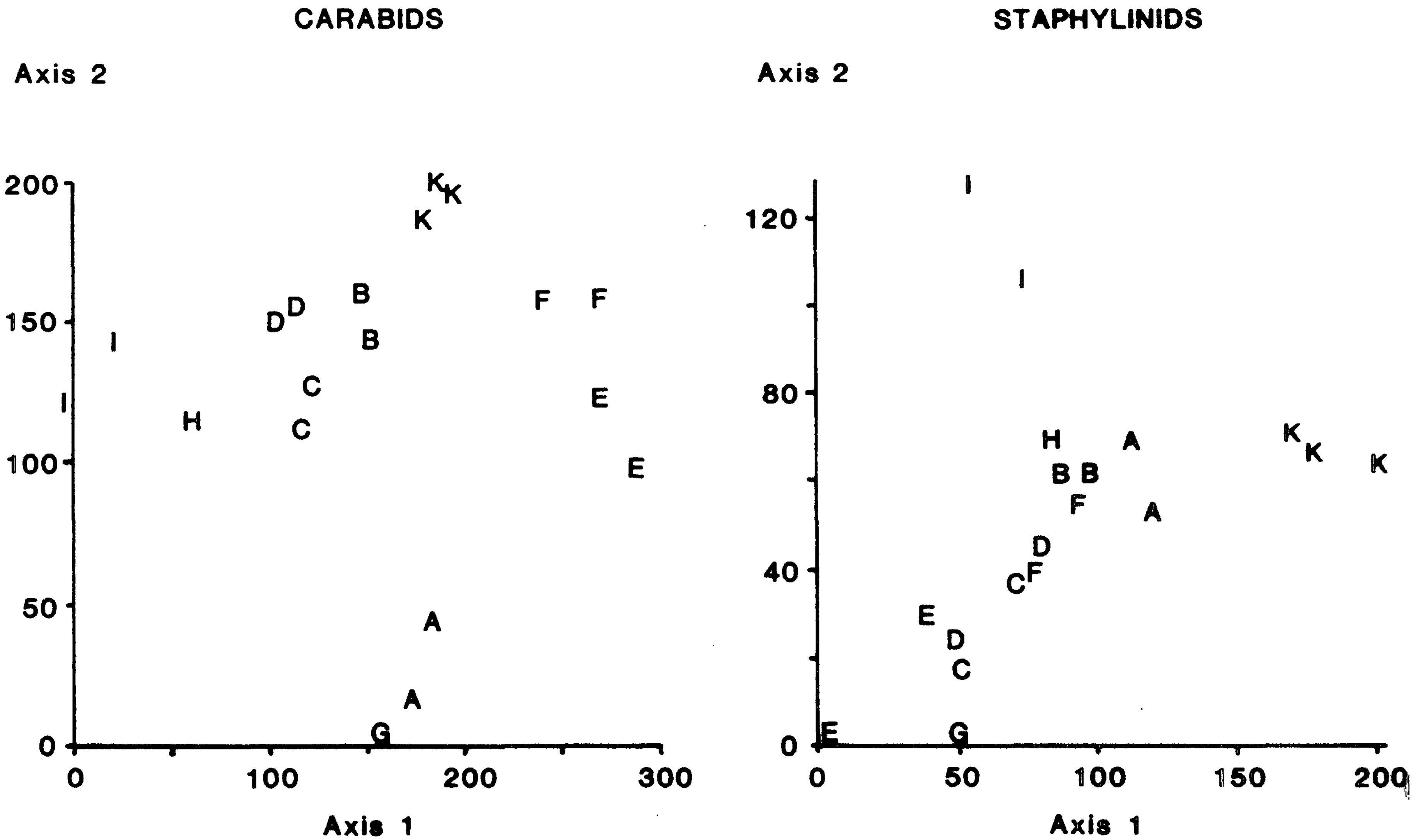
CHAPTER 8 THE BEETLE FAUNAS OF THE MOOR HOUSE LIMESTONE OUTCROPS

8:1 Introduction

The variation in carabid and staphylinid faunas between different Moor House sites resulted predominantly from fundamental differences in habitat type: sites located respectively on peat and mineral soil substrates possessed their own characteristic faunas (Section 5:4). However, between sites on apparently homogeneous limestone grassland there was still considerable heterogeneity in overall species composition (Figures 5.13 and 8.1, Table 5.11). All of the limestone outcrops possessed the same basic habitat characteristics; a well-drained calcareous soil supporting a closely grazed *Agrosto-Festucetum* sward, with the occasional occurrence of exposed limestone bedrock (Section 2:2). They did differ markedly from one another, however, in two important respects: altitude and extent. These two factors were not significantly correlated ($r = 0.11$, $df = 9$, $p = ns$). Both may have been influencing the composition of the beetle communities present on the outcrops. This possibility has been examined in detail by multiple regression analysis of the carabid and staphylinid data from these sites. Logarithms (base 10) of abundance have been employed in the regressions since, in theory, numbers of an animal population increase exponentially and not linearly with time. Logarithms (base 10) of outcrop area have also been employed, but various other measures of site size such as area *per se*, site diameter and the square root of area give similarly satisfactory correlations and could equally well have been used (cf Figure 8.4). The reasons for using the logarithmic function in the context of the Moor House outcrops are considered further in Section 8:3.

Figure 8.1

Ordination of the Moor House limestone sites according to the similarity of their carabid and staphylinid faunas in 1984 and 1985. Data are from sets of ten pitfall traps.



8:2 The influence of altitude

The limestone outcrops at Moor House ranged in elevation from 540m (site K) to 750m (site I; cf Table 2.1). Over this altitudinal range the numbers of carabids and staphylinids taken by pitfall trap in a year varied considerably: average numbers of beetles in samples taken on the lowest site (44 carabids and 559 staphylinids) were less than a third of those in samples from the highest site (236 carabids and 1842 staphylinids (Table 5.1). There was a significant positive relationship between altitude and beetle abundance overall (Table 8.1): carabid numbers increased by 62% and staphylinid numbers by 95% with every 100m rise in elevation. Total numbers of species taken, however, did not alter significantly with the change in altitude. As a consequence, there was also a significant increase in numbers of individuals/species with increasing elevation (Table 8.1). In the staphylinids this relationship was further manifested as a significant decline in alpha diversity with increasing altitude, from $\underline{a}$ = 10.7 (site K) to $\underline{a}$ = 7.3 (site I). Changes in altitude accounted for 62% of the variation in staphylinid $\underline{a}$ values between sites (Table 8.1). The rate of change in overall abundance and in numbers of individuals/species with changing altitude was not significantly different between carabids and staphylinids ($t = 0.14$ and 1.4 respectively, $df = 17$, p = ns).

Besides affecting the total abundances and alpha diversities of beetles present on an outcrop, altitudinal differences also accounted for much of the variation in beta diversity between the limestone sites: the clustering of limestone sites achieved by CLUSTAN (Figure 5.13) is seen to correspond to the altitudinal similarities between sites (cf Table 2.1). Moreover, a significant correlation existed between altitude and the scores on axis 1 in the DECORANA analysis (Table 8.2): in combination with the effect of site

Multiple regression analyses of carabid and staphylinid faunas on altitude and size of limestone outcrop at Moor House.

Table 8.1

Total numbers of species and individuals.

	Altitude of outcrop			Size of outcrop						
	Slope	se of slope	% change /100m	Slope	se of slope	% change /log.m	Constant value	Constant se	Corr. coeff.	Signif. (df=17)
STAPHYLINIDS										
No. species				3.26	1.33	8.4*	1.50	0.04	0.51	0.05
Log. individuals	0.29	0.04	95.0	0.12	0.04	27.9	0.81	0.40	0.90	0.001
Ind/species	14.8	1.6	71.2*	4.53	1.81	21.8*	-82.6	11.0	0.92	0.001
Log. ind/species	0.29	0.04	95.0				-0.59	0.22	0.90	0.001
Alpha diversity	-1.20	0.38	13.2*				21.6	2.4	0.79	0.001
CARABIDS										
No. species				-1.74	0.54	13.1*	1.25	0.04	0.62	0.01
Log. individuals	0.21	0.57	62.2	-0.24	0.07	42.5	1.39	0.40	0.80	0.001
Log. ind/species	0.19	0.06	54.9	-0.18	0.07	33.9	0.26	0.40	0.73	0.001

size, altitude accounted for 64% (carabids) and 75% (staphylinids) of the total variation along this principal axis of variation in faunal composition between sites (cf Figure 8.1). Since these methods of assessing beta diversities between communities operate primarily on differences in species composition, it is clear that the spectrum of species must be changing over the altitudinal gradient, and not merely their overall abundance. The nature of these significant differences in species composition with altitude is now considered.

Of the 145 staphylinid and 32 carabid species taken in traps at Moor House, respectively 20% and 13% were exclusively or predominantly montane or northern in their distribution (Fowler 1888, Goodier 1968, Lindroth 1974, Hammond pers. comm.). Although most of these species occurred throughout the altitudinal range encountered on the Reserve, their overall abundance was strongly correlated with elevation: numbers of montane staphylinid species, and the abundance of individuals of both carabid and staphylinid montane species, increased significantly with rising altitude (Table 8.3). Of the other more lowland or southern species, the staphylinids exhibited a significant decline in numbers of species with increasing elevation, decreasing by 11% with every 100m increase in altitude (Table 8.3), whilst the carabids showed no significant trend. The slopes of the regression lines between montane and lowland species components and altitude were not significantly different: decreasing numbers of lowland species at the higher altitudes were matched by an increase of the same magnitude in the numbers of montane species. As a result, overall numbers of species taken on a site did not change significantly with changing altitude (Table 8.1) despite the alteration in underlying species composition. This constancy in numbers of species was not, however, accompanied by a similar constancy in overall numbers of individuals taken on sites at different altitudes (Table 8.1).

Table 8.2

Beta diversities between outcrops (DECORANA scores).

	Altitude of outcrop			Size of outcrop			Constant			
	Slope	se of slope	% change /100m	Slope	se of slope	% change /log.m	value	se	Corr. coeff.	Signif. (df=17)
STAPHYLINIDS										
Axis 1 scores	-34.1	8.8	90.3*	57.8	10.1	64.1*	171	61	0.87	0.001
CARABIDS										
Axis 1 scores	-94.7	7.1	59.8*	-63.1	8.1	39.9*	898	49	0.97	0.001

Table 8.3

Montane and lowland species components.

	Altitude of outcrop			Size of outcrop			Constant			
	Slope	se of slope	% change /100m	Slope	se of slope	% change /log.m	value	se	Corr. coeff.	Signif. (df=17)
MONTANE SPECIES										
Staphylinids										
No. species	2.49	0.56	23.3*				-4.97	3.54	0.73	0.001
Log. individuals	0.42	0.06	163				0.02	0.38	0.86	0.001
Carabids										
Log. individuals	0.64	0.17	337				2.69	1.42	0.67	0.01
LOWLAND SPECIES										
Staphylinids										
No. species	-2.99	1.01	10.8*				35.4	7.0	0.79	0.001

Although montane species made only a minor contribution to the species richness of the fauna in general (13% of carabids, 20% of staphylinids), they had larger average population sizes at Moor House than did the more lowland species, comprising respectively 31% and 78% of the total carabid and staphylinid individuals taken on the limestone outcrops. In conjunction with this, the rate of increase of the montane component exceeded the converse rate of decrease of the lowland component with increasing elevation, and overall numbers of individuals of both carabids and staphylinids rose significantly (Table 8.1).

The relationships between montane and lowland species components and altitude may be examined in more detail within the various categories of staphylinid. Total numbers of Limestone species taken on an outcrop were significantly negatively correlated with altitude, decreasing by 13% with every 100m increase in elevation (Table 8.4). Total numbers of individuals, however, exhibited a strong positive relationship with altitude, more than doubling with every 100m rise in elevation. Once again, this apparent anomaly resulted from the montane and lowland components not fully compensating for one another along the altitudinal gradient: the lowland species decreased more markedly in numbers with increasing altitude than the montane species increased ($t = 3.05$, $df = 34$, $p < 0.01$; Table 8.5). This situation resulted from many of the latter species being present in very low densities at the lower altitudes as well as predominating at higher elevations. Thus overall species numbers were lower on the limestone grasslands at the higher altitudes where only montane species abounded compared to those at lower elevation where both lowland and montane species coexisted. Similarly, total numbers of individuals increased with a rise in altitude as a result of the montane species increasing in abundance of individuals at a significantly faster rate than the lowland species

Table 8.4

Peat. Limestone and Widespread species components.

	Altitude of outcrop			Size of outcrop						
	Slope	se of slope	% change /100m	Slope	se of slope	% change /log.m	Constant value	se	Corr. coeff.	Signif. (df=17)
PEAT SPECIES										
Staphylinids										
No. species				2.16	0.64	24.3	13.9	1.5	0.63	0.01
Log. individuals	0.32	0.08	109	-0.40	0.09	60.2	0.83	0.52	0.85	0.001
Log. ind/species	0.30	0.08	99.5	-0.28	0.09	47.5	-0.21	0.53	0.79	0.001
Carabids										
No. species				-2.74	0.40	47.1	12.1	1.0	0.86	0.001
Log. individuals				-0.64	0.09	77.1	3.17	0.22	0.86	0.001
Log. ind/species	0.16	0.07	44.5	-0.42	0.08	62.0	0.93	0.49	0.82	0.001
WIDESPREAD SPECIES										
Carabids										
Log. individuals				-0.41	0.10	61.1	1.81	0.23	0.72	0.001
LIMESTONE SPECIES										
Staphylinids										
No. species	-2.67	0.84	13.0	3.44	0.16	16.8	29.3	5.8	0.77	0.001
Log. individuals	0.31	0.05	104	0.23	0.06	69.8	0.28	0.37	0.86	0.001
Log. ind/species	0.37	0.05	134	0.13	0.06	34.9	1.20	0.35	0.89	0.001
Alpha diversity	-1.41	0.25					13.2	1.6	0.81	0.001
Carabids										
No. species				1.43	0.47	31.8	1.22	1.13	0.59	0.01
Log. individuals				0.26	0.12	82.0	0.90	0.28	0.48	0.05

Table 8.5

Montane and lowland Peat, Limestone and Nomadic species components (staphylinids only).

	Altitude of outcrop			Size of outcrop			Constant		Corr. coeff.	Signif. (df=17)
	Slope	se of slope	% change /100m	Slope	se of slope	% change /log.m	value	se		
LIMESTONE										
Montane species										
No. species	1.04	0.47	18.8*				-3.07	3.25	0.56	0.05
Log. individuals	0.43	0.06	169	0.17	0.07	47.9	10.5	0.4	0.88	0.001
Lowland species										
No. species	-3.71	0.74	24.8*	2.55	0.83	17.1*	32.3	5.1	0.83	0.001
Log. individuals	-0.23	0.06	69.8	0.26	0.07	82.0	2.72	0.40	0.82	0.001
PEAT										
Montane species										
No. species	1.03	0.29	29.7*	0.84	0.32	24.2*	-1.10	1.97	0.75	0.01
Log. individuals	0.51	0.12	223	-0.33	0.13	114	0.92	0.81	0.79	0.001
Lowland species										
No. species				-1.29	0.53	23.6*	8.45	1.26	0.51	0.05
Log. individuals	0.19	0.07	54.9	0.43	0.08	169	1.48	0.51	0.83	0.001
NOMADIC										
Montane species										
Log. individuals	0.36	0.13	130				-1.39	0.79	0.57	0.05
Lowland species										
Log. individuals	0.25	0.09	59.9				-0.17	0.57	0.48	0.05

decreased ($t = 2.35$, df = 34, $p < 0.05$). The compounded effects of decreasing numbers of species and increasing abundances of individuals at progressively higher altitudes produced a significant increase in numbers of individuals/species and a decline in alpha diversity of Limestone staphylinid species (Table 8.4).

Besides affecting the numbers and species composition of Limestone species, altitude apparently also had a marked influence on the other two major staphylinid categories taken on the limestone outcrops, the Peat and Nomadic species. Overall, Peat species showed a significant increase in abundance of individuals and in numbers of individuals/species taken on outcrops at increasing altitude (Table 8.4). This resulted from an increase in abundance not only of montane, but also of lowland Peat species on the higher sites (Table 8.5). The unexpectedly greater numbers of individuals of Peat species on outcrops at higher altitudes can be attributed to their restriction to the blanket bog being removed at these elevations where suitably wet and overcast conditions prevailed on all habitats (cf Sections 6:3 and 6:6). Both montane and lowland components of the Nomadic species category also exhibited an increase in abundance with a rise in altitude (Table 8.5). The anomalous increase in the latter component resulted not from the altitudinal change, however, but from the change in distance from the western escarpment (and lowlands beyond) which is highly correlated with altitude ($r = 0.9$, df = 10, $p < 0.001$): the majority of these species were immigrants entering the Reserve from the west as aerial plankton (see Section 7:3).

8:3 The influence of site size

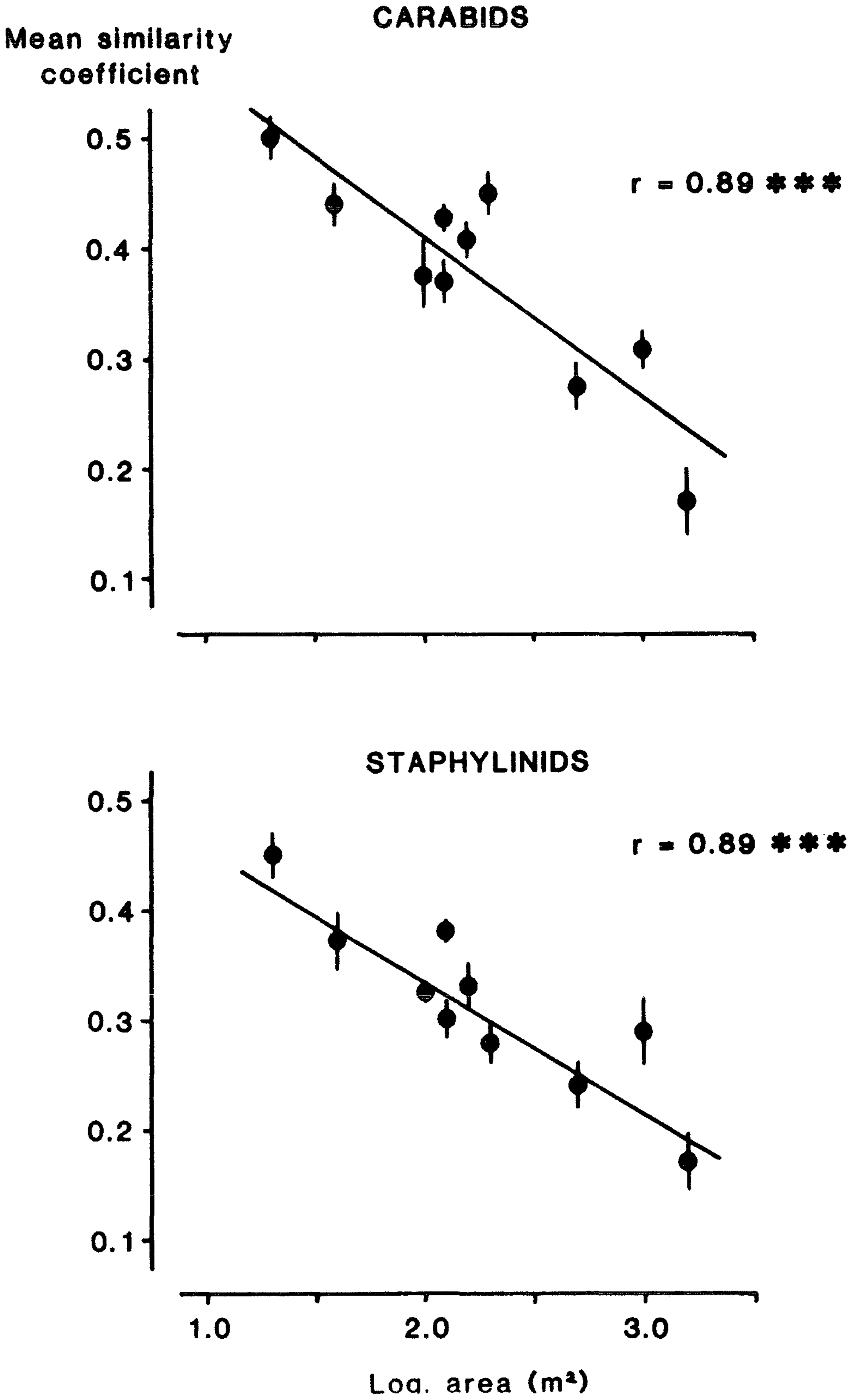
The limestone sites at Moor House ranged in size from 0.2ha (site E) to 14.0ha (site K). Over this size range both carabids and staphylinids showed considerable variation in total numbers taken (cf Table 5.11), but the trends exhibited by the two taxa were in exact opposition to one another. Numbers of staphylinid species and individuals were significantly and positively correlated with area of outcrop (Table 8.1), with species numbers increasing by 8% and individuals by 28% with every ten-fold increase in site size. The number of staphylinid individuals/species also increased significantly with increasing size of site (Table 8.1). In contrast, a significant negative relationship existed between site size and carabid numbers: numbers of carabid species decreased by 13% and individuals by 43% with each ten-fold increase in size of site. Average numbers of carabid species (11) and individuals (44) in samples taken from the largest site were respectively only 73% and 17% those present in samples from the smallest site (15 species and 252 individuals), and there was a significant change in numbers of individuals/species with an increase or decrease in site size (Table 8.1). As a result of the opposing species:area relationships between the taxa, the ratio of carabid to staphylinid species taken on a site increased significantly by 16% with every ten-fold decrease in outcrop size (Table 8.1): whereas carabids represented up to a third of all species and half of all individuals taken on the smallest site, they formed less than a quarter of species and a tenth of individuals on the largest site.

The positive species:area relationship evidenced in the staphylinid data is a well-known phenomenon (Arrhenius 1921, Gleason 1922, Preston 1962). The unexpectedly converse situation for the carabids, however, demands further examination of the data in order to explain such a marked difference in the relationships between the two taxa and site size. On all of the limestone outcrops at Moor House both carabid and staphylinid faunas possessed a component which was common to the blanket peat too which was shown to result predominantly from the dispersal of Peat species from the peat onto the limestone (Section 6:6). Numbers of Peat species and individuals of both taxa taken on individual outcrops decreased significantly with increasing size of site (Table 8.4). This relationship arose from the exponential decline in the degree of dispersal of beetles away from their normal habitat with increasing distance across the interface (Section 6:6). Since sampling was carried out at the centre of each limestone outcrop, few individuals of Peat species covered the greater distance from peat edge to trap on the larger outcrops compared with the shorter equivalent on the smaller sites. There was also a significant decline in the number of Peat individuals/species taken with increasing size of outcrop (Table 8.4). This occurred because even on the largest sites the chance of a species being represented by at least one vagrant individual in the traps at the centre of the outcrop was relatively high, although such a species would not be common at such a distance from its normal habitat. Within the Peat staphylinid species both montane and lowland species exhibited the same decrease in abundance with increasing size of outcrop (Table 8.5). Moreover, a similar negative relationship existed between site size and the abundance of individuals of Widespread carabid species: numbers increased by 61% with a ten-fold decrease in site size (Table 8.4). Since these species were mostly concentrated along the habitat interface, and appeared to be exploiting resources on the limestone and peat immediate to the interface but not at a great distance from it (cf Chapter 6), their contribution to the fauna at the centre of an outcrop, like that of Peat species, decreased as the size of the outcrop increased.

A significant negative correlation existed between the area of a limestone site and the mean similarity coefficient (modified Sørensen's Index) between its fauna and that of the blanket peat sites (Figure 8.2). Although carabid coefficients were similar to those for staphylinids, they were consistently and significantly higher than those for the staphylinids on the same site (paired $t = 3.41$, $df = 8$, $p < 0.01$). This trend reflects the greater contribution of carabid relative to staphylinid Peat species to the fauna on a limestone outcrop: averages of 5.9 Peat, and 7.4 Limestone carabid species were recorded on an outcrop in one year compared with 9.0 Peat and 20.5 Limestone staphylinid species. As a result, only 31% of all staphylinid, but 45% of all carabid, species typically taken on an outcrop were of intruding Peat species. Similarly, whereas Peat species only contributed an average of 16% to the total staphylinid individuals taken on an outcrop, in carabid samples they averaged 49% of all individuals. The greater influx of carabids relative to staphylinids off the surrounding blanket peat and into the limestone traps is explained in part by the difference in body size between the two taxa. The extent to which walking beetles penetrated habitats adjacent to their normal one was influenced greatly by their size (Chapter 6), and the staphylinids taken at Moor House, being typically smaller (1-13mm) than the carabids (4-25mm), were not able to penetrate the heart of the limestone outcrops to the extent that carabids were. Consequently, at the centre of even the smallest outcrops the contribution of invading Peat staphylinid species from the surrounding blanket peat was relatively low compared to that of the resident Limestone species, resulting in the overall decline in total numbers of staphylinids taken with decreasing outcrop size. In contrast, the considerable numbers of the larger and more mobile carabid Peat species reaching the centres of

Figure 8.2

Mean similarity coefficients between pitfall trap catches on limestone and blanket peat for carabid and staphylinid faunas at Moor House, in relation to area of limestone site. Standard errors are indicated. Significance level given by ***: $p < 0.001$.



the limestone outcrops surpassed the smaller contribution of Limestone species present, resulting in the observed increase in total numbers of carabid species and individuals with decreasing outcrop size.

When the complicating effects of intrusion by Peat species are removed, the resident Limestone faunas of staphylinids and carabids prove to be similarly influenced by changing size of outcrop: in both taxa, numbers of Limestone species increased significantly with increasing site size (Table 8.4). Within the staphylinids, numbers of lowland species, and abundances of individuals of both lowland and montane species, were similarly significantly reduced on the smaller outcrops (Table 8.5). Both flightless and flying staphylinid components exhibited the same positive correlation between species numbers and site size (Figure 8.3). A significant species:area relationship persisted for both taxa regardless of the measure of site size used (Figure 8.4), but by using logarithm (base 10) of area values could be derived for the various parameters in the species:area equation of Preston (1962; Table 8.6) which forms the basis of classical island biogeographical theory (MacArthur and Wilson 1963, 1967) and is returned to later in Chapter 9. Besides numbers of Limestone carabid and staphylinid species exhibiting a positive species:area relationship, the abundances of their individuals were also significantly positively related with size of outcrop, and there was a significant positive correlation between staphylinid Limestone individuals/species and outcrop size (Table 8.4).

There was no discernible pattern as to which species were absent on smaller sites, but the presence or absence of species on a site was influenced by altitudinal changes in species composition as well as by site size. However, those species common to pitfall catches on all sites (or all but one) proved to be characterized by either a relatively high abundance

Figure 8.3

Numbers of staphylinid Limestone species in pitfall trap catches in relation to area of limestone site at Moor House, comparing flightless and flying species. Significance levels given by *: $p < 0.05$.

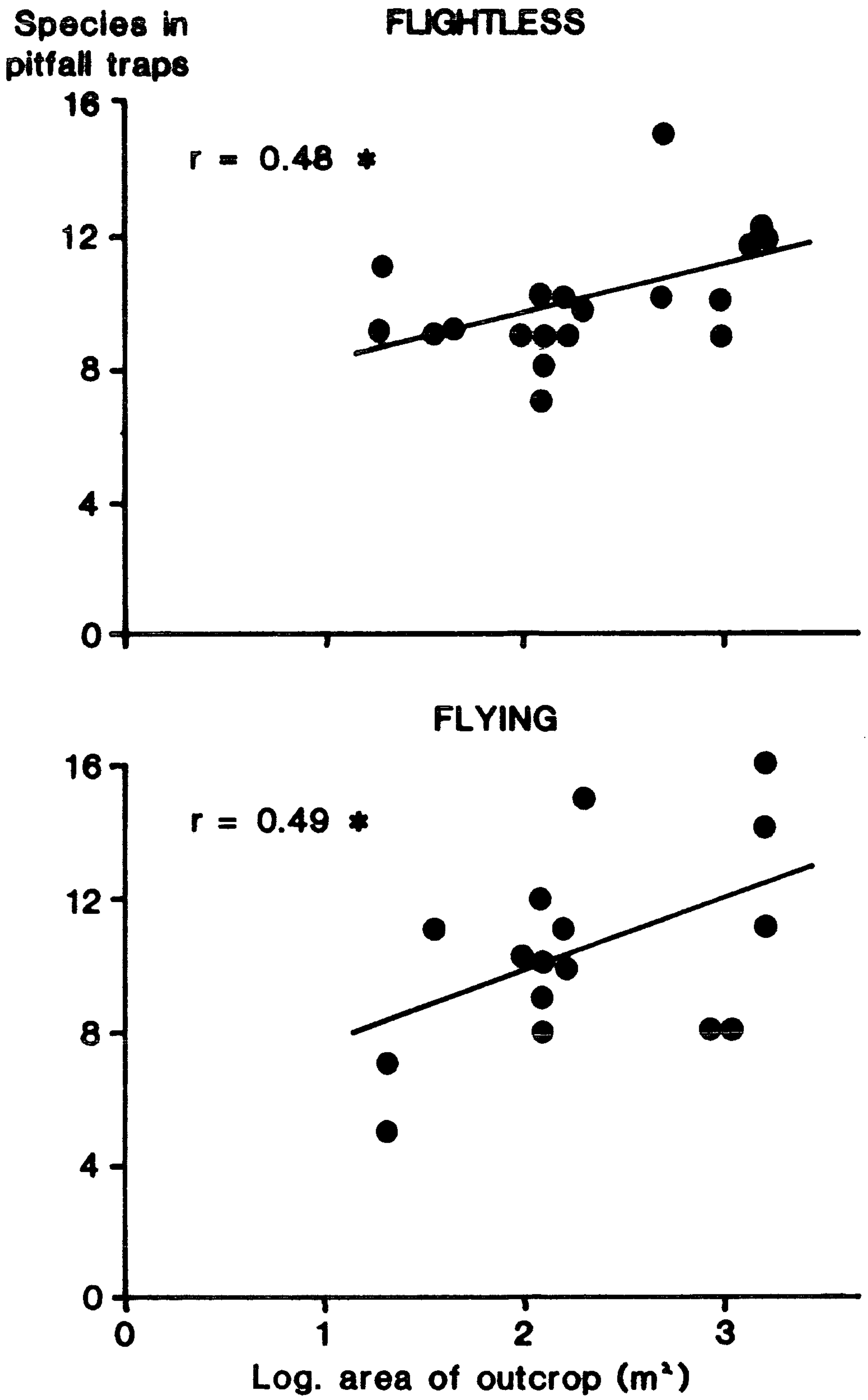


Figure 8.4

Numbers of carabid and staphylinid Limestone species in pitfall trap catches in relation to area of limestone site at Moor House, comparing different measures of site size. Significance levels given by *: $p < 0.05$.

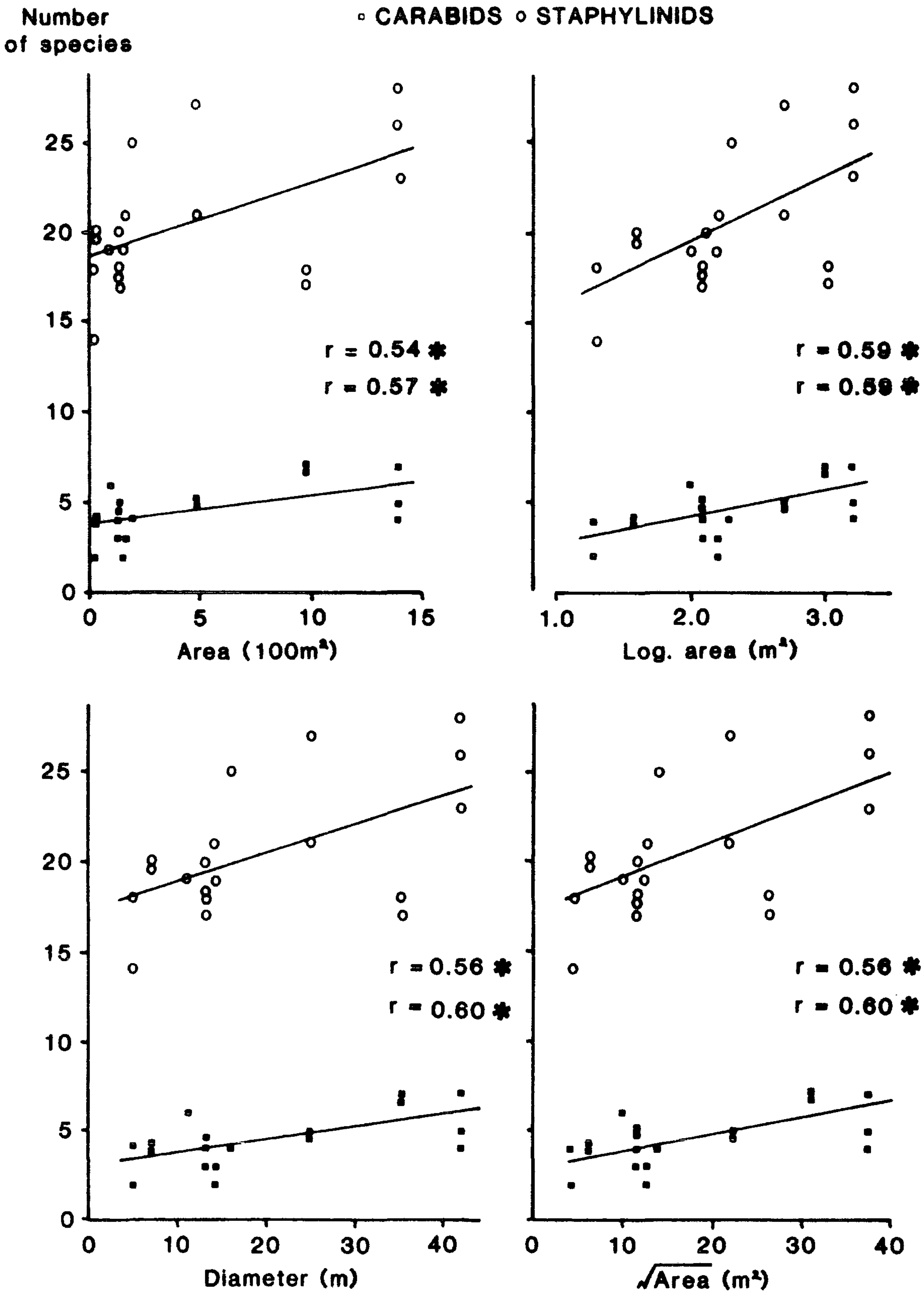


Table 8.6

Values for constants in species:area equation for carabids and staphylinids on limestone outcrops at Moor House.

Constant	Carabids	Staphylinids
z	0.13	0.07
c	21.4	13.8

where $S = c A^{z}$ or $\log S = \log c + z (\log A)$

where S = number of species

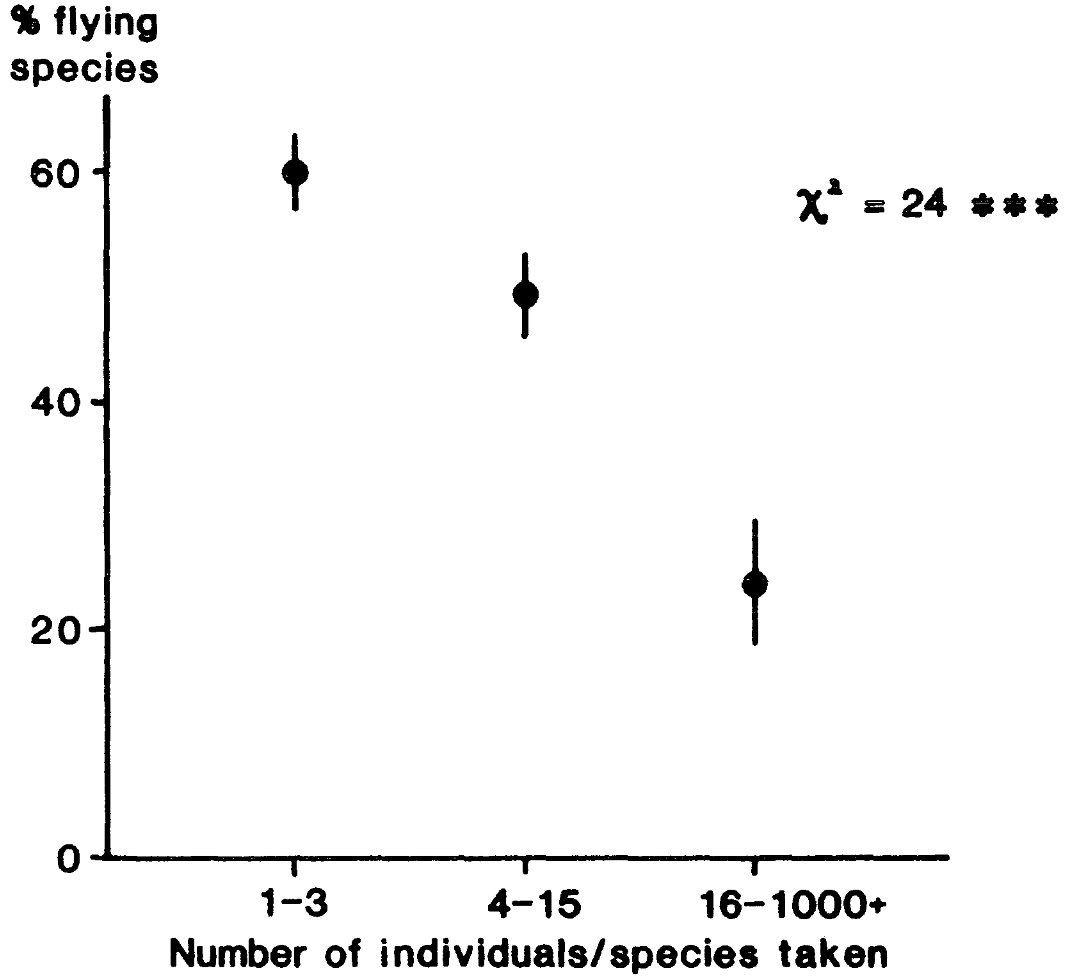
A = area of outcrop

c = constant measuring S/A

z = constant measuring rate of change in S with changing A (the carabid *Notiophilus aquaticus*, the staphylinids *Atheta tibialis* and *Liogluta nitidula*) or a capacity for flight (the staphylinids *Tachyporus chrysomelinus*, *T. pusillus*, *Mycetoporus lepidus* and *Amischa analis*). On individual outcrops, the abundances of different Limestone staphylinid species in pitfall trap catches varied considerably: some species were only taken once or twice whilst others were represented by more than 1000 individuals in a year's catch. The relative population densities of different species on a particular outcrop correlated most closely not with outcrop size, but with the capacity of a species for flight (Figure 8.5): significantly more of the rarest species (60%) were capable of flight than those which were frequently taken (25%). The ecological significance of this difference is considered in Chapter 9.

Figure 8.5

Proportion of staphylinid Limestone species capable of flight in relation to the abundance of their individuals taken in pitfall traps on limestone outcrops. Significance level given by ***: $p < 0.001$.



CHAPTER 9 GENERAL DISCUSSION

In this chapter two aspects arising from the general analysis of moorland carabid and staphylinid communities in earlier chapters are considered in more detail. In the first part the nature of flight activity in the two taxa at Moor House is further examined. In the second part the application of classical island biogeographical theory to the Moor House limestone outcrops and the concept of 'habitat islands' in general is discussed.

9:1 The nature of flight activity at Moor House

The level of flight activity exhibited by carabid communities at Moor House was very low: only 6% of all species caught by pitfall trap on the Reserve in 1984-5 was also taken in window traps. By contrast, flight was demonstrated in 57% of all staphylinid species similarly recorded on the ground surface on the Reserve. Both carabids and staphylinids have specific flight requirements with respect to windspeed, rainfall and temperature (Van Huizen 1977, 1979, Koskela 1979, Honek and Pulpan 1983): winds must be gentle (below about 7m/s) and rainfall absent or very low (below about 1.0mm/day) before flight is likely to occur. Even if these latter conditions are favourable, however, neither group will be able to fly unless its minimum temperature thresholds for flight activity are exceeded. The physiological nature and hence the level of these thresholds may well be comparable between the two taxa, such that at night or under overcast conditions their flight activity will be similarly dictated by the prevailing air temperature. However, during the day-time solar radiation, not air temperature, is likely to be the most influential factor in warming up the insect body, and unlike air temperature, solar radiation will be differentially effective according to insect body size and pigmentation. The smaller darker staphylinids may be expected to attain the temperatures necessary for flight more rapidly and at lower levels of radiation than the larger often paler carabids. The radiation factor is probably partially responsible for the lower temperature threshold of 16°C (daily maximum temperature) recorded by Van Huizen (1977, 1979) for flight activity by most diurnal carabid species in Holland compared with the average value of 19°C (at 2100h) of Honek and Pulpan (1983) for nocturnal carabids in central Bohemia. By comparision, Koskela (1979) has shown that for coprophilous staphylinids in Finland, air temperatures must exceed 11.1°C and 12.5°C before flight occurs in multi- and univoltine species respectively. These somewhat lower temperature values for staphylinids may represent a greater effectiveness of heat gain by solar radiation in these beetles rather than a lower physiological threshold _per se_, but this aspect remains to be investigated.

Average daily temperatures at Moor House seldom exceeded 12°C during the field season of 1984, and never rose above 11°C during that of 1985. Moreover, in the first half of May when staphylinid flight activity peaked, average daily temperatures were only about 9°C and 7°C in 1984 and 1985 respectively. According to the predictions of Van Huizen (1977, 1979), Honek and Pulpan (1983) and Koskela (1979) neither carabids nor staphylinids should have been recorded flying under such conditions (particularly in such abundance) if air temperature alone was the decisive factor. Hence the most plausible explanation for the marked difference in overall levels of flight activity between carabids and staphylinids at Moor House seems to be that air temperatures alone were too low to encourage flight in either taxon, but staphylinids were able to use to good advantage sporadic periods of high solar radiation which were insufficient to permit flight in carabids.

Koskela (1979) has shown, furthermore, that many coprophilous staphylinid species are capable of great flexibility in the timing of their diurnal flight activity at different seasons; a further adaptation towards the maintenance of continuous flight activity throughout the season, even in the cool and unpredictable climates of northern latitudes or high altitudes.

Within the staphylinids different categories of species were not characterized by the same general level of flight activity: Nomadic species were invariably capable of flight, whereas the number of Peat species taken in flight was negligible. Limestone and Widespread species exhibited intermediate levels of flight activity. The difference in flight activity observed between similar-sized species within a taxon cannot be so easily attributed to temperature effects. In this case it appears to have been the nature of the habitat or exploitable resource which was dictating the capacity for flight, with the level of flight activity correlating directly with the degree of permanence of the habitat or resource involved. This relationship between the level of flight activity within a taxon and the association of its species with either temporary or permanent habitats has been well documented for many insect groups (Hardy and Milne 1938, Freeman 1938, 1945, Southwood 1962, Greenslade and Southwood 1962, Johnson 1969, Hanski and Koskela 1977, etc). When a species occupies habitats of a temporary nature such as carrion, dung, or plants of seral communities (eg waste ground or fields) - all of which are in one locality for only a short period - then if it is to exploit fully all the available niches at any one time the species must have a high level of migratory movement geared to the rate of change of its habitat (Southwood 1962). In most beetles flight represents the normal means of such migration or dispersal: within the immediate habitat walking is used for trivial movement (Southwood 1962) and only rarely for long-range dispersal in the larger species (cf Den Boer

1970). Therefore, for species adapted to exploit invariably unstable habitats such as the sheep dung at Moor House, flight will always be essential. Such species retain their ancestral monomorphic macropterous or long-winged condition from generation to generation and polymorphism or loss of flight is highly unlikely (Hammond 1985) .

In contrast, for many species inhabiting relatively stable and permanent environments such as lakes, rivers, climax woodland, salt-marshes and heaths (Southwood 1962), or habitats that become increasingly stable through time (Den Boer et al. 1980), flight becomes unnecessary and even detrimental to their existence and there is a progressive selection towards flightlessness (Darlington 1943, Lindroth 1949, Southwood 1962, Den Boer 1970, 1971, 1977, 1979). This selection process usually involves the atrophy of wing musculature and/or a reduction in wing size of individuals in populations inhabiting stable sites, and ultimately gives rise to a monomorphic brachypterous or short-winged species. Species inhabiting sites which vary in stability may become wing dimorphic with largely brachypterous populations in the more stable localities, and predominantly macropterous populations in environments characterized by instability (Jackson 1928, Darlington 1943, Lindroth 1949, Den Boer 1970 etc.).

Compared to the highly transient microhabitats represented by sheep dung and carrion, the blanket peat and grassland habitats at Moor House were characterized by a relatively great stability of environment, having persisted in the same locality largely unchanged for even thousands of years (Godwin 1975, 1981). The comparatively low levels of flight activity exhibited by different categories of Settled staphylinid species at Moor House in relation to Nomadic species prove to be closely associated with a high degree of brachyptery within their populations (Table 9.1; Hammond pers. comm.). Such montane brachypterism is a common phenomenon where

Table 9.1

Wing condition of staphylinid and carabid species at Moor House

(after Houston 1970, Lindroth 1974, Hammond pers. comm.)

	Species categories				
	Peat	Limestone	Widespread	Vagrant	Nomadic
Staphylinids					
% Monomorphic macropterous	20	71	50	100	100
% Wing dimorphic	25	7	0	0	0
% Monomorphic brachypterous	55	22	50	0	0
Total species	20	45	16	7	60
Carabids					
% Monomorphic macropterous	22	38	50	100	
% Wing dimorphic	0	6	25	0	
% Monomorphic brachypterous	78	56	25	0	
Total species	9	16	8	2	

environments are characteristically of a permanent nature (Darlington 1943, Mani 1968, Brandmayr 1983). Although showing negligible flight activity on the Reserve regardless of habitat type, the carabid categories exhibit a pattern of wing condition comparable to that of the staphylinids (Table 9.1; Houston 1970, Lindroth 1974), suggesting that current inclement weather conditions rather than historical design may have been the cause of the present low flight activity observed in many species. Although both blanket peat and limestone grassland habitats appeared to be of a similarly permanent nature at Moor House, yet the level of flight activity exhibited by Limestone (and Widespread) staphylinid species was considerably higher than that of Peat species, and in both staphylinids and carabids the level of brachyptery in these categories was markedly lower than in the Peat species category (Table 9.1). This suggests that in some subtle way the limestone grassland outcrops and their peripheries constituted a far less stable or predictable habitat than the blanket peat. Part of the cause may lie in the relative stability of moisture regime of the two habitat types: the well-drained limestone grasslands and shallow peat habitats are subject to much greater changes in water relations than the more stable and moisture-retaining blanket peat. Houston (1970) recognized a similar trend between moorland habitat and degree of macroptery in carabid species at Moor House, with the proportion of macropterous species being highest on alluvial or flushed grasslands prone to flooding and lowest on the blanket peat. Brandmayr (1983) considered moisture stability to represent a second major axis (ecologial succession/dynamic stability being the first axis) determining the 'coenocline continuum brachyptery/macroptery' in carabids, and attributed montane brachyptery directly to the high dynamic and water stability characterizing these environments and not to altitude <u>per se</u>. He summarized the relationship as follows: 'Widely and continuously distributed homogeneous climax habitats with high dynamic and moisture stability select brachypterous species and forms. Small patchily distributed habitats, environmental heterogeneity, low dynamic and water stability of soil favour maintenance of high dispersal power.'(Brandmayr 1983).

Although the Limestone species of both taxa exhibit much higher levels of macroptery than their Peat counterparts, yet the degree of macroptery in the staphylinid Limestone species is considerably greater than in carabid Limestone species (Table 9.1) and was also manifest as active flight. This difference suggests a further possible explanation for the high numbers of flying Limestone species on the Moor House outcrops relative to those on the blanket peat: it may have been the direct result of a high level of immigration of such species from outside the Reserve which recolonized or supplemented existing populations on the outcrops each season. Small staphylinids are frequent components of the aerial plankton in the upper air (Hardy and Milne 1938, Southwood and Johnson 1957) and their apparent entry from the Eden valley has already been demonstrated. A seasonal 'rain' of potential colonists is easily envisaged. Carabids, on the other hand, seldom engage in high altitude dispersal, but mainly follow winds prevailing close to the ground surface (Lindroth 1949): comparatively little immigration of flying species onto the limestone outcrops within the Reserve is likely to occur, as evidenced by the meagre window trap catches. In view of the apparent unsuitability of weather conditions on the Reserve for carabid flight, it is very likely that most if not all of the flying carabids taken at Moor House were immigrants from outside. Of the five species taken in flight on the Reserve, only *Loricera pilicornis* was a common moorland species, and all species apart from *Bembidion guttula* are frequent components of flight trap catches elsewhere (Lindroth 1949, Den Boer 1971, Van Huizen 1979, Honek and Pulpan 1983). Apart from the cicindelids and certain species of *Bembidion*, carabids are weak fliers and their direction of flight is greatly influenced by the wind (Lindroth 1949). *Amara apricaria* and *Bradycellus harpalinus* may exhibit a migratory sequence between hibernation and reproductive habitats similar to that described for *Amara plebja* (Van Huizen 1977), and were caught up in air currents during their change of habitat such that migration became dispersal. These species, together with Trechus quadristriatus and Bembidion guttula are all typical of ruderal or fairly unstable habitats not characteristic of the Reserve (Lindroth 1974), and have most likely been carried in from the lowlands on the prevailing westerly winds. Houston (1970) proposed a similar explanation for the occasional winged individuals of these or other atypical species he caught at Moor House.

The considerably higher levels of immigration of staphylinid relative to carabid species would explain the relatively impoverished carabid faunas on the limestone outcrops at Moor House compared to those at Tailbridge, while average numbers of Limestone staphylinid species in the two localities remained similar: only Limestone carabid species able to maintain populations stable enough to resist extinction on an outcrop from year to year, or with sufficient dispersal power by walking to spread the risk of extinction (Den Boer 1977), were able to persist on the Moor House sites. This relationship between the species composition of the fauna on the outcrops and the dispersal powers of its member species is considered in more detail in the next section.

9:2 Island biogeography and the Moor House limestone outcrops

The present study has shown that the limestone outcrops at Moor House acted as true isolates of habitat for many of the carabid and staphylinid species present. Such species were apparently dependent upon environmental conditions or resources peculiar to limestone grassland and could not establish viable populations on the surrounding blanket peat. Their abundance on a limestone outcrop was influenced by outcrop size in the manner predicted by classical island biogeographical theory: greatest numbers of species were recorded on the largest outcrops, and fewest on the smallest.

According to the theory, the number of species present on an individual outcrop represented an equilibrium state resulting from a dynamic interaction between immigration rates and extinction processes. At the species level, the relative importance of these latter functions depended upon two major attributes of a species: a) its ability to resist extinction by systematic pressures on or stochastic perturbations of its local populations (Shaffer 1981), and b) its powers for dispersal and (re)colonization of outcrops to compensate for local extinctions (Den Boer 1979). Den Boer (1979) regards the extinction of local carabid populations or 'interaction groups' as a common phenomenon not merely for species living in unstable or temporary habitats, but also for those inhabiting more permanent and stable environments. He defines an interaction group as 'a group of individuals living on a site having spatial dimensions which do not substantially exceed the average distances covered by the individual members during their normal patterns of activity' (Den Boer 1977, 1979). The interaction groups for two carabid species 6-8mm and 10-12mm long are estimated to cover 1.5ha and 15ha respectively (Baars 1979). When the dimensions of the inhabited area greatly exceed the distances normally covered by individuals (as would be expected for flightless carabid and staphylinid populations on the blanket peat at Moor House), then an interaction group will gradually merge into others around it. Because even the seemingly most uniform of habitats are in fact generally quite heterogeneous (Margules, Higgs and Rafe 1982) with local differences in microenvironment and resources, fluctuations in the abundance of contiguous interaction groups will occur asynchronously, with the effect of extreme conditions in one locality being compensated by more moderate conditions in others. Thus between generations the risk of wide fluctuations leading to extinction is spread unequally over many local groups and the composite population remains relatively stable (Den Boer 1977, 1979). Evidence for such a stablization of numbers and 'spreading of risk' has been provided by a series of long-term field experiments on two carabid species which showed that the fluctuations in annual reproductive rate of a large panmictic population were confined within much narrower limits than those of the local interaction groups of which it was composed (Den Boer 1971).

The limestone grasslands at Moor House, like the blanket peat, constituted a relatively permanent and stable habitat compared to wasteland, fields or other successional habitats. They may also be expected to have possessed a similar heterogeneity of microhabitat, such that local interaction groups were subject to stochastic extinction. However, whereas in extensive non-isolated habitats, such as the blanket peat, local populations could be rapidly replenished by individuals dispersing on foot from contiguous areas when fluctuations within them led to extinction, recolonization of the small and highly isolated limestone outcrops would be much more difficult. The size of the outcrops was such that they may have been capable of accommodating only a single interaction group of many of the larger species (cf Baars 1979, Den Boer 1979), and their isolation was such that only in populations of species with exceptional powers for dispersal would any degree of interaction and associated 'spreading of risk' have been possible. Under these circumstances selection appears to have operated in favour of two alternative strategies. Carabid and flightless staphylinid species had comparatively low powers of dispersal, a minimal possibility of interchange of individuals between outcrops and immigation of individuals from outside the Reserve was highly unlikely. The only flightless species which persisted on individual outcrops appeared to be those which maintained sufficiently large or stable populations from year to year that stochastic extinction was avoided. Flightless staphylinid species were typically taken in greater numbers on a site than were their flying counterparts. On the more extensive outcrops the greater degree of heterogeneity of habitat and the larger number of interaction groups which could exist allowed more species to persist than could do so on the smaller outcrops.

The alternative strategy pursued by many staphylinid species inhabiting the limestone outcrops as sparse populations was to retain a capacity for flight and hence a more effective means of dispersal between outcrops. Although individual interaction groups ran a high risk of being made locally extinct by stochastic events within the immediate environment, this was compensated for by the species engaging in high levels of flight activity each season which allowed it to recolonize outcrops where temporary extinction had occurred, or to supplement populations that were in danger of soon becoming so. Thus in a sense, the population as a whole was analogous to the composite of contiguous interaction groups found on the blanket peat, in that flight allowed these Limestone species a similar degree of interaction and 'spreading of risk' between isolated outcrops as walking did for Peat species on the blanket peat. It has been noted that most flight activity in these species occurred regularly each spring. Den Boer (1979) suggests that such a regular annual dispersal is necessary in order to increase sufficiently the chance of (re)founding populations, since conditions will not always be favourable for a successful settlement. Besides possibly offering a greater variety of niches and the potential for larger more stable populations to these flying species, larger outcrops may have possessed more of such species than smaller outcrops simply because they presented a larger interception area to flying immigrants (Connor and McCoy 1979).

Besides area, isolation is predicted to influence the number of species on an island, but in a negative fashion (MacArthur and Wilson 1963, 1967). The evidence for the immigation of flying individuals from a larger 'reservoir' of grassland species to the west of the Reserve supports this prediction: the number of flying staphylinids (and aphids) sampled on or over the limestone outcrops at Moor House diminished with increasing distance from this source area.

Although the presence of flying species on the Moor House outcrops is easily accounted for as an inevitable seasonal immigration of species within the aerial plankton, yet the persistence of the flightless species, which may have existed as such for many thousands of years, requires further explanation. The origin of such flightless Limestone species may go back to the Boreal era at least 3000 BP when climatic conditions were suitably clement to permit an extensive growth of birch, willow and juniper woodland at Moor House up to an altitude of 760m (evidenced by fossil tree stumps; Godwin 1975, 1981). On patches of skeletal soil such as the limestone outcrops, however, which were too unstable to permit the growth of trees, a high montane grassland perhaps covered with a thin hazel and juniper scrub but otherwise free from trees may have persisted. These habitats would have provided a refuge for plant communities requiring unshaded base-rich soils (Pigott 1956, Pennington 1969) and also for their associated grassland faunas. With the deterioration of climate that marked the Boreal/Atlantic transition (about 2800 BP), blanket bog growth resumed and the birch woodland was waterlogged and superseded by the extensive blanket peat cover still present today (Godwin 1975) . The limestone grasslands persisted, however, presumably retaining many of their original grassland species and maybe also acting as refuges for some former woodland species.

Although the limestone outcrops at Moor House possessed a core of resident species within their carabid and staphylinid faunas which conformed to classical island biogeography theory, yet in every case a large proportion (sometimes the greater part) of the species present were not representative of the limestone grassland habitat at all, but were either 'edge' species exploiting the transitional habitat along the outcrop boundary, or species invading from the surrounding blanket peat. The influence of this influx became progessively greater as an outcrop became increasingly smaller in size and had major repercussions upon the species richness, diversity and composition of the local fauna. Contrary to many faunas in real island situations, population densities of Limestone carabid and staphylinid species on the smaller islands did not match or exceed those on the larger islands, but were consistently lower. Such a positive area:density relationship is often attributed to competition between species (eg MacArthur 1958). Since numbers of Limestone species also declined with decreasing site size it is unlikely that competition between resident species was the cause, but rather competition from the Widespread and invading Peat species for limited resources. This phenomenon of increasing interference from adjacent habitats as habitat island size decreases has been observed in other such systems. Janzen (1983) noted that areas of conserved pristine forest are increasingly susceptible to immigration of animals and plants from neighbouring anthropogenic successional habitats as they are reduced in size. Mader (1984) demonstrated a considerable increase in the total numbers of species present in wooded islands as a result of the occasional penetration of numerous field species, and an associated change in the local species composition of the woodland with growing influence of the surrounding areas. He estimated that the proportion of non-characteristic carabid species would exceed that of former resident species in woodland isolates 2-5ha in extent, and suggested that very small islands (less than 0.5ha) may be composed entirely of 'edge' with no remaining 'core' area. Levenson (1981) came to a similar conclusion. Webb and Hopkins (1984) showed a similar increase in the number of invertebrate species at a point on small heathlands compared to the number at a comparable point on larger heaths, and again attributed it to a greater edge effect on the smaller heathland fragments.

The implications of this influx of non-representative species onto a habitat island with regard to the acceptability of general ecological principles such as species:area relations are considerable, and are especially important when such habitats are being assessed for conservation purposes. Besides highlighting the inevitable contamination of the resident fauna and alteration in species composition which occurs, the present study has demonstrated how highly misleading such a parameter as species richness is as an indication of the quality of a habitat: whereas the staphylinids exhibited a positive species:area relationship overall, the carabids gave the exact opposite trend with species numbers being highest on the smallest outcrops. This difference between the taxa resulted primarily from their difference in body size and dispersal power. Resident carabid faunas on the limestone outcrops were relatively impoverished compared to those of staphylinids because of their low powers for long-range dispersal and colonization but relatively high minimum patch requirements to avoid extinction (Rosenzweig 1975, Den Boer 1979). Moreoever, because of the general propensity for flight within the staphylinids, many flying species recorded on the outcrops were simply vagrants and unlikely to become established there. (Williamson (1981) reckoned that the turnover producing the equilbrium between immigration and emigration involved only such casual species.) With regard to the resident species on the blanket peat, however, because those in both taxa were predominantly flightless, the influx of carabid individuals from the surrounding blanket peat onto the limestone outcrops was relatively higher than that of staphylinids owing to their greater dispersal powers on foot. Thus, overall, the numbers of Peat species dictated the species:area relationship for carabids, but the numbers of Limestone species had the greatest influence on this relationship for staphylinids. These opposing trends illustrate how different animal groups can exhibit very different overall responses within the same system, and indicate the necessity for detailed autoecological studies of the organisms concerned when designing nature reserves or otherwise attempting to understand the local ecosystem (McCoy 1982). Species characteristic of a habitat type must first be distinguished from all other invading or eurytopic species before a useful assessment of the quality of a habitat island can be made. Designs and models based upon measures of species richness and the species:area relationship alone (Diamond 1975, Wilson and Willis 1975) are clearly unsatisfactory if the aim is to conserve endangered species or those most representative of a habitat.

SUMMARY

1. The ground beetle (carabid) and rove beetle (staphylinid) faunas of contrasting moorland habitats were studied in two localities in northern England.

2. In 1984-5, the beetle faunas of ten isolated limestone outcrops, six sites within the intervening blanket peat, and two adjacent areas of untreated and improved *Juncus* moor on the Moor House National Nature Reserve, Cumbria, were investigated.

3. In 1986, the beetles present along a 200m transect between extensive areas of limestone grassland and blanket peat at Tailbridge Hill, Cumbria, were studied.

4. Samples of the surface and aerial faunas were collected fortnightly during the field season (April-October) using pitfall and window traps respectively. Limited soil sampling and examination of sheep dung was also carried out.

5. Totals of 5417 carabids of 44 species and 22544 staphylinids of 157 species were recorded in pitfall and window traps on the two study areas. One carabid and 46 staphylinids (89% larvae) were present in soil samples. A total of 299 staphylinids of 12 species was taken in sheep dung.

6. Average numbers of beetles caught at Moor House varied consistently between habitats. Averages of 158 carabids of 13 species and 802 staphylinids of 39 species were taken in pitfall traps on the limestone outcrops, and 15 common species were taken solely on this habitat. Averages of only 31 carabids of 6 species and 256 staphylinids of 20 species were taken in pitfall traps on the blanket peat, and only one common species was recorded on this habitat alone. Five species of

carabid and staphylinid were common on both limestone and blanket peat sites.

7. Average numbers of beetles caught at Tailbridge showed no consistent pattern between habitats. Averages of 233 carabids of 13 species and 762 staphylinids of 29 species were taken in pitfall traps on the limestone grassland at least 50m from the habitat interface, and five common species were taken only on this habitat. Averages of 346 carabids of 16 species and 183 staphylinids of 26 species were taken in pitfall traps on the blanket peat at least 50m from the habitat interface, and seven common species were recorded on this habitat only. Three species of carabid or staphylinid were common on both limestone and blanket peat sites.
8. Williams' $\underline{a}$ was shown to be the best measure of within-site diversity in the beetle faunas on the limestone outcrops at Moor House when compared with the indices $\underline{S}$, $\underline{H}$, $\underline{D}$ and $\underline{d}$.
9. $\underline{a}$ values of staphylinids were invariably higher than those of carabids on the same site, but both taxa showed a similar pattern of alpha diversity between pitfall trap catches from different sites. $\underline{a}$ values were lowest on the blanket peat sites (2.3: carabids; 5.0: staphylinids) and highest on the *Juncus* moor sites (4.7: carabids; 12.2: staphylinids). Diversities on the limestone outcrops lay between these extremes (3.6: carabids; 9.0: staphylinids.
10. The programs CLUSTAN and DECORANA were used to analyse the pattern of beta diversity between pitfall trap catches at Moor House. Habitat type constituted the major source of variation in species composition of carabid and staphylinid catches. At a similarity level of 0.5 (based on a modified version of Sørensen's index) catches from blanket peat, improved and untreated *Juncus* moor, and limestone grassland formed

discrete clusters.

11. Species of carabid and staphylinid taken at Moor House and Tailbridge were classed as Settled or Nomadic according to the spatial and temporal stability of the habitat or resource with which they were associated.

12. Settled species were further classed as Peat (33 species), Limestone (67 species), Widespread (28 species) or Vagrant (11 species) according to their relative abundances on the major habitat types.

13. Nomadic species were further classed as Dung (36 species) or Non-dung (26 species). Dung species were taken predominantly on the limestone grasslands, where the highest concentrations of sheep dung were to be found.

14. Considerable interchange of carabid and staphylinid species occurred across the habitat interface between limestone grassland and blanket peat on both study areas, with 5% of Peat species occurring up to 100m onto the limestone, and 5% of Limestone species being taken up to 100m onto blanket peat at Tailbridge.

15. Flight capacity significantly influenced the extent and magnitude of dispersal of staphylinids away from their normal habitat: 27% of individuals of Limestone species capable of flight were taken on the peat habitats at Tailbridge, compared to only 2% of those of flightless species. The incidence of macroptery in individuals of the wing dimorphic Peat species <u>Mycetoporus</u> <u>clavicornis</u> taken on limestone (56%) was significantly higher than in those taken on blanket peat (20%).

16. Body size was an important factor in the relative dispersal of flightless species away from their normal habitat. Whereas 60% of flightless Limestone staphylinid species 5-12mm were caught at least 25m onto blanketpeat, only 18% of those 1-4mm were taken this far from the limestone grassland.

17. Moisture requirements of different Peat carabid species significantly influenced their dispersal onto the limestone. Although comprising 65% of all individuals of Peat species taken on blanket peat 100m from limestone at Tailbridge, Wet species formed only 31% of the total at 25m, and were completely absent at 100m onto the limestone habitat. They were significantly less abundant on the limestone outcrops at Moor House in the drier 1984 season than in the wetter conditions of 1985.

18. Besides altering the local species composition, the interchange of species between habitats resulted in a 54% increase in species richness and a doubling of $\underline{a}$ values for pitfall catches of both carabids and staphylinids on limestone 2m from the interface compared to those at 100m onto the same habitat at Tailbridge.

19. Flight activity within the two taxa was very different: only 7% of carabid, but 55% of staphylinid species taken in pitfall traps at Moor House and Tailbridge were also caught in window traps on these study areas. A further three carabid and 38 staphylinid, species were taken in window traps only.

20. Of the twelve carabids taken in flight at Moor House only one was of a common moorland species. Climatic conditions on the Reserve during 1984-5 were not condusive to carabid flight, with average daily temperatures below 12°C and less than six hours of bright sun per day. The evidence suggests that the flying individuals caught there were vagrants from further afield.

21. The level of flight activity exhibited by staphylinid species at Moor House was related to the degree of permanence of the habitat occupied. All Nomadic, but only 41% of Settled, species were capable of flight, and 71% of all individuals of Nomadic species recorded were taken in window traps compared to only 21% of those of Settled species able to fly.

22. Settled staphylinid species exhibited a peak of flight activity in May which was concurrent with a general increased abundance in pitfall trap catches at this time. Very little flight activity was recorded in late summer and autumn. Nomadic species showed two peaks of flight activity in May and September but were taken frequently in window traps throughout the field season.

23. Settled species were exploiting resources that were spatially and temporally predictable within areas of permanent habitat; flight was apparently largely confined to an annual dispersive phase early in the season. Nomadic species were exploiting transient and spatially unpredictable resources; flight was essential throughout the field season to keep pace with the change in resource distribution.

24. Only 10% of Peat staphylinid species were capable of flight at Moor House compared to 52% of Limestone and 38% of Widespread species. Only 6% of all individuals of these flying Peat species were actually caught in flight compared to 20% of individuals of Limestone species.

25. This difference in flight activity was related more to the extent and spatial distribution of the two habitats than to marked differences in their stability. Peat species could compensate for local population extinctions by walking into the locality from contiguous areas of blanket peat. Limestone species formed discrete and isolated populations on the various outcrops. They appeared either to avoid local stochastic extinction by maintaining large and stable populations on individual outcrops, or to compensate for it by being able to fly regularly between outcrops to supplement or re-establish local populations.

26. The majority of insects in flight over a habitat at Moor House were of local origin, either from the immediate locality or from neighbouring moorland habitats, but there was also evidence of a large input of winged

staphylinids and aphids in aerial plankton carried over from the Eden valley by prevailing westerly winds in the second half of the field season. Two carabid, seven staphylinid and 32 aphid species taken on the Reserve were atypical of moorland, and a further two carabid and 78 staphylinid species were represented in window traps by only one or two individuals and were previously unrecorded at Moor House.

27. Altitude was an important factor influencing the species composition of the carabid and staphylinid faunas on the Moor House limestone outcrops. The contribution of montane species increased by 23% (staphylinids) and that of lowland species decreased by 11% (staphylinids) with every 100m rise in elevation. The greater rate of change in the montane species component resulted in an overall increase in numbers of individuals present on outcrops at the higher elevations: by 95% (staphylinids) and 62% (carabids) with a 100m increase in altitude.

28. Numbers of Limestone carabid species taken on the limestone outcrops at Moor House increased by 32% with every ten-fold increase in site size. Numbers of Limestone staphylinid species similarly increased by 17%. These species:area relationships conformed to the predictions of classical island biogeographical theory.

29. Numbers of flightless Limestone carabid and staphylinid species were higher on larger outcrops which could sustain more species with sufficiently large population densities to resist extinction. The outcrops were too small to allow the existence of many Limestone carabid populations, resulting in a greatly impoverished carabid fauna (averaging 4.5 species, 42 individuals) compared to that at Tailbridge (7.5 species, 163 individuals).

30. Limestone staphylinid species, with smaller minimum patch sizes and a greater capacity for flight, were not so affected by the extent and

distribution of limestone habitat (averaging 21 species, 650 individuals at Moor House; 20 species, 610 individuals at Tailbridge). Numbers of flying Limestone staphylinid species may have been higher on larger outcrops because such sites presented a greater interception area to immigrants from other outcrops or from outside the Reserve.

31. Numbers of Peat species taken on the limestone outcrops at Moor House increased significantly by 24% (staphylinids) and 47% (carabids) as site size declined. Peat species averaged 31% (staphylinids) and 45% (carabids) of all species and 16% (staphylinids) and 49% (carabids) of all individuals taken on an outcrop. The relatively high influx of carabids from the surrounding blanket peat resulted in an overall negative relationship between total numbers and site size in carabids whereas these variables were positively correlated in staphylinids.

32. The limestone outcrops at Moor House functioned as true isolates to many (Limestone) species, but differed from real islands in their subjection to considerable invasion of non-resident species from surrounding habitats. The respective influences of these two components must always be analysed and taken into account in any consideration of the fauna of 'habitat islands'.

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