Ecological studies on wading birds (Charadrii) in some upland areas of Britain

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ECOLOGICAL STUDIES ON WADING BIRDS (CHARADRII) IN SOME UPLAND AREAS OF BRITAIN

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ABSTRACT

Factors affecting the diversity and abundance of wading birds during the breeding season were studied on an area of moorland and marginal hill farmland in part of Upper Teesdale.

Several vegetation types, on both peat and mineral soils, were available as breeding sites. Low vegetation height and an open, treeless habitat favoured by most wader species was maintained by a combination of management for grouse moor and sheep grazing.

The interpretation of multivariate analyses suggested that vegetation type and altitude were the most important determinants of distribution for Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin. Wader species richness and abundance decreased with altitude, approximately one species being lost for every 100m increase in altitude. Both relationships were independent of vegetation type and were thought to be food-related.

Within the marginal hill farmland, fields with a cover of *Juncus effusus* exceeding 5% had the highest breeding densities of waders and were preferentially selected by Lapwing, Redshank, Snipe and Curlew. The proximate factors involved in the selection of fields by these species were typically associated with wet habitats, e.g. marshy patches, the cover and distribution of *J. effusus*, and flat areas. Species richness was greatest on the large, wet, unmanaged fields. Only Lapwing commonly bred on the drier hay meadows.

Three wader species, Common Sandpiper, Oystercatcher and Ringed Plover were notably restricted to bodies of permanent standing water. Of these only Common Sandpiper were abundant, breeding densities varying in accordance with stream width and the number of shingle banks which were used as feeding areas. The formation of Cow Green Reservoir in 1970 seems to have been responsible for attracting Ringed Plover as a new breeding species to Upper Teesdale.

Changes of land use in upland areas have important consequences for many wader species. From a consideration of factors affecting the diversity and abundance of wading birds in Upper Teesdale, the implications of such changes were discussed with reference to the management and conservation of upland areas as habitats for breeding waders.

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INTRODUCTION

Natural selection has caused plant and animal species to become adapted to specific environments. As a result, most organisms are non-randomly distributed, their pattern of distribution being ultimately dependent on the differential survival of individuals in different habitats. This spatio-temporal distribution and abundance of organisms is the basis of ecology. For species whose members are capable of locomotion, natural selection has determined the evolution of a mechanism whereby they can recognise the habitats to which they are adapted, individuals moving on until they find a suitable area. An understanding of this process of habitat selection, and any other factors which may influence distribution, is essential in the conservation of species. The main concern of this study was to evaluate factors affecting the variety and abundance of wading birds during the breeding season on an area of moorland and marginal hill farmland in part of Upper Teesdale. As British uplands are being changed by land improvement schemes for agriculture and the establishment of extensive conifer plantations, the need for such information is becoming increasingly urgent since many areas of prime wader breeding habitat are being destroyed or are under threat.

The present study is set against extensive background knowledge since Upper Teesdale has long been an area for research sponsored by universities and research councils. Some of the most intensive studies on British moorlands have been carried out on the Moor House National Nature Reserve and information from this area formed part of the U.K.'s contribution to the International Biological Programme. The construction of Cow Green Reservoir, completed in 1970, gave a new impetus to scientific studies as impoundment caused the loss of part of Teesdale's relic ice age flora. Donations to the

Teesdale Trust from Imperial Chemical Industries Ltd., the chief beneficiary of the new reservoir, helped fund research projects over a ten year period, primarily to document the effects of flooding. Clapham (1978) gives details of this work. Much of the research has been of a botanical nature, or concerned with invertebrates, and relatively little attention has been given to vertebrates. In recent years 83 species of birds have been recorded nesting in Upper Teesdale and, although this is not a large number for such an extensive area, the abundance of certain groups, such as the waders, makes Teesdale of considerable interest (Coulson 1978).

The distribution of a species may be governed by environmental limitations, powers of dispersal and behavioural responses. Behavioural responses may be towards other organisms or to the environment (i.e. habitat selection). Two species with the same ecology cannot survive in the same region if they are competing for a resource which is in short supply (Gause 1934). Thus, the presence of competitors can modify the distribution of a species. Birds can withstand great variations in climatic conditions (Lack 1933) and having good powers of dispersal can move before lethal conditions become operative. Therefore, at least on a local scale, interactions with other organisms and habitat selection are likely to be the most important determinants of avian distribution, given that the species could survive in the area on other grounds.

Habitat selection is common throughout the animal kingdom but it is for birds that most evidence is available. Being mainly diurnal and relatively conspicuous, particularly during the breeding season, birds are amenable to study. Also, the laying of eggs in a nest indicates prolonged habitat utilization.

"Birds are guided to their breeding stations by a primarily innate reaction released by certain environmental stimuli, on the principle of summation of heterogeneous stimuli, as in instinctive activities in general. The threshold for the release of the reaction is dependent on the internal motivation of the bird" (Hildén 1965). Since the response to the habitat is innate it allows consistent evaluation of alternative sites (McFarland 1977). Understanding the mechanism for the selection process has been greatly aided by the distinction between ultimate and proximate factors first proposed by Baker (1938). Ultimate factors are those which affect survival rate and hence modify habitat selection through evolution. They are the features the environment must possess to ensure the individual's survival and are the underlying causes for the breeding of each species in its specific environment. Hildén (1965) considered that the ultimate factors for birds were:

1) food
2) requirements imposed by the structural and functional characteristics of the species
3) shelter from potential predators and adverse weather.

Proximate factors are the environmental stimuli to which a bird responds directly. They need have no biological significance and, therefore, may not confer any immediate survival value. Proximate factors do however enable individuals of a species to recognise a habitat to which they are adapted by eliciting the settling reaction. Hildén's (1965) categories of proximate factors were:

1) features of landscape and terrain
2) nest-, song-, feeding-, drinking- and vantage-sites
3) food
4) other animals, either conspecifics or individuals of a different species.

Thus food can act in both a proximate and ultimate sense but is usually only a proximate factor for species which are specialized feeders. Each environmental variable can act in either a positive or negative way. Waders may be attracted to open areas while such localities would be unsuitable for species such as the Tree Pipit which needs a song-post. Similarly, social breeders may be attracted to areas where breeding pairs have already settled, while species showing no clear-cut sociality may be repelled by the presence of conspecifics already having a territory.

The theoretical effects of ultimate factors on evolution have been discussed by Brock (1914), Lack (1944) and Thorpe (1945) and many authors have emphasized that the perceptual basis of habitat selection must also be taken into account, referring to proximate factors by a variety of names. Brock (1914) referred to "mental bias", Lack (1933, 1937, 1940) and Miller (1942) to "psychological factors" and Moreau (1935) to "subjective factors". However, Klomp (1953) was the first person to clearly distinguish between proximate and ultimate factors in the field. He found that the Lapwing avoids breeding in fields with trees (proximate factor) because they were less able to defend nests and chicks from predacious crows (predation being the ultimate factor) than in open areas. A proximate factor may provide an index of a biologically important, but less readily measured, environmental variable. Thus Klomp found Lapwing preferred a brown or grey-green field colour (proximate factor) as this was indicative of low vegetation height later in the season (ultimate factor), Lapwing being unable to walk in tall vegetation and having courtship displays and feeding methods suited to a short sward. Klomp also suggested a survival value in the brown-coloured fields as they afforded better camouflage to eggs and young.

Each species responds to the pattern of the environment by a group of specific search images which are genetically determined (Tinbergen 1951). The proximate factors used by an individual are therefore based on the ancestral habitat. Lack (1933) found Ringed Plover only on gravel areas in the Brecklands although they were structurally suited to occupying areas of short grass. In this way, the response to certain proximate factors can sometimes restrict a species' distribution. Although such responses are inherited they can be modified by site tenacity (Thorpe 1945), experience (Svardson 1958) or imprinting (Klopfer 1963, Wecker 1963), all of which can in some instances lead to the occupation of new habitats. On returning to the breeding area, if environmental changes have occurred, the site tenacity of individuals may still cause the birds to settle and so occupy a new habitat. If such changes are not selectively disadvantageous, newly-hatched chicks may imprint onto the "new" habitat and so perpetuate its use. This has been suggested to explain the change in habitat of the Curlew from nesting on bogs to becoming an inhabitant of pasture and arable land (Peitzmeier 1952).

For any avian species, a breeding area must fulfil two purposes. It must provide an area in which adults can survive and contain suitable nest sites. Thus, there may be two stages in the selection of a breeding site. Elliott (1975) considered these to be:

1) selection of factors characteristic of the general habitat to which the species is adapted.
2) selection of the exact nest site.

Hildén (1965) further sub-divided the first stage so that some proximate factors may be sufficient to initiate a settling response thereby allowing birds to explore a variety of sites. When more than one suitable area is available the bird chooses the one which exceeds the threshold for the release of the settling reaction by the broadest margin. For some species, such as hole- or cliff-nesting birds, the nest site requirements are so exacting that general habitat requirements are of secondary importance and the settling reaction may not be released unless a suitable nest is present. By contrast, in wading birds selection of the general habitat is of more importance and nest sites are apparently chosen "casually" (Landsborough-Thompson 1964). For waders, whose nest site requirements are not exacting, in choosing a suitable generalized breeding area nest sites (e.g. grass tussocks, patches of easily friable ground in which to make a scrape) will almost invariably be present. However, Elliott (1975) and Rankin (1979) have demonstrated that the siting of wader nests is not an entirely fortuitous process.

Elliott (1975) developed a model to describe the mechanism for nest site selection. This is reproduced here, with some modifications, to describe the selection of a breeding area.

$$\sum_i a_i . y_i > b_k . K$$

Where, for a given species:

y_i is the i^{th} relevant factor relevant to the habitat selection mechanism,

a_i is a measure of the relative importance of the i^{th} proximate factor,

K is the level of accumulated stimuli required for the settling reaction

b_k is a factor which modifies the threshold required for the settling reaction, and is dependent on the internal motivation of the k^{th} individual.

The model incorporates a summation of stimuli and states that when that summation exceeds some threshold level the settling reaction will occur. This is in keeping with the mechanism of habitat selection outlined by Hildén (1965). Sometimes one key stimulus may outweigh all others and in its absence other stimuli are never sufficient to induce the bird to settle. There is, therefore, a weighting system for each factor. The innate releasing mechanism is responsive to "a combination of only very few environmental stimuli" (Tinbergen 1948) and, of these, even fewer are essential. Also, since the threshold of response depends on the motivation of the bird at a given time, the number of proximate factors necessary to cause the settling response may be diminished if the internal motivation is sufficiently high. Thus, different proximate factors may sometimes be used by members of the same species. At the species-level, each species may be expected to respond to their own characteristic set of proximate factors as different species are adapted to different habitats.

The principal aim of this study was to determine the factors involved in the selection of a breeding area by wading birds in part of Upper Teesdale. There have been many general surveys of wader breeding habitats such as those for the Lapwing (Nicholson 1938-9, Lister 1964, Imboden 1971), Redshank (Thomas 1942), Dunlin (Soikelli 1964), Golden Plover and Dunlin (Yalden 1974) and Oystercatcher (Heppleston 1971), and works such as the British Trust for Ornithology's Atlas of Breeding Birds (Sharrock 1976) have pinpointed the sites used by British breeding waders. However, such studies have been essentially descriptive and there have been few attempts to relate variations in distribution to the entire range of habitats available. Apart from the work of Klomp (1953) and Taylor (1974) on Lapwing habitats and the assessment of nest-site selection of various wader species breeding on saltmarsh by Elliott (1975) and Rankin (1979) there have been no detailed studies to determine the proximate and ultimate factors responsible for wader distribution.

Measures of the relative abundance of the various wader species in different habitats in Upper Teesdale between 1978 and 1980 were used to give a preliminary index of habitat preferences. Multivariate analyses were then performed to evaluate the extent to which specific variables may have influenced the distributions of the waders. These analyses produced equations analagous to the weighting and summation of various factors which are necessary to elicit the settling reaction as proposed by Hildén (1965). Understanding the relative importance of factors which influence the selection process is potentially of value in the management and conservation of breeding habitats. By favourably manipulating the relevant factors, the abundance of selected species could in some cases be increased, and sub-optimal habitats may be made more acceptable.

SECTION 1

THE STUDY AREA

Upper Teesdale (54^{o} 40'N, 2^{o}20'W) lies in the highest part of the northern Pennines. The study area, 105km^2, is in the centre of a large, relatively undisturbed area, a roadless rectangle averaging 14.5km wide and 30km long. Geologically this is part of a fault-bounded structural unit, the Alston Block. The lower Silurian and Ordovician strata are overlain by a series of alternating beds of Carboniferous limestone, sandstone and shale which now dominate the surface geology. Also outcropping is a dolerite intrusion known as the Whin Sill. Where this occurs on the Upper Teesdale N.N.R. it has metamorphosed part of the limestone strata and it is here that the rare sugar limestone and its associated flora is found.

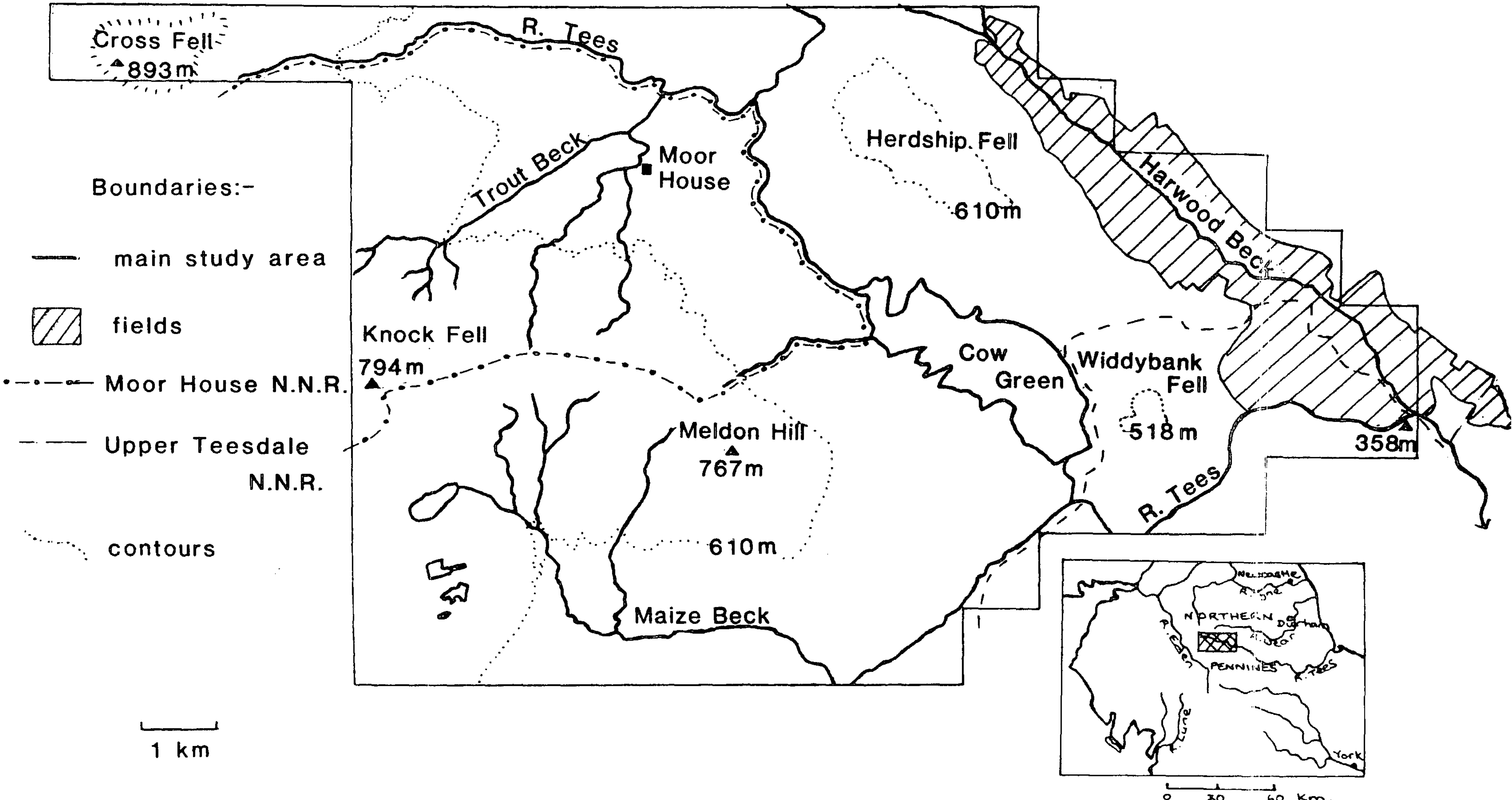
The study area is delimited by natural features - the River Tees lies to the north and Maize Beck to the south, whilst the east and west boundaries are the Harwood Beck valley and the summit ridge of the Pennines between Cross Fell and High Cup Nick (see Map, Fig. 1).

The area provides an altitudinal range of over 500m, descending from 893m on the summit of Cross Fell, the highest part of the Pennines, down a gentle dip slope to 358m in the south of the Harwood Beck valley. The western half has been dissected into east-west trending ridges by small, shallow, rapidly flowing streams of the Tees catchment. This then falls gently to the Cow Green basin before rising to the main ridge in the east, Herdship Fell (Fig. 1).

For such a remote and sparsely populated area Upper Teesdale is exceptional in having had three meteorological stations maintained for a number of years (Pigott 1978). Manley (1936, 1942 and 1943)

<u>Figure 1</u>

The study area in Upper Teesdale.


Cross Fell
893m
R. Tees
Trout Beck
Moor House
Herdship Fell
610m
Harwood Beck
Boundaries:-
main study area
fields
Moor House N.N.R.
Upper Teesdale N.N.R.
contours
Knock Fell
794m
Cow Green
Widdybank Fell
518m
358m
Meldon Hill
767m
610m
R. Tees
Maize Beck
1 km
Newcastle
R. Tyne
NORTHERN
Durham
R. Wear
R. Eden
PENNINES
R. Tees
R. Lune
York
0 30 60 Km

started records at Moor House (556m) and Dun Fell (847m) (see Fig. 1), the sites having supplied records to the Meteorological Office since 1952 (when the area around Moor House was declared a National Nature Reserve) and 1963 respectively. In 1968, on the Upper Teesdale N.N.R. (Fig. 1), an additional station was set up at 510m on Widdybank Fell.

The climate of Moor House is cool, wet and windy; oceanic and subarctic rather than temperate and has been likened to that at sea level in southern Iceland (Manley 1936 and 1943). The summers are cool and wet and the monthly mean temperature exceeds 10^{o}C in July and August only. Rainfall is about 1900mm yr^{-1} falling irregularly but with late autumn usually being the wettest period. Ground frosts may occur in every month and snow often lies on part of Cross Fell (893m) until the middle of May or early June. The tendency for cloud to form over Teesdale is a marked feature of the climate and causes a reduction in the amount of solar radiation reaching the ground (Pigott 1978a).

The adiabatic lapse rate for mean temperatures in this part of England is about 0.67^{o}C per 100m increase in altitude (Manley 1943, Pigott 1978a, Harding 1979). Therefore, between the highest and lowest altitudes of the study area an average temperature difference of about 3.6^{o}C would be expected which is about 71% of the mean annual temperature (this being 5.1^{o}C for Moor House (Heal, Jones and Whittaker 1975)). Accompanying the altitudinal decline in temperature is a decrease in the length of the growing season by over two weeks for every 100m increase in altitude, the growth period being based on the length of time that mean temperatures exceed 5.5^{o}C. In Teesdale the growing season at 450m (a representative altitude for much of the pasture in the Harwood Beck valley) is from 18 April to 23 October while at 670m (on the fell tops) it is from 4 May to 16 October (Manley 1952).

Detailed accounts of the geology and a soil map have been produced for the Moor House N.N.R. (Johnson and Dunham 1963, Hornung 1969). The geology of the whole of Upper Teesdale is reviewed by Johnson (1978). Blanket peat, usually more than 1m deep, covers more than 50% of the study area, an underlying layer of boulder clay giving impeded drainage. As the depth of blanket peat increases it becomes more unstable and erosion occurs. On the western plateau-like area this has caused the formation of peat hags which now cover c. 10-15% of the blanket bog. In the absence of peat,soil type is dependent on the presence of glacial drift and its thickness, the underlying bedrock influencing the soils wherever drift is thin or absent. On the limestone exposures as drift increases in thickness soils vary from rendzinas and brown calcareous soils where the drift covering is less than 30cm deep, to acid brown earths (drift 30-60cm deep) and peaty gleyed podzols or peaty gleys where drift is greater than 60cm deep (Bradshaw and Jones 1976). Around the larger streams strips of alluvium have developed.

The altitudinal gradient and range of soil types provides for a varied flora. Along the eastern edge of the area, up the Harwood Beck valley, is a strip of marginal hill pasture. Here some 200 fields have been enclosed, about half having been managed as hay meadows for at least the last 125 years and some probably two to three times longer than this (Roberts 1978). There is no arable land, the remaining fields being grazed by cattle and sheep. The size of the fields, the majority of which are walled, varies from under 0.5ha to over 60ha although around 50% have areas of 1-10ha. Both organic and inorganic fertilizers are applied, usually on a yearly basis, to the hay meadows, while a few of the better pastures receive only occasional treatments and others none at all. There has been little or no use of herbicides.

The meadow grades into rough pasture and then open moorlands which are sheep grazed and usually managed as grouse moor, although in parts burning has been sporadic.

Calluneto - Eriophoretum (McVean and Ratcliffe 1962) is the characteristic and dominant plant community of the acid, waterlogged peat and covers most of the western half of the study area. In places it is replaced by increasing proportions of *Eriophorum vaginatum* (see section on vegetation).

Areas of uninterrupted bog are usually less than 10ha and are separated by streams, erosion channels, grassland areas, flushes or man-made features such as spoil heaps and footpaths. The grassland areas at higher altitudes are composed of relatively species-rich Agrosto-Festucetum, Nardetum sub-alpinum and Juncetum squarrosi sub-alpinum.

Apart from the strip of lowland pasture in the east, most of the study area is close to or above the treeline (550m) and is one of the most isolated parts of England. For centuries the breeding birds in this area have been relatively free of human disturbance. However, there is evidence that man colonized the region from the late Mesolithic period, about 3000 B.C. onwards. Sheep farming was introduced and later mining. Mining for lead, barytes and zinc was once extensive, the peak of mineral production being the 1850s and 60s, also a period of peak population. This dwindled along with the population at the end of the nineteenth century due to difficulty in working the mines and the importation of cheap, easily won foreign ores, and finally ceased altogether in 1947. Spoil heaps from shafts or underground levels dug in search of ore remain in many places. There are also areas of gravel or silt polluted by heavy metals from the crushing and washing of ore.

The amount of pollution from lead and other heavy metals has much influence on the flora of some of the spoil heaps, but for the most part the vegetation is a fragmentary Agrosto Festucetum (Eddy, Welch and Rawes 1968).

Today virtually the only human settlement is along the eastern strip in the Harwood Beck valley, an area probably first settled around 1100 A.D. (Roberts 1978).

THE VEGETATION

Upper Teesdale has become famous for the peculiarity and richness of its flora. Some species of the flora are not known elsewhere in the British Isles (e.g. *Minuartia stricta*) and several are arctic-alpine or alpine (e.g. *Bartsia alpina, Gentiana verna, Myosotis alpestris)*. However, interesting though the rarities and atypical members of the flora area, it is the dominant members of the plant communities that are most likely to influence the distribution of the avifauna.

On both the National Nature Reserves within the study area major phytosociological studies have been undertaken. The Moor House N.N.R. was originally chosen as a representative expanse of typical Pennine Calluneto-Eriophoretum blanket mire. It also has a wide range of acidic and basic grasslands typical of northern England. A detailed vegetation map of the area was produced by Eddy, Welch and Rawes (1968).

The Upper Teesdale N.N.R. is internationally important for its arctic alpine plant refugium and the unusual habitats of the sugar limestone outcrops, the open calcareous flushes and the unstable river banks. The construction of the Cow Green reservoir, completed in autumn 1970, was a stimulus to further research in the area and phytosociological work began on the south-eastern shores of the reservoir and on Widdybank Fell. For detailed vegetation maps of the area see Bradshaw and Jones (1976).

Some of the principal factors influencing the dispersion of waders across the study area are associated with vegetation type and structure. An appreciation of which plant communities are available is therefore central to understanding the distribution of the birds. Table 1 summarizes the characteristics of the most common vegetation types. (For vegetation see Bradshaw and Clark (1965), Bradshaw and Jones (1976), Eddy, Welch and Rawes (1968), Jones (1973), Pigott (1956) and Ratcliffe (1978); for soil types see Hornung (1969), Johnson and Dunham (1963) and Johnson (1978) and Pigott (1978b)). Calluneto-Eriophoretum is the most commonly occurring plant community on the study area. On flat areas with deeper peat and many pools it becomes replaced by Trichophoro-Eriophoretum. This, however, has little extent, being confined to small localized areas with a high water table.

Within any of the vegetation types associated with peat, areas of erosion can be found. In places this has led to the formation of peat hags. Other species are then able to invade the bare peat, underlying drift or bedrock. Thus the recolonizing vegetation of the eroding bog is usually more species rich. Total vegetation cover is lower than for the other plant associations.

A number of grassland communities are interspersed with the blanket bog thus forming a vegetational mosaic. Sometimes these are only small patches but nevertheless they can sustain an alternative, and often rich, invertebrate food supply for the breeding birds.

Table 1 Characteristics of the main vegetation types occurring on the study area

VEGETATION TYPE	DOMINANT SPECIES	SOIL TYPE	STRUCTURE	LOCATION
1. Calluneto-Erophoretum	*Calluna vulgaris* *Eriophorum vaginatum*	Peat	Mature community - *Calluna* bushes 30-40cm tall alternating with tussocks of *Eriophorum*. Beneath is an almost complete moss carpet, usually *Sphagnum rubellum*.	Predominates on the blanket bog. Usually on sloping ground; few pools; peat layer c. 2m deep.
2. Eriophoretum	*Eriophorum vaginatum*	Peat	Tussocks. Increase in amount of *Festuca ovina* and *Deschampsia flexuosa* where grazed. Sometimes with *Juncus squarrosus*.	Can occur at higher altitudes than 1. as *Calluna* is adversely affected by frosts
3. Nardetum sub-alpinum	*Nardus stricta*	Alluvium, drift soils	Tussocks. *Juncus squarrosus* sometimes co-dominant. *Agrostis tenuis* and *Anthoxanthum odoratum* usually have good cover.	Occurs on e.g. alluvial terraces of larger streams, central ridge Moor House N.N.R., parts of Herdship Fell.
4. Festucetum	*Festuca ovina*	Mineral soils - base deficient brown earths, brown podsols to iron-humus podsols, podsol rankers	Even closely grazed turf; often springy due to thick ground layer of mosses. Less herb rich than 5. - *Gallium saxatile* the only dicotyledon to approach constancy.	Sandstone outcrops.
5. Agrosto-Festucetum	*Agrostis tenuis* *Festuca ovina*	Mineral soils - brown earths, rendzinas, well drained alluvium	Dry species rich grassland. Short, evenly grazed turf. Moss layer incomplete. Basiphilous herbs abundant (e.g. *Thymus drucei, Trifolium repens, Prunella vulgaris)*.	At all altitudes where soil conditions suitable. Limestone outcrops.
6. Meadow	Variable - grasses usually having high cover are: *Festuca rubra* *Anthoxanthum odoratum* *Holcus lanatus* *Agrostis stolonifera* *Cynosurus cristatus*	Mineral soils	Widely varying vegetation heights depending on grazing regime. Hay meadows ungrazed in summer. Species rich; herbs have high cover in relation to grasses. Characteristically has *Troleus europeus, Geranium sylvaticum* and *Cirsium heterophyllum*.	Almost entirely in the Harwood Beck valley in some of the enclosd fields and part of the river banks.

Agrosto-Festucetum can grade into Festucetum, Nardetum sub-alpinum or species-poor Juncetum squarrosi sub-alpinum. The latter is a community having tufts of *Festuca ovina* and *Deschampsia flexuosa* between rosettes of *Juncus squarrosus*. It has less extent than any of the vegetation types in Table 1 but occurs on the central ridge of the Moor House N.N.R. and on some alluvial terraces. Grassland dominated by *Molinia caerulea* occurs locally but is not extensive.

The upland grassland areas are selectively grazed by sheep and support higher densities than the blanket bog (Table 2). On blanket bog grazing intensity decreases as the proportion of heather increases. Grazing not only affects vegetation height but, in the long term, may also modify the vegetation type which in turn may have repercussions on wader distribution. The deposition of dung on these areas is of importance as it enhances the food value to the birds due to the attraction of dung associated fauna.

Table 2. Grazing intensity of sheep on moorland (Data from Moor House N.N.R.).

Vegetation type	No. of sheep per ha	
Blanket bog	0.02 - 0.6	Welch and Rawes 1966
Nardus grassland	c.2 - 3	Rawes and Welch 1964
Festucetum	2 - 4	Welch and Rawes 1964
Agrosto-Festucetum	3 - 13	Rawes and Welch 1966
Juncus squarrosus grassland	1 - 2	Rawes and Welch 1966, Eddy, Welch and Rawes 1968

In earlier periods of post-glacial history a large proportion of drier ground below 600m probably carried trees or small shrubs which have subsequently been denuded during the main phase of deforestation.

Adequate regional evidence for this is provided in the pollen record (Raistrick and Blackburn 1932, Turner *et al.* 1973). The woodland is now replaced by the enclosed pastures of the hill farms and a grassland/heather moor complex on the fells. The eastern strip of the study area, now covered by lowland pasture, has a variety of field types ranging from the herb-rich hay meadows to the species poor rough pasture. The hay meadows even today reflect the presence of the once extensive woodland, typical woodland species such as the wood anemone (*Anemone nemorosa*) and woodland cranesbill (*Geranium sylvaticum*) contributing to the species diversity (Bradshaw and Clark 1965). The grazed meadows are less species rich but still have a high proportion of broad leaved grasses. Some are poorly drained and have varying amounts of *Juncus effusus*. Many of these are cattle grazed whilst the poorer, rough pastures where broad-leaved grasses are less prevalent are almost exclusively sheep grazed.

There are a few trees scattered up the Harwood Beck valley and there is a small conifer plantation at Langdon Beck. Several smaller plantations have been made on the Moor House N.N.R. Woodland alongside the riverbanks does not occur until as far south as High Force.

THE INVERTEBRATES

The majority of invertebrates are usually connected in some way to the type of vegetation a particular area supports, either because they directly feed on the plants, or because they are predators of plant feeders. The extremes of wetness, pH, mineral content and vegetation on the mosaic of peat and mineral soils found on the study area provide two distinct habitats. Table 3 summarizes the faunal characteristics of these sites. Table 4 summarizes the differences between the main invertebrate groups on peat and mineral soils.

Upper Teesdale is at a boundary of two faunal types which here exist side by side but show little overlap. The sub-arctic or alpine fauna of the peat areas has a different spectrum of species to the mineral sites which are characterized by species with a mainly central European distribution. Only 47% of the total number of species are common to both habitats (Coulson and Butterfield pers. comm.).

In general the fauna of the enclosed pasture in the Harwood Beck valley is similar to that of the upland grasslands but with a slightly increased species diversity, especially in the hay meadows. The patterns of seasonal abundance of invertebrates are also similar for these areas. The invertebrates of the lowland pasture area are discussed more fully in Section 3 where the results of pitfall trapping and soil sampling are also presented.

The most important prey species available to the birds are likely to be, due to their abundance, size and biomass, Coleoptera, Araneae, some species of Diptera and Lumbricidae. Opiliones can almost certainly be excluded from the diet of waders due to their life cycle. Overwintering eggs hatch to first instar larvae in May but appreciable biomass is not attained until the fourth or fifth instar is reached in late July/August.

Dung associated fauna may also be an important additional food supply for breeding waders. Sheep graze most of the moorland area from April to November whilst the marginal hill pasture is cattle grazed from spring to autumn and sheep grazed in the spring and winter. Lapwing, both adults and chicks, were frequently observed probing cowpats. Sheep selectively graze the upland grassland patches but pass through areas of blanket bog and so even here dung is

Table 3. Faunal characteristics of peat and mineral soils within the study area.

	PEAT	MINERAL
Faunal type	Most groups so far examined exhibit a typically northern, sub-arctic or alpine fauna. Strong affinities with fauna of northern Scandinavia.	Characterized by species with a mainly central European distribution which also occur on lowland sites in Britain.
Biological activity (Cragg 1961)	On the basis of % organic content biologically less active than mineral sites.	More biologically active than peat.
Seasonal availability (Nelson 1971, Coulson and Whittaker 1978)	Peak abundance in mid May to June when more than 80% of the yearly total biomass is available. Peak mainly due to *Tipula subnodicornis* and *Molophilus ater*.	Period of abundance 3x longer than that on peat - mid May to mid August with a fairly high level up to end of October. Peak biomass only c. $^{1}/_{10}$ that of the peak on peat but this is spread more evenly therefore total biomass is higher. A succession of different invertebrates available.
Invertebrate abundance (Coulson and Butterfield pers. comm)	Mean standing crop, maximum 7g dw m^{-2}. Fewer species than on mineral soils. Fewer individuals than on mineral soils.	Mean standing crop, average 45g dw m^{-2} 1.12 x more species than on peat. 1.41 x more individuals than on peat.

Table 4. A comparison of the invertebrates on peat and mineral soils.

	PEAT	MINERAL
Coleoptera (Coulson and Butterfield pers. comm.)	Carabidae have a summer peak of activity of adults (mainly due to *Carabus* sp.). Biomass - high in spring, low in autumn, higher than on mineral soils	Fairly constant biomass throughout season. Greater variety of species but lower biomass than on peat.
Araneae (Cherrett 1961)	Only $^{71}/_{580}$ British species recorded at Moor House. No. per m^2 on *Calluna/Eriophorum* 133-155	*Juncus squarrosus* grassland 213-470 per m^2 Limestone grassland (grazed) 29- 77 per m^2 but Duffey (1962) on other limestone grassland areas found densities up to 841.9m^2. Pitfall traps on lowland pasture (this study) showed Lycosidae predominated on wetter sites, Linyphiidae more prevalent on drier areas.
Opiliones	*Mitopus morio* largest and most common species. Peak biomass summer and autumn is 10-30x greater than on mineral soils (Coulson and Butterfield pers. comm.)	In general smaller species of lower biomass (e.g. *Oligolophus agrestis* and *Oligolophus palpinalis*). Pitfall traps on the lowland pasture yielded very low numbers.
Diptera	Tipulidae have largest biomass - peak emergence late May/early June due to *Tipula subnodicornis, Trichyphona immaculata* and *Molophilus ater* (Coulson 1959). Empididae are second most important biomass contributor - spring peak, progressive decrease to autumn (Coulson and Butterfield pers. comm.)	Tipulidae less abundant on alluvial sites - 3 smaller peaks, *Tipula varipennis* (late May/early June), *Tipula paludosa* (July and August), *Tipula pagana* (October) (Coulson 1959). *Tipula paludosa* is the predominant Tipulid on lowland pasture (this study). Here Dipterans were mainly small acalypterate flies and the yellow dungfly (*Scathophaga stercoraria*).
Lumbricidae	Virtually none. *Calluna* 0.1 - 0.5 per m^2 *Eriophorum* 0.01 per m^2 (Svendsen 1955)	$^{14}/_{27}$ British species at Moor House (Svendsen 1957). Density sometimes exceeds that of lowland areas (80-400 per m^2) although the majority of estimates lie within this range.

deposited although in much smaller amounts. Cragg (1961) estimated that the number of sheep and amount of dung deposited on mixed moor, *Juncus squarrosus* moor and limestone grassland was 1:4:6. On the virtually ungrazed hayfields of the lowland pasture there may still be a rich dung associated fauna due to the spreading of dung as organic fertilizer.

Succession of fauna on sheep dung has been described by, for example, Olechowicz (1974) and Pisolkar (1980). Cordilurinae and Muscidae flies visit the dung and so wading birds may be able to capture both the visiting adults and their larvae which develop in the dung. Also available to the birds are the adults and larvae of dung beetles (*Aphodius* species), Hydrophilid and Staphylinid beetles and some lumbricid worms. Olechowicz (1974) has estimated that around $15g/m^2$ of animal biomass (33% being due to dipteran larvae) is produced by sheep dung on upland pasture.

Mohr (1943) has recorded a similar succession of invertebrates in cattle droppings. As far as productivity is concerned Papp (1971) reared a dry fly mass of, on average, 0.5% of the dung dry weight, the total weight of flies developing occasionally exceeding 2%. These results are similar to those of Laurence (1954) who estimated that 1/80 of the dung weight was equivalent to the developing larval mass and that each pat contained on average 1000 individuals. Thus dung provides a localized but easily detectable, readily obtainable and abundant invertebrate food supply.

In Upper Teesdale breeding waders have, therefore, two main types of feeding area available to them. The blanket bog has a well defined community of invertebrates, is species-poor, being particularly deficient in lumbricids, but with a rich dipteran element.

Enchytraeidae, which are too small to be of use to the birds, are a major contributor to the biomass. Nevertheless, there is an abundance of Tipulidae. *Tipula subnodicornis* is the dominant high moorland form and this is likely to be the main prey available to the breeding waders. Coulson (1962) found that the highest densities of final instar larvae occurred on *Juncus squarrosus* moor (170 per m^2). *Eriophorum* moor was almost as productive (70-100 per m^2) whilst *Sphagnum* bog had much lower densities (14-36 per m^2) but a more stable population.

The mineral soils have a higher biomass than the peat, Lumbricidae being the main contributor. Of further advantage to the birds is that due to the typically wet summers in upland areas earthworms do not usually aestivate. There is, therefore, an abundance of food available from May to October, a spring flush on the peat in May and June being followed by a high, sustained level of invertebrates on the mineral soils in summer and autumn.

SECTION 2

WADERS OF MOORLAND AND MARGINAL HILL FARMLAND

The habitats used by British breeding waders have been described in broad terms by many authors but relatively little quantitative information exists, particularly for upland areas. It is necessary to compare the relative frequency of occurrence of a species with the availability of the whole range of habitat variables in a given location to demonstrate whether certain habitats are more favoured than others and selection is occurring. Most studies relate only to apparent preferences since few take into account the relative availability of different habitats. Exceptions to this are the work of Taylor (1974), Yalden (1974), Wilson (1978) and Fuller (1981) but only Taylor in her study of Lapwings breeding on marginal hill pasture assessed the impact of a wide variety of habitat variables.

The study area in Upper Teesdale provided a variety of habitats over a range of altitudes from 358m to 893m. The distribution of the diverse wader population could therefore be examined with respect to certain geographical and biotic factors. Of the wader species breeding in Teesdale, six occurred in sufficiently large numbers to make statistical analysis of their distributions possible. A further three species, Common Sandpiper, Oystercatche and Ringed Plover, were restricted to the river systems and the margins of large bodies of standing water and are considered separately in Section 4. In this section the distributions of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin are examined in relation to vegetation and altitude. Overlap between the species is also considered and the importance of a variety of habitat variables in determining the distribution of the waders is assessed using multivariate techniques.

Multivariate procedures aid in identifying relationships between a dependent variable and an array of predictor variables and are especially useful in elucidating the relative importance of intercorrelated habitat variables as predictors. However, due to certain limitations the techniques must be used with caution (see e.g. Richardson 1974).

Discriminant analysis has been used to differentiate species distributions (e.g. Green 1971, Bertin 1977, Gochfield 1978). It has also been used to compare sites at which a structure is present or absent; Rankin (1979) compared nest-sites with non-nest (random) samples for several wader species breeding on a saltmarsh. Similarly, Riechert (1976) delineated for certain orb-weaving spiders the factors which controlled web-site selection.

Multiple regression analysis has also been a useful interpretive tool in many studies. It has been used to determine factors controlling the abundance and size of prey in spider webs (Brown 1981), the effect of nesting density in the Kittiwake on hatching date and hatching success (Dixon 1979), variation in the growth rates of tern chicks (Dunn 1972) and in forecasting daily variations in the amount of bird migration (Richardson 1974

In the present study, discriminant function analysis has been used to assess differences between areas in which waders were found from those in which they were absent, and stepwise multiple regression was used to investigate factors influencing their breeding densities.

Methods

In 1978 an area of 105 km^2 in part of Upper Teesdale (Fig. 1) was surveyed to examine the distribution and abundance of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin in relation to various habitat characteristics. A square with 1 km sides, based on the National Grid, was taken as the standard sample unit (subsequently referred to as km square).

i) Counts of birds

Each km square within the study area (on Ordnance Survey Sheet 91) was visited between the third week in April and the middle of June. Earlier visits would probably have resulted in low counts of birds, the vagaries of the weather early in the season often causing delay in the final settlement of the birds' territories. Counts late in the breeding season are undesirable and some pairs may have moved their broods considerable distances from the nest site; also failed and early breeders may have formed post-breeding flocks or left the area altogether. Thus counts were commenced when the pre-breeding flocks (Lapwing, Golden Plover and to a lesser extent Curlew and occasionally Dunlin) had broken up on the lower pasture area in the east of the study area and preliminary visits to the higher altitudes showed the birds to be well distributed on the fells and actively displaying. Counts were restricted to April and early May, when the birds were displaying, and late May/early June when many of the waders had newly hatched young and were vociferous and easy to locate. Counts were not made during the incubation period when all species, except Lapwing, became more secretive and were less easy to detect.

Waders cannot be adequately censused by the "mapping method" (IBC Committee 1969). Delimiting territories and nest finding was impossible over such a large scale, therefore a compromise was used. Estimates of the number of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin were made by walking a transect across the centre of each km square, the positions of all waders seen or heard being noted. Svensson (1978) recommended that in an open habitat at least four visits were necessary to achieve 90% overall census efficiency. However, due to the size of the area, difficulties in reaching the upper fells, the shortness of the season, particularly in view of the optimum times to count the birds, and the number of days of rain, thick mist or strong winds which made census work unreliable, this was not possible. It was considered that one "well-timed" visit was likely to yield more applicable data than a mean count of several visits if some of these would have to be made at less optimum times for counting certain species or under poor weather conditions. (Snipe, for example, drum less frequently in wind, rain or dense fog (Tuck 1972)). Moreover, since the study was essentially comparative, absolute population estimates were not necessary. Each km square was therefore censused once and the adequacy of the counts was assessed by making a repeat visit to 36km squares. A comparison of the first and second counts for these squares showed that the species differences between visits were not significantly different (paired 't' test, t = 0.86, d.f. = 35, n.s.; mean difference in species between the first and second counts = -0.083 ± 0.10). Also the number of individuals detected did not significantly differ between visits (paired 't' test, t = 0.83, d.f. = 35, n.s.; mean difference in the number of individuals between the first and second counts = -0.25 ± 0.30). Of the total number of species and individuals recorded in each km square the efficiency of any one visit was 80.1 ± 4.1% for the number of species and 75.1 ± 4.2% for the number of individuals. Therefore one count was considered acceptable for the purposes of the present study. The numbers of waders should, however, be regarded as representative estimates of the breeding population rather than absolute numbers.

A necessary assumption of the census technique is that there is an equal probability of detecting all species. In practice this is unlikely to be true as some species are more difficult to census than others. Numbers of Snipe recorded were probably underestimated as birds some distance from the transect line would not have been flushed. Similarly numbers of Dunlin may be underestimates, particularly on the fell tops where the frequently windy conditions make their calls difficult to detect. The fact that the majority of the counts were made either early in the season when adult birds were displaying, or later on, as young were hatching, should have minimised these problems. Also, the exposed nature of upland sites makes the detection of individual birds far more likely, and over greater distances, than in a less open habitat such as woodland. The openness of the terrain also makes it possible to follow the flight paths of birds when flushed, thus reducing the risk of overestimating population density.

It is further assumed that there is an equal probability of detecting each species in each km square. However, differences in terrain between the squares may be expected to cause some discrepancy. For example, a km square with many undulations may be less reliably censused than a square with more even topography.

There was little evidence of non-breeders occurring in the study area. Only one flock (10 Golden Plover, not in summer plumage) was encountered in the middle of the breeding season; these birds have been excluded from the counts.

In 1979 and 1980, 57 of the original 105 km squares were surveyed to monitor any changes in the size or distribution of the wader population.

ii) Measurement of habitat variables.

A series of variables were selected that measured habitat characteristics which were considered to be potential influences on the distribution of the waders. Measurements of these variables were made in each of the 105 km squares of the study area. Certain features of the habitat may vary within an area as large as a square kilometre.

Where such variation occurred, measurements were made according to the situation that was predominant in the area under consideration. Thus, for example, measurements of vegetation height relate to the vegetation type which had the largest extent within the km square.

The method of measuring the habitat variables which were considered of potential importance as factors controlling the distribution of the waders are summarized in Appendix 2.

iii) Analysis

In 1979 and 1980, 57 of the 105 km squares surveyed in 1978 were revisited. These squares were representative of the whole study area in terms of vegetation types and altitude. Kendall's rank correlation coefficient indicated that the proportions of vegetation types in the 1978 and 1979/80 samples (Table 5) were significantly similar ($\tau = 0.97$, $P < 0.01$). A slightly smaller range of altitude was covered in the 1979/80 sample but the proportions of km squares within 50m altitude zones were not significantly different from the distribution of altitudes throughout the entire study area (Kendall's rank correlation coefficient, $\tau = 0.56$, $P < 0.02$) (Table 6). Therefore, the distribution of species in 1979 and 1980 should be directly comparable with the distributions observed in 1978.

Table 5. The number of km squares classified as a particular vegetation type for the whole study area, 1978, and for the section surveyed in 1979 and 1980.

	Meadow	*Festuca*	*Nardus*	*Eriophorum*	*Calluna/ Eriophorum*	*Calluna*
1978 (N=105)	6	14	3	32	47	3
1979/80 (N=57)	6	9	3	13	25	1

Table 6. The number of km squares within 50m altitude zones for the whole study area, 1978, and the section surveyed in 1979 and 1980.

	Altitude range									
	350-400m	401-450m	451-500m	501-550m	551-600m	601-650m	651-700m	701-750m	751-800m	801-850m
1978 (N = 105)	3	3	13	20	23	21	11	9	0	2
1979/80 (N = 57)	3	3	12	18	10	8	1	2	0	0

There was no evidence of any significant changes in the selection patterns or distribution of the waders between years. Considering the same 57 km squares that were surveyed in all three years, the densities of each wader species were significantly correlated between years (Appendix 3). Moreover, correlation coefficients between numbers of each species and habitat variables showed that significant correlations were in most cases consistent over the three year period (Appendix 4). Therefore, for most of the analyses in this section the data on counts of waders has been combined over the three breeding seasons 1978, 1979 and 1980. For the 57km squares surveyed in each year the mean number of each species per km square was calculated to the nearest whole bird. For analyses considering the total number of species present per unit area the mean number of species per km square over the three year period was used. For the remaining 48km squares of the study area the data are based on the series of counts for 1978 only.

Multivariate analysis.

Multivariate techniques are useful in elucidating the response of one, or several, species to a range of habitat variables. The potential effects of the habitat variables (Appendix 2) on the distribution of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin were considered from two viewpoints: (a) effects on presence or absence of a species, and (b) effects on density.

(a) Presence or absence of a species.

Discriminant function analysis is suited to data of a categorical nature. It was, therefore, used to determine if km squares with a particular wader species present could be distinguished from km squares in which that species was absent i.e. that selection of a breeding area was occurring. Discriminant analysis produces an equation based on linear additive functions of the predictors which gives the best discrimination between the various categories of the dependent variable (here presence or absence of birds). The set of constants for the equation are such that the discriminant scores produced have the largest possible ratio of between categories variance to within categories variance (Richardson 1974). The analyses were performed by the SPSS Discriminant Programme (see Nie *et al.* 1975).

To distinguish between areas (km squares) with and without each wader species, the array of habitat factors described in Appendix 2 were used as discriminating variables. Any highly intercorrelated variables which had to be removed from the regression analyses (see (b)) were also removed from the discriminant analyses. The set of variables found to influence presence or absence could, therefore, be compared directly with those affecting density to see if the variables involved were the same in each case.

A stepwise method was used so that variables were selected for entry into the analysis on the basis of their discriminating power. A variable was eligible for entry only if its partial F ratio was significant ($P < 0.05$). This is a test for the statistical significance of the amount of centroid separation between groups added by a particular variable above and beyond the separation produced by variables already entered. At each step a similar test is made of all variables previously selected to see whether each variable still adds significant discriminatory power given the other variables now in the equation. Due to interrelationships between variables, it is possible that as more variables are entered, some of those selected earlier no longer contribute significantly to the group separation. Such variables were then removed from the analysis. The stepwise criterion used was Rao's V, a generalized distance measure along discriminant function axes in geometrical space. Variables were sequentially selected to maximize Rao's V (i.e. give maximum group separation) until the addition to Rao's V became insignificant or all remaining variables failed the F-test. The change in V has a chi-square distribution with 1 d.f. therefore a minimum value associated with a desired level of statistical significance is easily set.

The discriminating power of the function finally derived from the set of habitat (predictor) variables was inversely related to the value of Wilks' Lambda which the programme transformed into a chi-square statistic. The overall significance of the function was, therefore, easily assessed. The magnitude (but not the direction) of the standardized discriminant function coefficients indicated the relative contribution of each variable to the discriminant function. The unstandardized coefficients, and the constant, were incorporated into a prediction equation. The mean discriminant scores for each group along a function are the group centroids. The mid-point between the centroids for the two groups represents, therefore, the borderline discriminant score for predicting the presence or absence of the wader species under consideration. The classification routine of the programme identified each case (km square) as belonging to a particular group (species present or species absent) on the basis of its discriminant score. The percentage of cases correctly classified indicated the accuracy of the discrimination and reflected the extent to which the species concerned exhibited habitat selection as mediated by the proximate habitat factors under consideration.

(b) Density.

Factors influencing the density of each wader species (number of individuals per km square) were investigated using an SPSS Stepwise Multiple Regression Programme (see Nie *et al.* 1975). Variables important in determining the density of a particular species may, but need not necessarily, be the same as those factors which determine presence or absence. So that the effect of habitat variables on density only was considered, all km squares in which the species was not recorded were excluded from the analysis. Confounding effects of species absence were thus removed.

Multiple regression analysis fits a linear additive equation to the data. The equation can then be used to predict the dependent variable (density of a particular wader species). The reliability of predictions made by the equation is measured by the square of the multiple correlation coefficient, R^2, which indicates the percentage of the variation in density of birds accounted for by the observed relationships between density and the predictor variables. In a stepwise analysis the relative contribution of each predictor variable in accounting for the observed variation in the dependent variable (bird density) is also determined.

At each step of the analysis the variable added to the equation is the one which gives the greatest increase in R^2 i.e. makes the greatest improvement in predictive ability. Variables were allowed to enter the equation only if they made a significant improvement to its predictive capabilities (based on the 'F' value of the variable as it entered the equation being significant, $P < 0.05$) (see Nie *et al.* 1975).

A high degree of intercorrelation (multicolinearity) between independent (predictor) variables may cause problems in multiple regression analysis (see Nie *et al.* 1975). To overcome these problems the correlation matrices of habitat variables were examined and in instances of highly intercorrelated variables ($r < 0.80$) only one of the variables was used in the analysis, as recommended by Nie *et al.* (1975).

Bivariate scattergrams of each habitat variable with each wader species were checked to see if any relationships were obviously non-linear and required transformation before analysis, or that some correlations were spurious i.e. due to one particularly high or low point in the sample. Possible violations of the assumptions of linearity, normality and homoscedasticity that are made in regression analysis were checked for by examination of residuals (see e.g. Draper and Smith 1966, Nie *et al.* 1975, Bibby and Toutenburg 1977).

Results

i) General distribution of waders.

Figures 2-7 show the distribution maps for six wader species - Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin, found within the study area in 1978. Lapwing, Redshank and Snipe had almost identical distributions. The largest part of the populations of these three species occurred along the eastern strip of the study area on the enclosed lowland pasture, with only scattered pairs extending onto the moorland. By comparison, the Golden Plover population showed much wider dispersion across the study area. The pattern is the reverse of the Lapwing, Redshank and Snipe distributions, the majority of the Golden Plover breeding on the moorland away from the lower pasture area to the east.

Figures 2 - 7.

Distributions of the numbers of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin located in each 1km square within the study area in 1978.

Lapwing

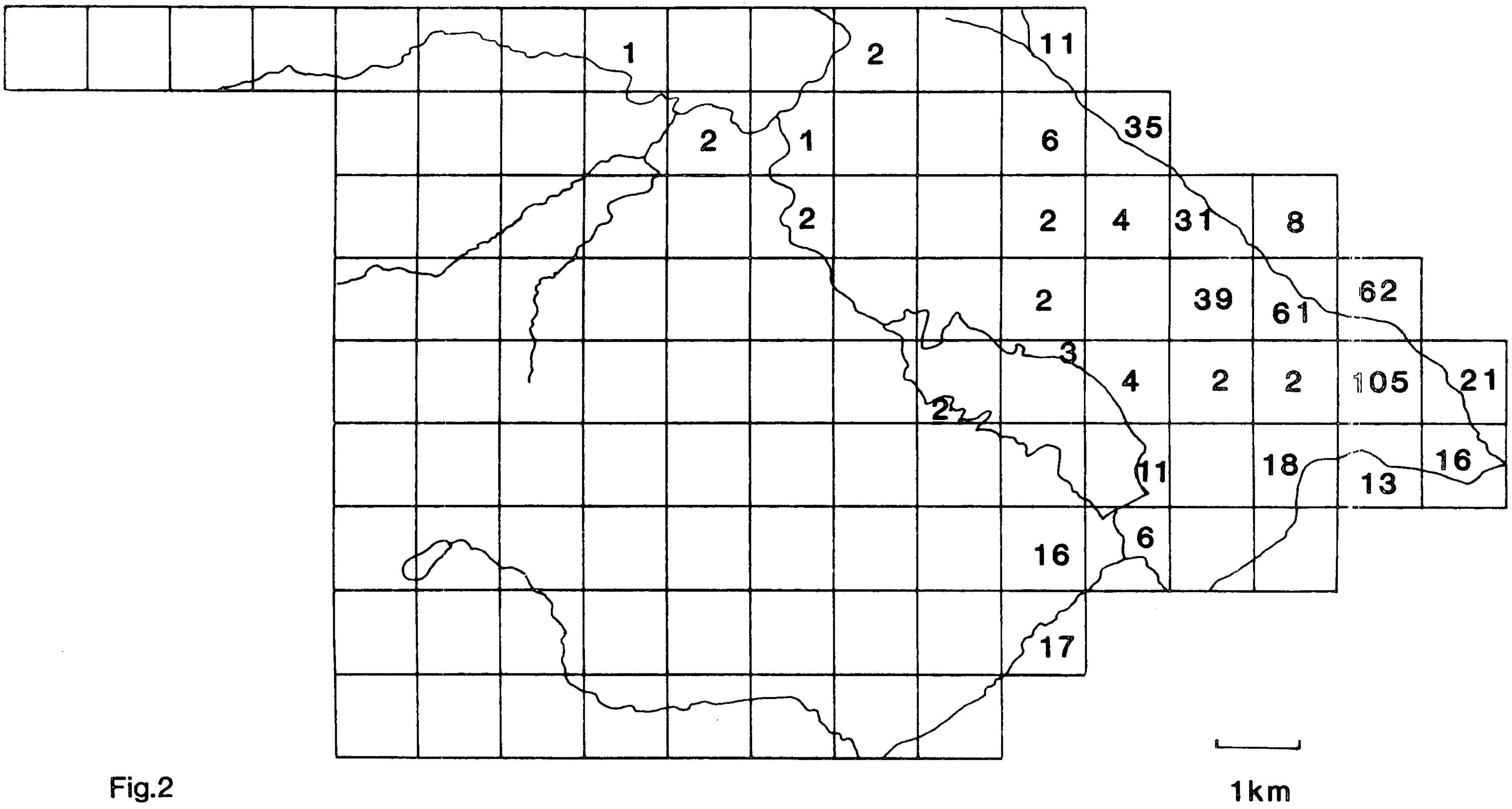


Fig.2

Redshank

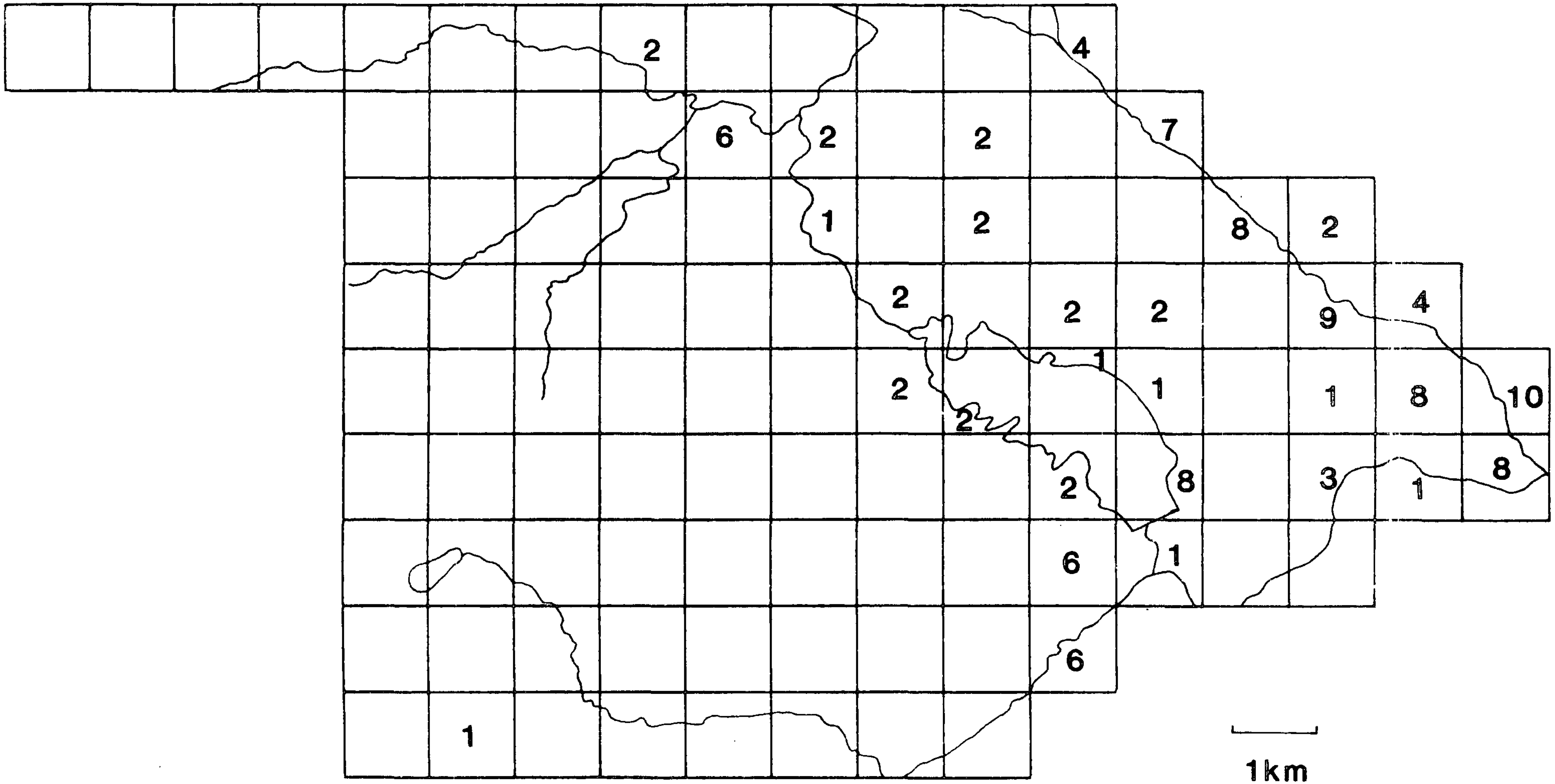


Fig.3

Snipe

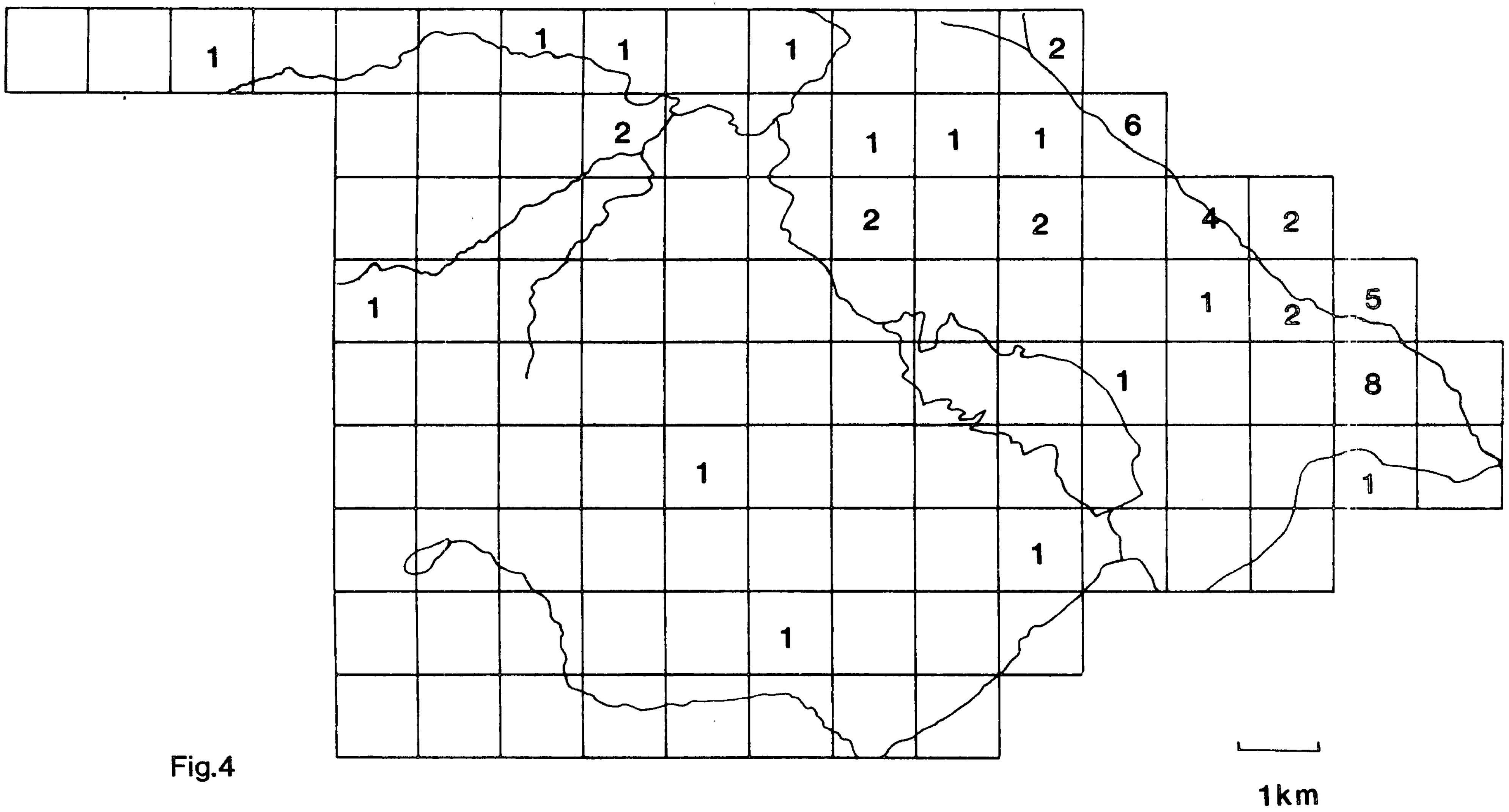


Fig.4

Curlew

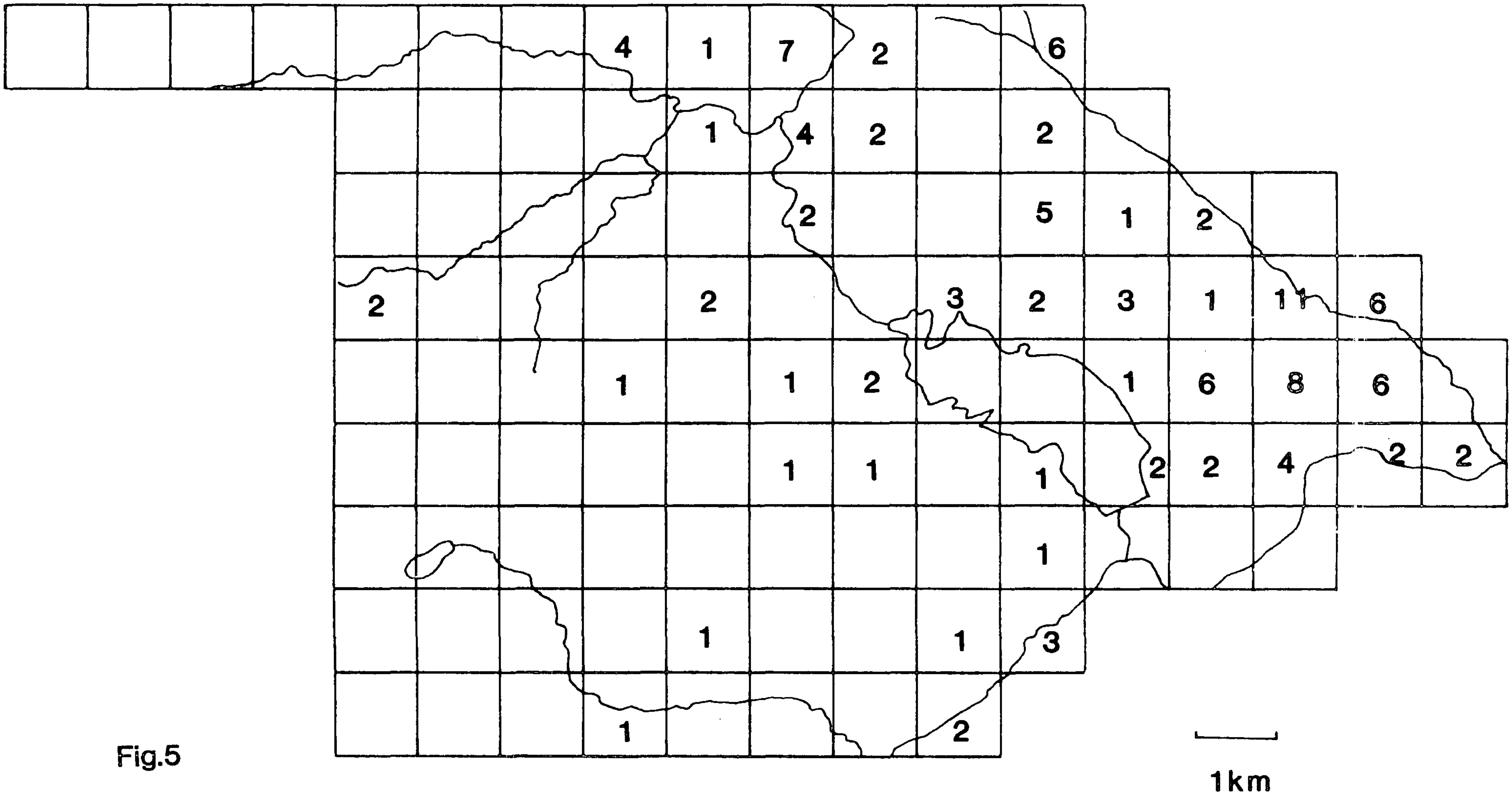


Fig.5

Golden Plover

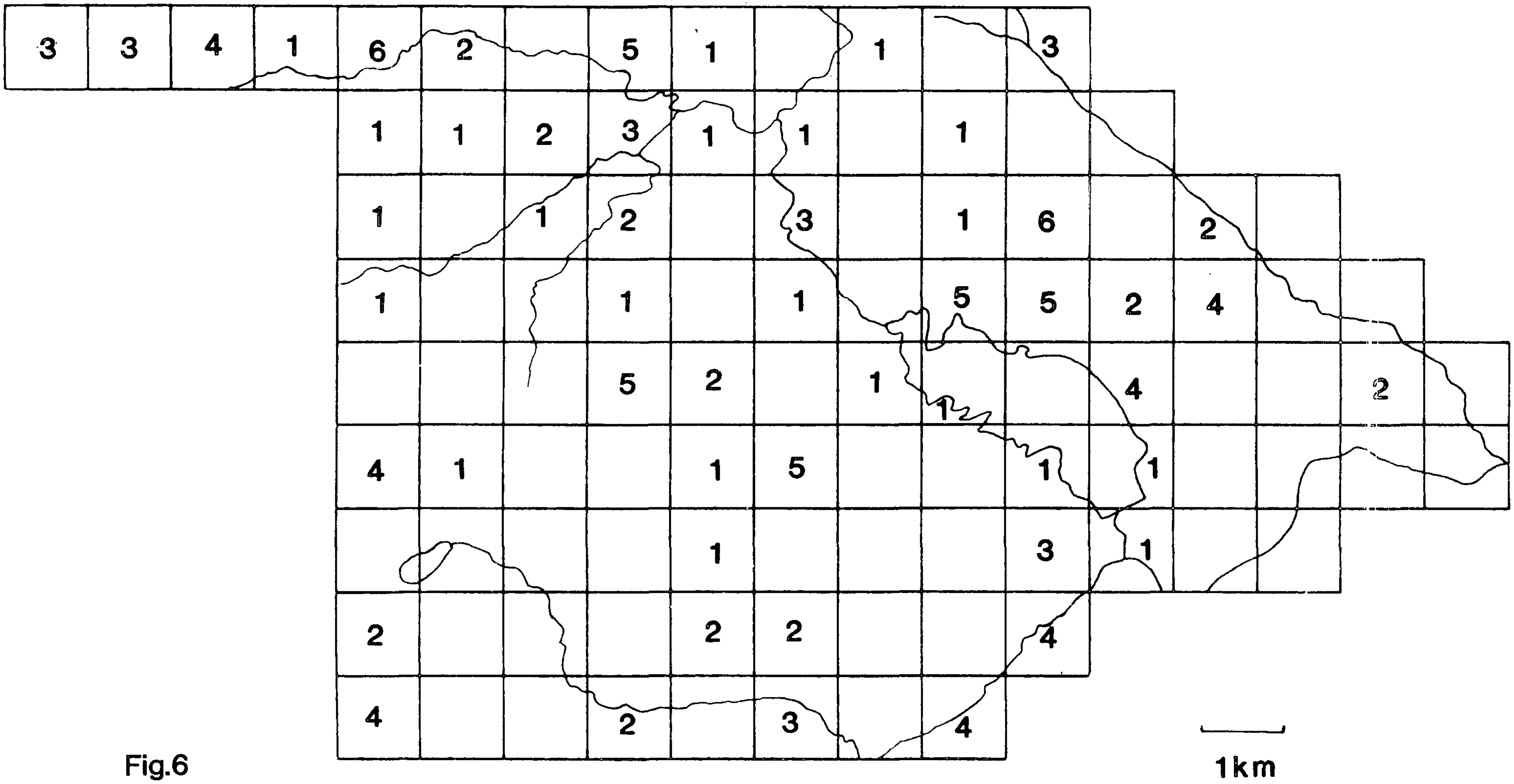


Fig.6

Dunlin

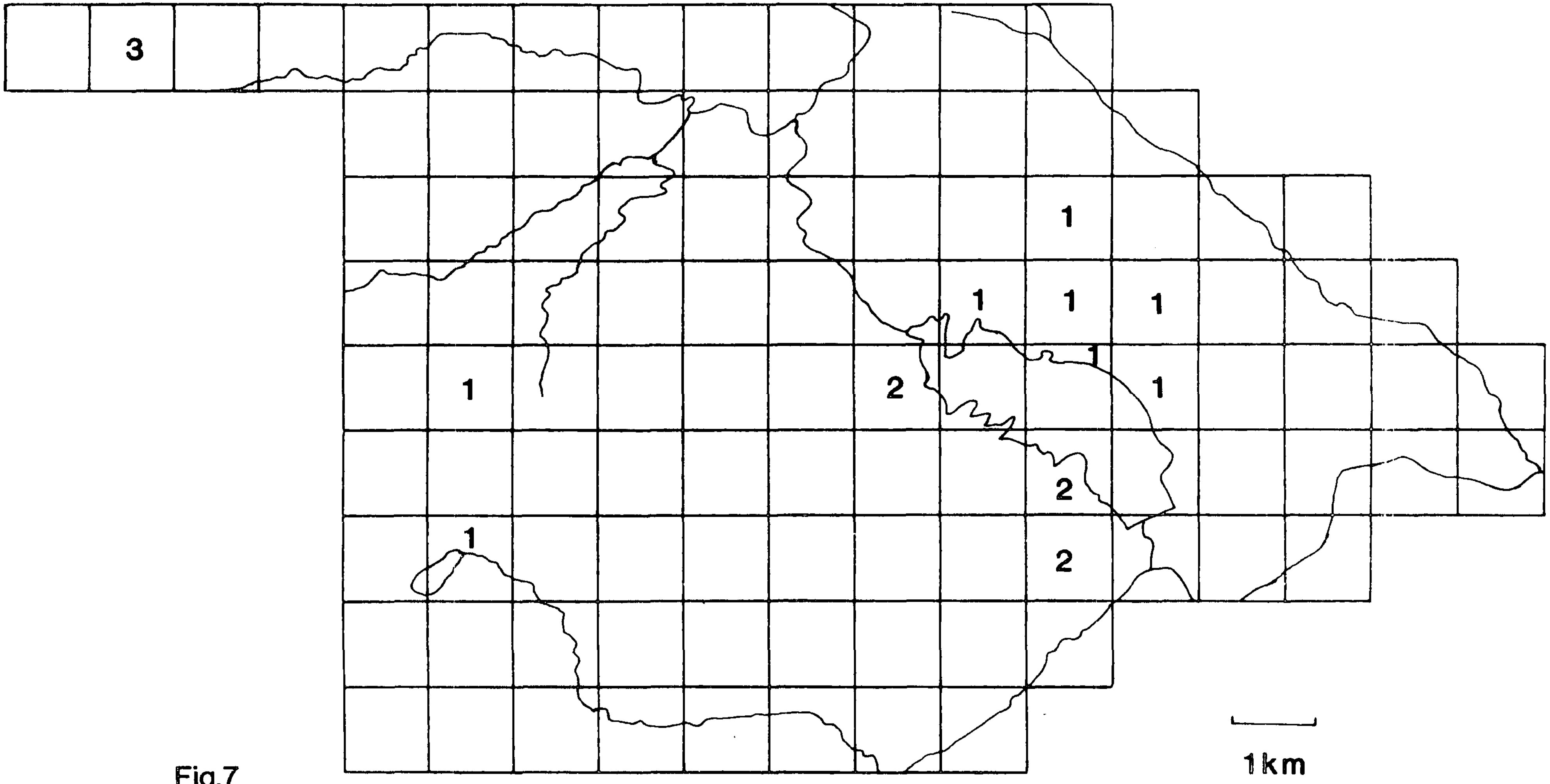


Fig.7

Curlew showed a pattern intermediate to the two forms described above. They extended over the whole of the eastern half of the study area. High numbers occurred on the lower fell slopes around the lowland pasture although many pairs were located at increased altitudes where they seemed to be particularly associated with the main river valleys.

Dunlin were less abundant than most of the wader species that breed in Upper Teesdale. Cow Green Reservoir is a major attracting influence and the majority of the Dunlin population congregates on its shores to feed, breeding pairs holding territories on the adjacent fell slopes. The remainder of the Teesdale population is restricted to the higher fell tops, mainly on the more plateau-like areas where there are pools and tarns.

The departure of a distribution of organisms (in this case birds per km square) from randomness can be tested by comparing its mean and variance. In a Poisson distribution the variance divided by the mean is unity. A value significantly less than one implies overdispersion while a value significantly greater than one indicates aggregation (Southwood 1966). The extent to which the distributions of the waders satisfy a Poisson model can be tested by the formula:-

$$\chi^2 = \frac{S^2(N-1)}{\bar{x}}$$

where $\bar{x}$ = mean number of birds per 1km square

S^2 = variance

Table 7 gives the values for the coefficient of dispersion for each wader species and the results of the χ^2 test for significant departure from unity. None of the distributions of birds observed in 1978 satisfied the Poisson model. All species were found to be significantly aggregated ($P < 0.001$) suggesting that selection of specific areas is likely.

Table 7. The mean number of birds per km square and the coefficients of dispersion of six wader species within the study area in 1978. The results of the χ^2 test of the Null Hypothesis that the coefficients are not significantly different from unity are also given. Based on 105 km squares.

Species	No. of birds per 1km square $\bar{x}$	Coefficient of dispersion $s^2/\bar{x}$	χ^2 (104 d.f.)	P
Lapwing	4.81	44.07	4585	< 0.001
Redshank	1.10	4.88	504	< 0.001
Snipe	0.47	3.22	334	< 0.001
Curlew	1.12	3.55	184	< 0.001
Golden Plover	1.24	2.15	223	< 0.001
Dunlin	0.16	1.56	162	< 0.001

ii) Changes in the wader populations within the study area during the breeding seasons of 1978-1980.

In order to assess any changes in the populations of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin during the three years of the study, 1978-80, 57km squares within the study area were surveyed each breeding season. Differences in the number of km squares occupied, the total number of birds present, and the corresponding changes in density between 1978, 1979 and 1980 are given for each wader species in Table 8. During this period there were no significant changes in the populations of Lapwing, Redshank and Snipe either in terms of range, population size or breeding density. Curlew numbers showed a significant decrease with little corresponding contraction in the range, thus producing significantly lower breeding densities in 1980 compared with 1978. By contrast, Golden Plover numbers increased. The number of km squares they occupied increased only slightly, therefore densities in 1980 were significantly higher than those observed in 1978. The Dunlin population showed a significant increase in the number of breeding birds, the range extension, although not significant being sufficient to maintain similar densities in all three years.

The 57 km squares surveyed each year were representative of the whole study area (105 km squares) in terms of vegetation types and altitude (see Methods). Thus the observed changes in the wader population should be representative of the entire study area. The possibility that the apparent changes in some of the wader populations were due, wholly or in part, to redistribution within the study area between breeding seasons cannot, however, be eliminated.

In spite of the fact that the 1978-79 winter was particularly hard and that the bad weather continued up to 19 May 1979 in Upper Teesdale, with almost daily blizzards, there was no evidence of any changes in the densities of the wader populations between the breeding seasons of 1978 and 1979.

Table 8. Population changes of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin in part of the study area between 1978 and 1980. Based on the same 57 km squares for all years.

(a) The number of km squares occupied and the results of the χ^2 test to assess changes in the range of each species.

	No. of km squares occupied				
	1978	1979	1980	χ^2	
Lapwing	27	26	32	1.52	n.s.
Redshank	26	23	25	0.34	n.s.
Snipe	15	13	16	0.43	n.s.
Curlew	29	22	22	1.34	n.s.
Golden Plover	29	35	33	1.46	n.s.
Dunlin	7	9	15	4.27	n.s.

(b) The number of individuals present and the results of the χ^2 test to assess changes in population size.

	No. of birds				
	1978	1979	1980	χ^2	
Lapwing	499	529	571	4.91	n.s.
Redshank	107	110	117	0.47	n.s.
Snipe	38	55	44	3.26	n.s.
Curlew	88	73	54	8.10	$P < 0.05$
Golden Plover	69	96	110	9.48	$P < 0.01$
Dunlin	10	19	56	41.96	$P < 0.001$

(c) Mean density changes (numbers of birds km^{-2}) and standard errors together with the results of a paired 't' test for the density changes in the individual km squares.

	Mean change in density		
	1978-1979	1979-1980	1978-1980
Lapwing	0.48±1.20 n.s.	0.72±0.78 n.s.	1.26±1.73 n.s.
Redshank	0.04±0.29 n.s.	0.13±0.36 n.s.	0.11±0.35 n.s.
Snipe	0.17±0.17 n.s.	-0.22±0.25 n.s.	0.30±0.19 n.s.
Curlew	-0.28±0.26 n.s.	-0.35±0.24 n.s.	-0.63±0.24 $t = 2.62^{**}$
Golden Plover	0.39±0.31 n.s.	0.26±0.33 n.s.	0.76±0.38 $t = 2.00^{*}$
Dunlin	0.17±0.11 n.s.	0.69±0.38 n.s.	0.85±0.44 n.s.

* $P < 0.05$
** $P < 0.01$
n.s. not significant

iii) The effect of vegetation on the distribution of waders.

Six predominant vegetation types were distinguished in the survey (Table 1). These occurred over sufficiently large areas to enable classification of each km square according to one dominant vegetation type.

Waders were present in 76% of the 105 km squares surveyed in 1978 whilst in 1979 and 1980 88% and 93% of the 57 squares examined were occupied. All km squares with meadow as the predominant vegetation type were utilized whilst the other vegetation types were used in varying proportions in 1978 (Table 9). A greater proportion of squares with *Festuca, Eriophorum* and *Calluna / Eriophorum* were used by the waders in 1979 and 1980. This was not a result of the reduced sample size in the final two years of the study; the increase is still apparent if the same 57 km squares are compared in all three years (Table 9). The increase in the number of squares occupied is to be expected from the changes detected in some of the wader populations (Section 2, ii).

Presence or absence of wader species.

Considering first the presence or absence of each species within the km squares, Table 10 indicates the number of km squares occupied by each wader species in 1978 with respect to the dominant vegetation type recorded in those areas. From these data it would appear that there is a considerable amount of overlap between species. However, the distribution of birds in relation to the frequency of available habitats does show some differences. Table 11 indicates where each species occupies more than 50% of the available habitat, or, for less abundant species the vegetation type which has more than 50% of their total number of occurrences, in terms of km squares.

Table 9. Percentage of km squares of different predominant vegetation types in which breeding waders were located in 1978, 1979 and 1980. Based on the presence or absence of Lapwing, Redshank, Snipe, Curlew, Golden Plover or Dunlin in each km square.

	Meadow	*Festuca* grassland	*Nardus* grassland	*Eriophorum*	*Calluna/ Eriophorum* co-dominant	*Calluna*	TOTAL AREA
a) Whole study area 105 km squares							
1978	100	86	67	78	72	33	76
	(N=6)	(N=14)	(N=3)	(N=32)	(N=47)	(N=3)	(N=105)
b) Part of study area, the same 57 km squares surveyed in all 3 years							
1978	100	100	67	85	76	0	82
1979	100	100	100	92	80	0	88
1980	100	100	100	100	88	0	93
	(N=6)	(N=9)	(N=3)	(N=13)	(N=25)	(N=1)	(N=57)

N = no. of km squares surveyed

Table 10. Number of 1 - km squares of different predominant vegetation types occupied by each wader species in 1978.

	Meadow	*Festuca* Grassland	*Nardus* Grassland	*Eriophorum vaginatum*	*Calluna*/ *Eriophorum* co-dominant	*Calluna*
Frequency of 1-km squares	6	14	3	32	47	3
Lapwing	6	8	0	9	7	0
Redshank	6	7	0	9	9	0
Snipe	5	5	0	8	6	0
Curlew	3	8	2	17	12	0
Golden Plover	1	9	2	16	25	1
Dunlin	0	1	0	8	3	0
No waders	0	2	1	7	13	2

Table 11. Habitat preference of waders as shown by utilization of more than 50% of the available 1-km squares in 1978.

	Vegetation type					
	Meadow	*Festuca* Grassland	*Nardus* Grassland	*Eriophorum*	*Calluna/ Eriophorum* co-dominant	*Calluna*
Lapwing	X	X				
Redshank	X	X				
Snipe	X					
Curlew	X	X	X	X		
Golden Plover		X	X	X	X	
Dunlin				(X)		

X >50% of available 1-km squares occupied

(X) >50% of the total number of 1-km squares occupied by that species (species too rare to occupy a large proportion of the habitat.

This then gives some indication of the preferred vegetation types. Golden Plover was the only species to show preference for *Calluna/ Eriophorum* but potentially could overlap with Curlew and Dunlin on *Eriophorum* and Curlew on *Nardus*. Lapwing, Redshank, Snipe and Curlew all used more than 50% of the available km squares with meadow, whilst Lapwing, Redshank, Snipe and Golden Plover could all potentially occur together on *Festuca*. More species show a preference for meadow and *Festuca* grasslands and it is therefore likely that there will be a greater chance for interaction between the waders occurring on these sites.

Number of individuals.

A more accurate reflection of vegetation preferences shown by the waders is given by considering actual numbers of birds present on each vegetation type, and not merely their presence or absence in a particular km square. Figure 8 shows the percentage of the population within the study area found on different vegetation types for the six wader species. The data have been combined for 1978, 1979 and 1980 (see Methods).

Kendall's rank correlation can be used to evaluate the extent to which the distributions of any two species across the study area are similar in terms of the vegetation types selected. The coefficient ranges from -1 to +1. A significant tendency towards -1 indicates separate patterns of distribution. A significant tendency towards +1 indicates similar distributions.

The data show almost identical distributions for Lapwing, Redshank and Snipe (Fig. 8) and the coefficients between the distributions of these species were significant (Table 12). The pattern for Golden Plover is opposing and complementary to these

Table 12. Kendall's rank correlation coefficients for paired wader species and species with habitat availability to show similarities in the distribution patterns of wading birds in part of Upper Teesdale, 1978-80.

	Lapwing	Redshank	Snipe	Curlew	Golden Plover	Dunlin
Lapwing		***1.00	**0.83	0.47	-0.14	0.28
Redshank			**0.83	0.47	-0.14	0.28
Snipe				0.62	0.14	0.43
Curlew					*0.69	**0.83
Golden Plover						0.57
Dunlin						
Habitat	0.14	0.14	0.29	*0.69	***0.93	**0.86

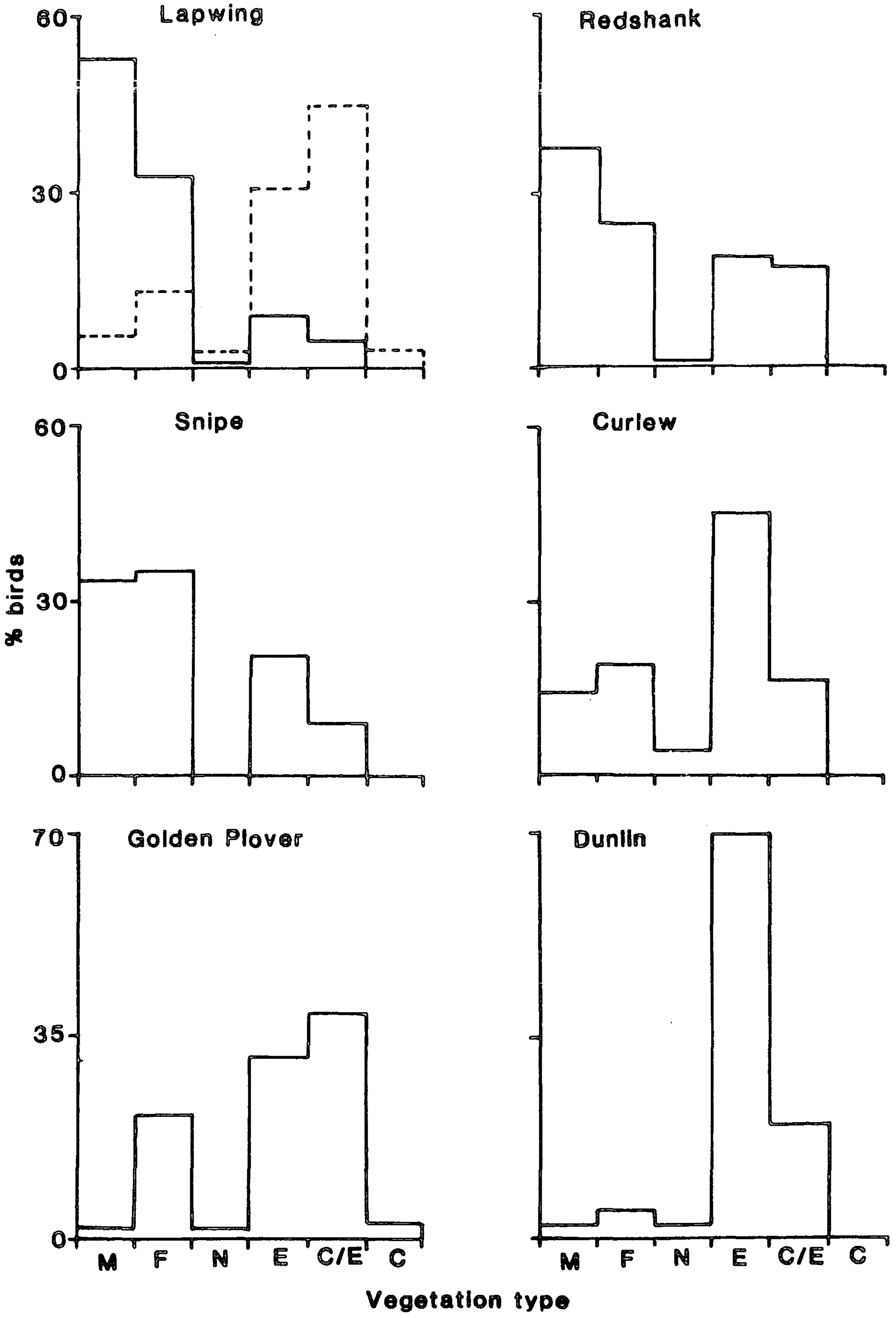
* $P<0.05$

** $P<0.02$

*** $P<0.01$

Figure 8. Percentage of the population of each of six wader species found on different vegetation types in part of Upper Teesdale in 1978-80. Hatched line indicates the percentage of km squares classified as a particular vegetation type.

M = meadow
F = *Festuca* grassland
N = *Nardus* grassland
E = *Eriophorum*
C/E = *Calluna/Eriophorum*
C = *Calluna*



Lapwing
Redshank
Snipe
Curlew
Golden Plover
Dunlin
60
30
0
60
30
0
70
35
0
% birds
M
F
N
E
C/E
C
M
F
N
E
C/E
C
Vegetation type

and shows no correlation with their distributions. The distribution of Curlew is intermediate between the above two patterns, although it is significantly correlated with that of the Golden Plover. Dunlin show the most restricted selection of vegetation types, 70% of their population being located on km squares where *Eriophorum* is predominant. This preponderance of Dunlin on cotton-grass areas, the vegetation type which also has the highest number of Curlew, leads to a significant correlation between the distribution patterns of these two species. No two species showed significantly dissimilar distribution patterns (i.e. significant negative values of Kendall's rank correlation coefficient).

The percentage similarity in the distribution patterns of any pair of species can be calculated using the formula according to Whittaker and Fairbanks (1958) and Southwood (1966):-

$$\%\ \text{similarity} = \Sigma \min (a, b, \ldots\ldots. x)$$ where a, b, ...x are the percentages of each species occurring in different habitats

Table 13 gives the percentage similarities in the distribution patterns of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin with respect to vegetation type for both pairs of species and each species with the availability of vegetation types in 1978-80. Again the results indicate that Lapwing, Redshank and Snipe have very similar distributions (% similarity > 75%), the degree of similarity being much less for all other pairs of species. The distribution of Golden Plover follows the frequency of vegetation types much more closely than any other species (% similarity = 91.5%).

Any species may show:-

a) selection of certain habitats

b) no selection of habitats. Individuals occur at random or are spaced evenly. In either situation their distributions will follow the availability of habitats, more individuals being present in the habitats having the largest extent.

Rank correlation methods can in some cases help to identify whether habitat selection is occurring by comparing the distribution of a species with habitat availability. Comparing the proportions of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin occurring on the different vegetation types with the availability of habitats (Table 12), Kendall's rank correlation coefficient indicates that Curlew, Golden Plover and Dunlin each have a significant association with the distribution of habitat types. However, an inherent weakness of rank correlation methods is that they do not take into account the magnitude of each category, merely its rank. Thus a situation where a species is selecting the most frequently occurring habitats is not always distinguished from that of a randomly distributed species which is following the availability of habitat types. It is therefore not possible to determine whether the correlations obtained for Curlew, Golden Plover and Dunlin are due to their lack of selectivity of vegetation types or whether these arise because they happen to be selecting *Eriophorum* and *Calluna/Eriophorum*, the most frequently occurring habitats. However, the fact that the distributions of Lapwing, Redshank and Snipe show no significant correlation with the frequency distribution of the predominant vegetation types indicates the possibility of strong selection for meadow and *Festuca* grassland.

Table 13. Percentage similarities of the distribution patterns of six wader species with respect to vegetation type for paired species and species with habitat frequency, 1978-80.

	Lapwing	Redshank	Snipe	Curlew	Golden Plover	Dunlin
Lapwing		76.4	80.4	48.3	38.1	21.7
Redshank			87.1	70.7	61.7	45.3
Snipe				64.2	54.0	37.7
Curlew					71.9	71.9
Golden Plover						60.8
Dunlin						
Habitat	33.3	56.9	49.2	68.9	91.5	60.5

A more accurate indication of selection is obtained using selection ratios. This takes into account both the abundance of a particular species and the availability of the habitat (Hunter 1962).

$$\text{Selection ratio (S.R.)} = \frac{\text{proportion of observations of species A in habitat x}}{\text{proportion of habitat x in the study area}}$$

The selection ratio has a skewed distribution ranging from zero to infinity. 0 to 1 indicates that there is no evidence of selection whereas any value above 1 indicates selection of a particular habitat, in this case km squares of a certain predominant vegetation type.

Table 14 gives the selection ratios obtained for Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin on the six predominant vegetation types in 1978-80. Several of the values obtained were only a little above 1. Therefore standard errors for the selection ratio were obtained by the formula:-

$$\text{S.E. of selection ratio} = \frac{100\sqrt{\frac{pq}{N}}}{\%\ \text{habitat x in study area}}$$

where p = unit probability of species A occurring in habitat x

$q = 1 - p$

N = total number of species A in all habitats of the study area

Variance and error for the denominator is negligible.

It was considered that there was significant evidence of selection ($P < 0.05$) only if:-

$$\text{S.R.} - 2\ \text{S.E.} > 1$$

Table 14. Selection ratios and standard errors for wader species located on different vegetation types 1978-80.

	Meadow	*Festuca*	*Nardus*	*Eriophorum*	*Calluna/ Eriophorum*	*Calluna*
Lapwing	*9.29 ± 0.37	*2.45 ± 0.15	0.20 ± 0.11	0.30 ± 0.04	0.10 ± 0.02	0
Redshank	*6.62 ± 0.78	*1.83 ± 0.29	0.29 ± 0.29	0.63 ± 0.12	0.39 ± 0.08	0
Snipe	*5.95 ± 1.14	*2.69 ± 0.49	0	0.68 ± 0.18	0.21 ± 0.09	0
Curlew	*2.53 ± 0.63	1.47 ± 0.30	1.44 ± 0.71	*1.49 ± 0.17	0.37 ± 0.08	0
Golden Plover	0.35 ± 0.20	*1.64 ± 0.25	0.70 ± 0.40	1.04 ± 0.12	0.89 ± 0.09	0.93 ± 0.46
Dunlin	0.44 ± 0.43	0.38 ± 0.26	0.87 ± 0.86	*2.30 ± 0.24	0.45 ± 0.14	0

The selection ratios indicate that meadow and *Festuca* grassland were the preferred vegetation types, each being selected by four species (Lapwing, Redshank, Snipe and Curlew, and Lapwing, Redshank, Snipe and Golden Plover respectively). Only Curlew and Dunlin showed significant selection of *Eriophorum* whilst *Nardus* and *Calluna* were not selected by any of the species. There was no evidence of selection of the most frequently occurring habitat, *Calluna/Eriophorum*, although the highest percentage of Golden Plover was found on this vegetation type. Each species showed significant selection of at least one vegetation type.

Breeding density.

Examination of breeding densities eliminates any bias in analysis due to unequal availability of habitats. Figure 9 shows the breeding densities of the six wader species on different vegetation types in 1978-80. The data have been combined (see Methods) to show the average densities over the three year period. However, between years each species showed the same pattern of density changes from one vegetation type to another. A useful comparison can be made with the results in Figure 9 and the percentage frequency distributions of the various species (Fig. 8). A habitat may contain a large proportion of a population but the birds need not necessarily be at high density if that habitat is extensive. For Lapwing, Redshank, Snipe and Dunlin changes in density between vegetation types closely reflected and reinforced the percentage distribution pattern - vegetation types carrying the higher percentages of the population also had higher densities of that bird. Densities of Curlew and Golden Plover were virtually unaffected by vegetation type. Most individuals of these species

Figure 9. Breeding densities (mean number of birds per km square) of six wader species on different predominant vegetation types in part of Upper Teesdale 1978-80

Error bars = 95% confidence limits

Numbers over bars indicate sample sizes (number of km squares).

Symbols for vegetation types as for Fig. 8

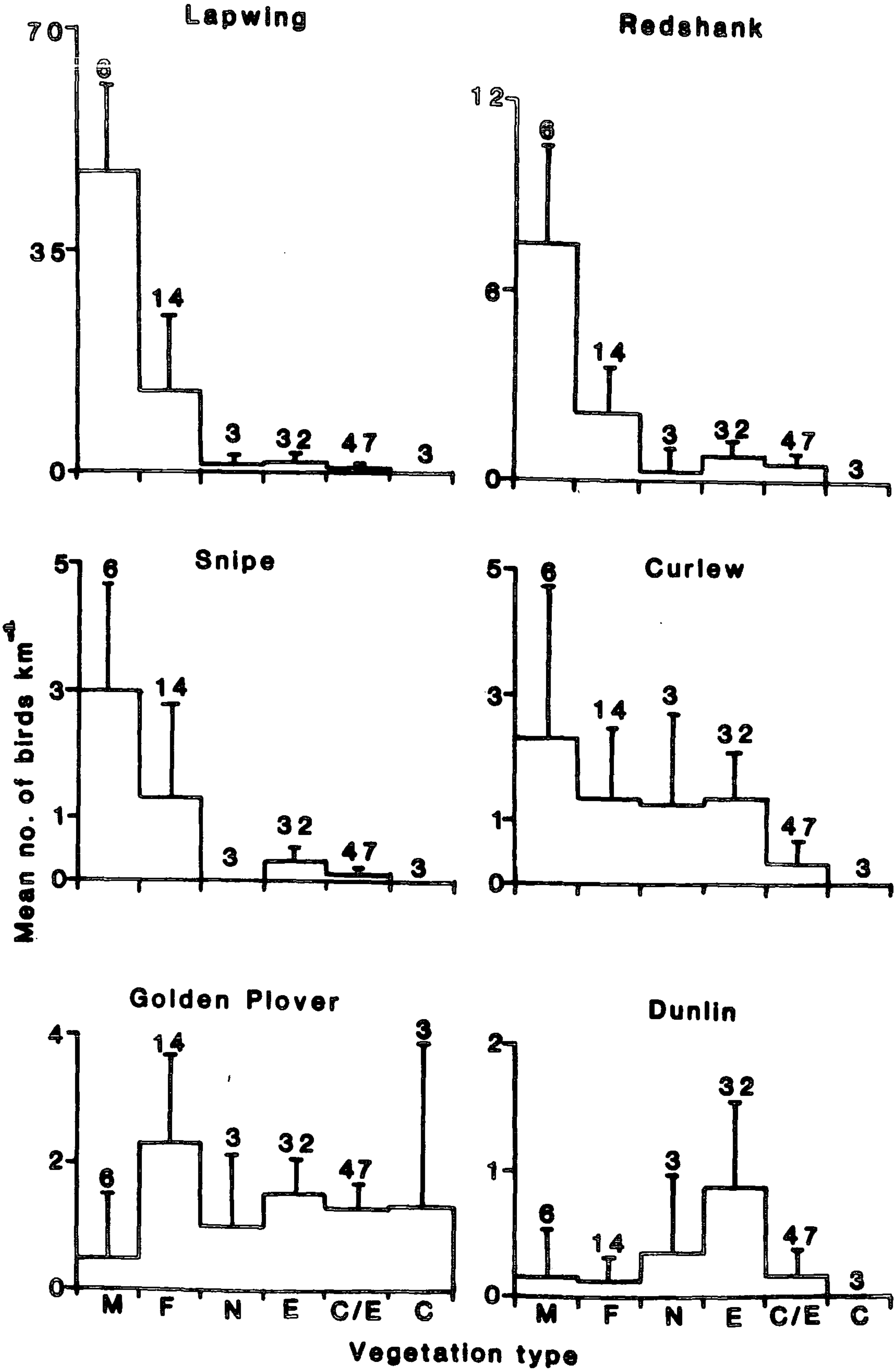

Lapwing
70
35
0
6
14
3
32
47
3
Redshank
12
6
0
6
14
3
32
47
3
Snipe
5
3
1
0
6
14
3
32
47
3
Curlew
5
3
1
0
6
14
3
32
47
3
Golden Plover
4
2
0
6
14
3
32
47
3
Dunlin
2
1
0
6
14
3
32
47
3
M
F
N
E
C/E
C
M
F
N
E
C/E
C
Mean no. of birds km⁻¹
Vegetation type

Table 15. Breeding densities of waders (mean number of birds per km square ± 1 S.E.) on grassland and blanket bog 1978-80.

	Meadow, *Nardus* and *Festuca* grasslands (N = 23 km squares)	*Eriophorum*, *Calluna/Eriophorum* and *Calluna* (N = 82 km squares)	Student's 't'
Lapwing	20.30 ± 5.32	0.90 ± 0.24	3.64 ($P < 0.001$)
Redshank	3.26 ± 0.80	0.54 ± 0.12	3.36 ($P < 0.005$)
Snipe	1.61 ± 0.52	0.20 ± 0.05	2.70 ($P < 0.01$)
Curlew	1.61 ± 0.45	0.73 ± 0.17	1.83 (n.s.)
Golden Plover	1.70 ± 0.47	1.37 ± 0.16	0.66 (n.s.)
Dunlin	0.17 ± 0.08	0.44 ± 0.15	1.59 (n.s.)

n.s. = not significant

occur on blanket bog areas but densities on these sites were similar to those on grassland areas.

Mineral soils supported significantly higher densities of Lapwing, Redshank and Snipe than areas where blanket bog predominated (Table 15). Although the same trend was apparent for Curlew and Golden Plover, the differences are not significant. Nearly all the Dunlin occurred on blanket bog and although the density was higher, the difference is not significantly different to that recorded on grassland sites.

Species number and species diversity.

Not only do mineral sites support higher densities of certain species but they also have more species. The mean number of species present on each vegetation type in 1978 is shown in Table 16. This also gives the Shannon-Weiner index of species diversity (see e.g. Southwood 1966):-

Index of diversity, $H(S) = -\sum_{i=1}^{S} P_i \log_2 P_i$

where S = total number of species in the sample

and P_i = proportion of the total number of birds which consists of species i

Table 16 also gives values for Student's 't' test to compare differences between the mean number of species per km square and the species diversity index for paired vegetation types.

The diversity index has two components:-

1) the number of species
2) the evenness of individuals. Maximum evenness will occur if each species has an equal number of individuals present in the area being considered (Lloyd and Ghelardi 1964, Tramer 1969, Hill 1973, Peet 1974).

Table 16. Mean number of species, the Shannon-Weiner Index of species diversity, and standard errors, for waders located in different vegetation types in part of Upper Teesdale in 1978.

	Meadow	*Festuca* Grassland	*Nardus* Grassland	*Eriophorum*	*Calluna/ Eriophorum*	*Calluna*
Mean no. of species	3.50 ± 0.43	2.71 ± 0.50	1.33 ± 0.66	2.03 ± 0.28	1.36 ± 0.21	0.33 ± 0.33
Shannon-Weiner Diversity Index	1.17 ± 0.09	0.85 ± 0.20	0.64 ± 0.32	0.79 ± 0.13	0.39 ± 0.10	0 ± 0
N (number of km squares)	6	14	3	32	47	3

Values of Student's 't' to compare mean number of species in paired vegetation types

	F	N	E	C/E	C
M	1.20	2.75*	3.42*	4.47*	5.84*
F		1.67	0.24	2.49*	3.97*
N			0.98	0.04	1.36
E				1.91	3.93*
C/E					2.63*

Values of Student's 't' to compare diversity index in paired vegetation types

	F	N	E	C/E	C
M	1.46	1.59	2.40*	5.80*	13.00*
F		0.56	0.25	2.06*	4.25*
N			0.43	0.75	2.00
E				2.44*	6.08*
C/E					3.90*

Significant values (P < 0.05) are indicated by *

Table 17. Mean number of wader species per km square in different vegetation types 1978-80 .

Vegetation type	Mean no. of species per km square	S.E.	No. of km squares
Meadow	3.60	0.35	6
Festuca grassland	2.52	0.48	14
Nardus grassland	1.67	0.51	3
Eriophorum	2.07	0.25	32
Calluna/Eriophorum	1.40	0.18	47
Calluna	0.33	0.33	3

Values of student's 't' to compare mean number of wader species in paired vegetation types

	F	N	E	C/E	C
M	1.82	*3.12	*3.56	*5.59	*6.80
F		1.21	0.83	*2.18	*3.76
N			0.70	0.50	2.21
E				*2.17	*4.20
C/E					*2.85

* $P < 0.05$

The correlation between the number of species and the species diversity index gives a measure of the contribution of the species number component to the diversity index. For the 1978 data this plot was linear ($r = +0.92$, $N = 105$, $P < 0.001$) and 85% of the variation in the diversity index could be explained simply by the number of breeding wader species. Thus the evenness component appears to be relatively unimportant in this situation. The diversity of wading birds, in this part of Upper Teesdale can, therefore, be adequately described by counting the number of species and measures of abundance are, for this purpose, of little consequence. Other workers have also reached similar conclusions when evaluating bird species diversity (e.g. Tramer 1969).

Table 17 gives the average number of species per km square for each vegetation type over the three year period 1978-80. (As in previous analyses in this section, Common Sandpiper, Oystercatcher and Ringed Plover have been excluded since they are restricted to the aquatic habitats and are not selecting vegetation type *per se*.) Meadow had significantly more species than any of the peat areas and *Festuca* grassland held significantly more species than *Calluna*/*Eriophorum* or *Calluna*. *Calluna* was the most species-poor vegetation type having significantly fewer species than all other types except *Nardus*. The number of species found on *Eriophorum* was intermediate between those of meadow and *Festuca* grassland and heather sites.

iv) The effect of altitude on the distribution of waders.

Superimposed on the influences of vegetation type are the effects of altitude. Figure 10 shows the altitudinal distribution of six wader species within the study area in 1978-80. The pattern of availability of altitudes follows a normal distribution. Lapwing, Redshank and Snipe showed selection of lower altitudes, their distributions being skewed to the left. Over 50% of their populations occurred below 500m. Dunlin and Golden Plover occupied the same range of altitudes, their peak occurrence coinciding at 500-550m. Almost 75% of the Curlew were located below 550m. Again their distribution follows a pattern intermediate between those of Lapwing, Redshank and Snipe, birds characteristic of the lowland pasture, and Golden Plover and Dunlin which occur almost entirely on the higher fells. Only Golden Plover and Dunlin were found above 750m.

Figure 11 illustrates diagramatically for the 1978 data:-

a) the association between species

b) the degree of overlap and where this occurs

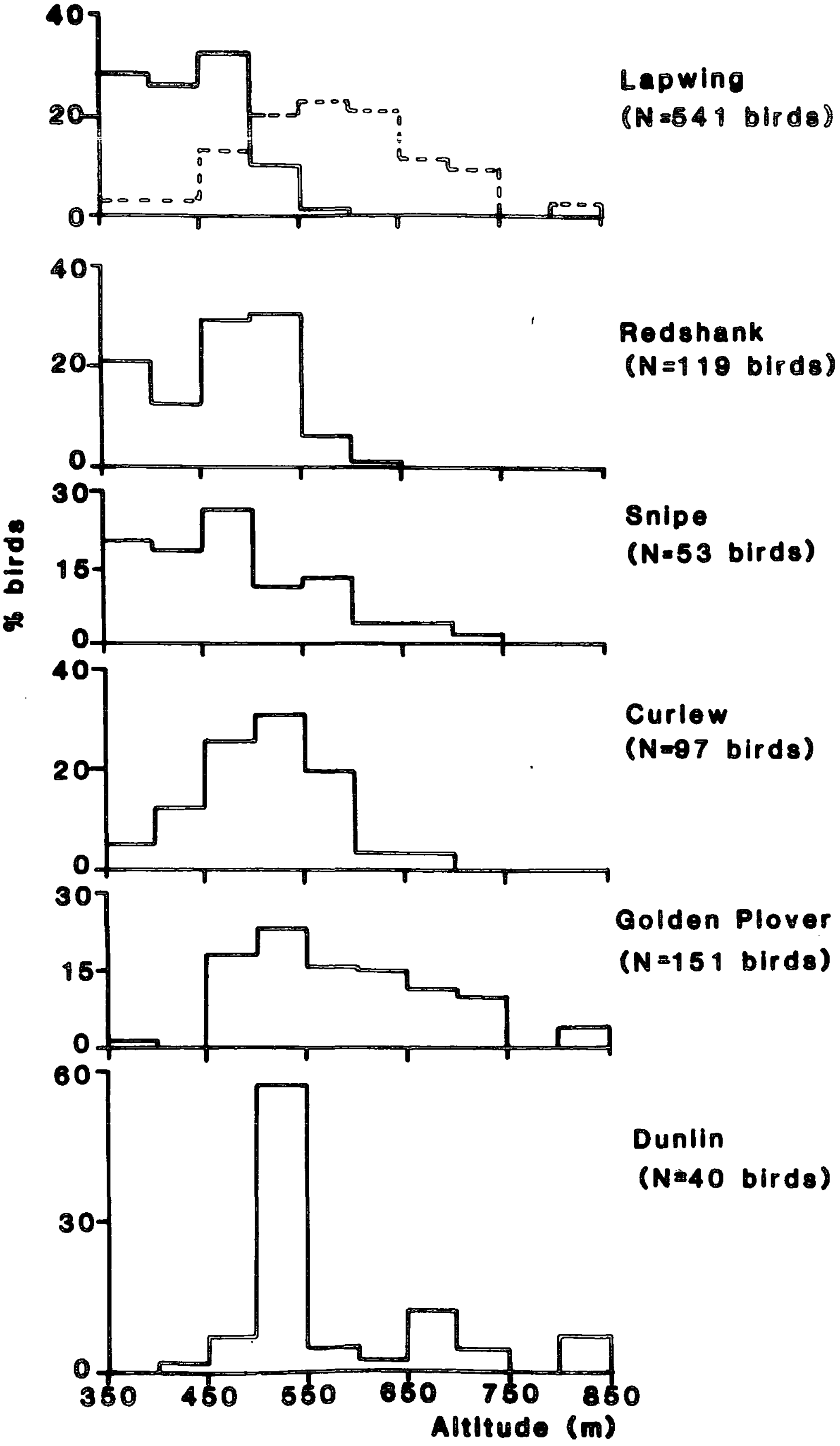
c) the extent to which each species occupies the study area.

The presence of each species within each km square and the altitude at which it occurs is indicated. Where two or more species were found in the same square they are joined together by a line. Species occurred together much more frequently below 600m than they did above this altitude. Between the lowest altitudes, 389m, and 500m, Lapwing, Redshank, Snipe and Curlew commonly occurred together and were associated less frequently with Golden Plover. No km squares within this range had only one species present. This area relates principally to the lowland pasture of the Harwood Beck Valley.

Most overlap between species was found between 500 and 550m, decreasing towards 600m. These altitudes coincide with the Cow Green Basin which is the only part of the study area where all six species were found together.

Figure 10. Percentage frequency distribution in relation to altitude for each of six wader species found within the study area in 1978-80.

- The hatched line indicates the percentage frequency distribution of altitudes within the study area, each of the 105 km squares being classified according to its median altitude.



Lapwing
(N=541 birds)
Redshank
(N=119 birds)
Snipe
(N=53 birds)
Curlew
(N=97 birds)
Golden Plover
(N=151 birds)
Dunlin
(N=40 birds)
% birds
40
20
0
40
20
0
30
15
0
40
20
0
30
15
0
60
30
0
350
450
550
650
750
850
Altitude (m)

Above 600m the range of wader species found is reduced. This represents the higher fells and mainly concerns the Moor House to Cross Fell region. No Lapwing were observed and there was only one occurrence of Redshank. Golden Plover was the most abundant species, although there were isolated occurrences of Snipe, Curlew and Dunlin. Very little overlap between species was observed compared to the lower areas. Dunlin and Golden Plover are the characteristic waders of higher moorland areas and were the only species found to extend to Cross Fell.

Figure 12 shows the relationship between the number of wader species and altitude for the three breeding seasons 1978, 1979 and 1980. In all years there was a decrease in species richness with increasing altitude, the regression lines indicating that, on average, about one wader species is lost for every 100m increase in altitude.

Within the study area, as altitude increases, mineral soils give way to a predominance of peat and vegetation type changes. Figure 13 shows the changing proportions of grassland sites across the altitudinal gradient of the study area. However, these changes do not explain the altitudinal decline in the number of wader species. Within both grassland and blanket bog sites the number of species per km square still showed a significant decrease with increasing altitude ($r = -0.72$, d.f. = 21, $P < 0.001$ and $r = -0.37$, d.f. = 80, $P < 0.001$ respectively; Figure 14).

Parallelling the altitudinal decline in the number of species was a decrease in the number of birds per km square. The effect was again apparent on both grassland and blanket bog sites, ($r = -0.75$, d.f. = 17, $P < 0.001$ and $r = -0.54$, d.f. = 62, $P < 0.001$ respectively), densities decreasing as altitude increases up to a height of around 650m after which there was little change in numbers (Fig. 15).

Figure 11. Diagrammatic representation of the altitudinal range of six wader species in the study area and the degree of overlap between species in 1978. Lines indicate where species occur jointly within the same km square. For clarity, a hatched line is used wherever species adjacent on the figure are not also present.

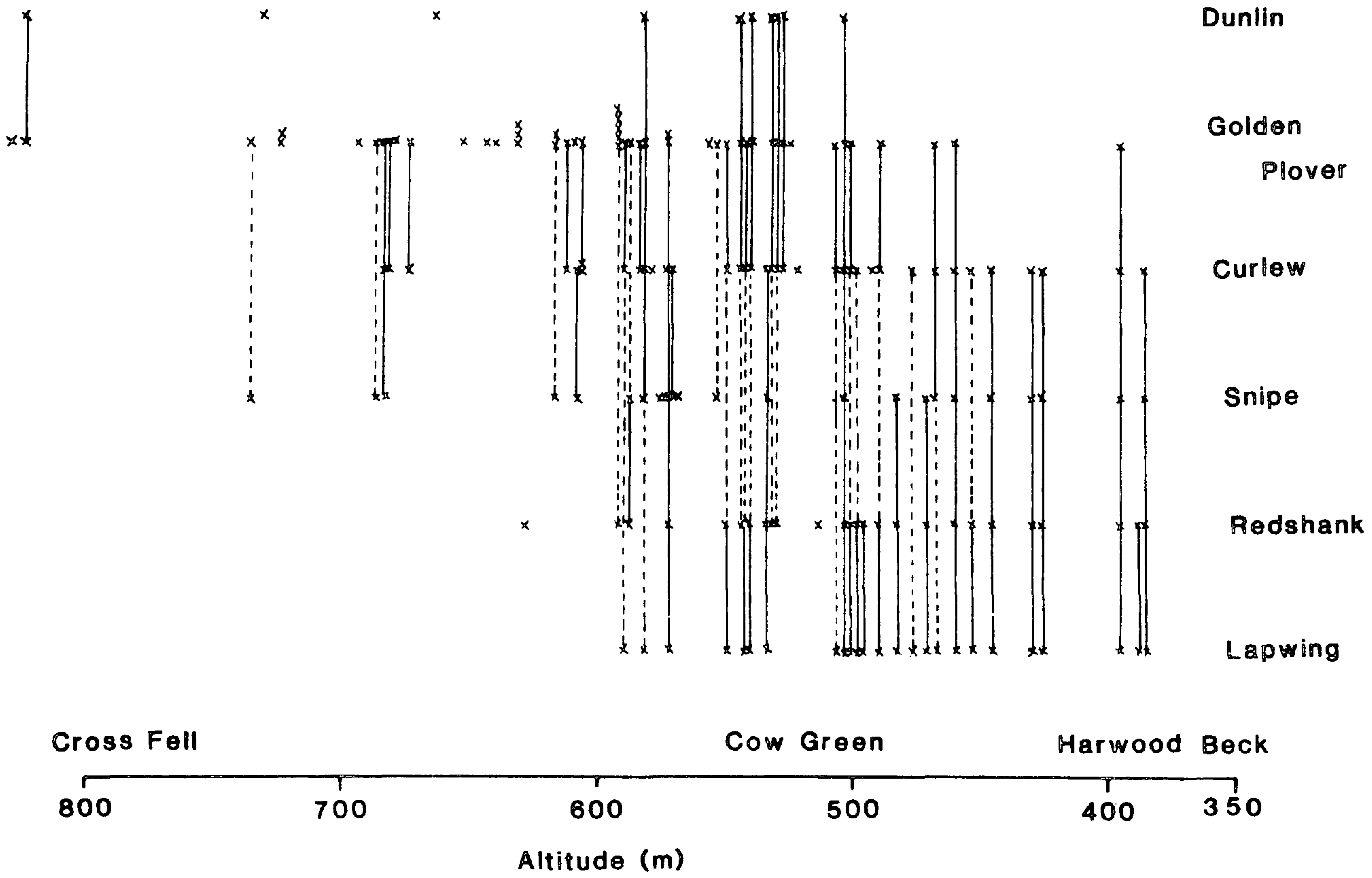

Dunlin
Golden Plover
Curlew
Snipe
Redshank
Lapwing
Cross Fell
Cow Green
Harwood Beck
800
700
600
500
400
350
Altitude (m)

Figure 12. Relationship between the number of species of wading birds and altitude in part of Upper Teesdale in 1978, 1979 and 1980.

-Mean values and 95% confidence limits are plotted for 50m altitude intervals. Where sample sizes were less than four, adjacent 50m altitude intervals have been grouped. Numbers above error bars indicate sample sizes (number of km squares).

Due to unequal sample sizes the regression lines have been fitted to the individual points.

Regression equations:-

1978 $y = -0.0094x + 7.29$

$r = -0.51$

d.f. = 103

$P < 0.001$

1979 $y = -0.013x + 9.0$

$r = -0.58$

d.f. = 55

$P < 0.001$

1980 $y = -0.010x + 8.05$

$r = -0.51$

d.f. = 55

$P < 0.001$

x = altitude (m) y = No. of species per km^2

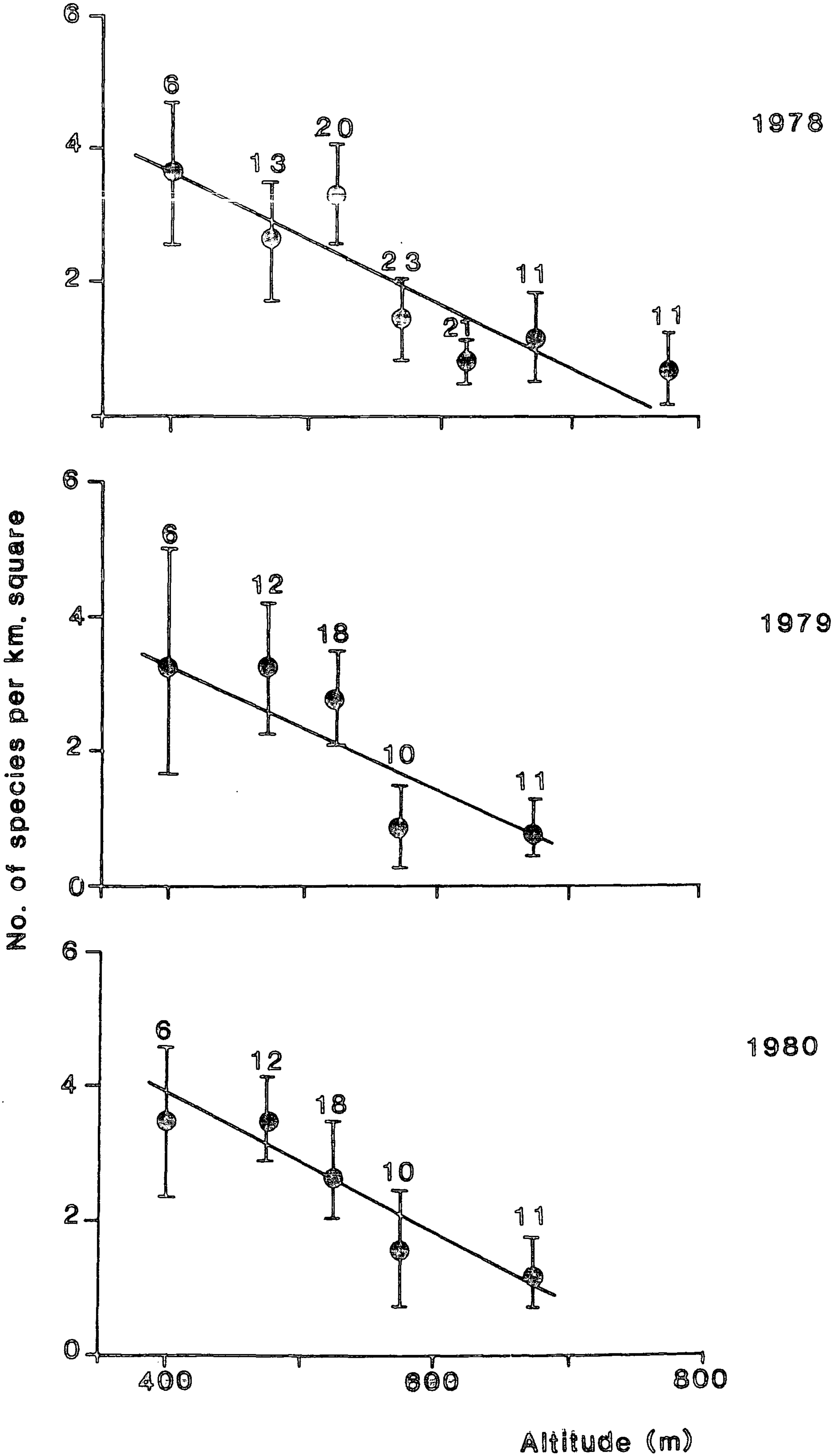

6
4
2
6
13
20
23
21
11
11
1978
6
4
2
0
6
12
18
10
11
1979
6
4
2
0
6
12
18
10
11
1980
400
600
800
No. of species per km. square
Altitude (m)

Figure 13. Percentage of km squares within 50m altitude ranges that are predominantly grassland, as opposed to blanket bog.

- Numbers over bars indicate sample sizes (number of km squares).

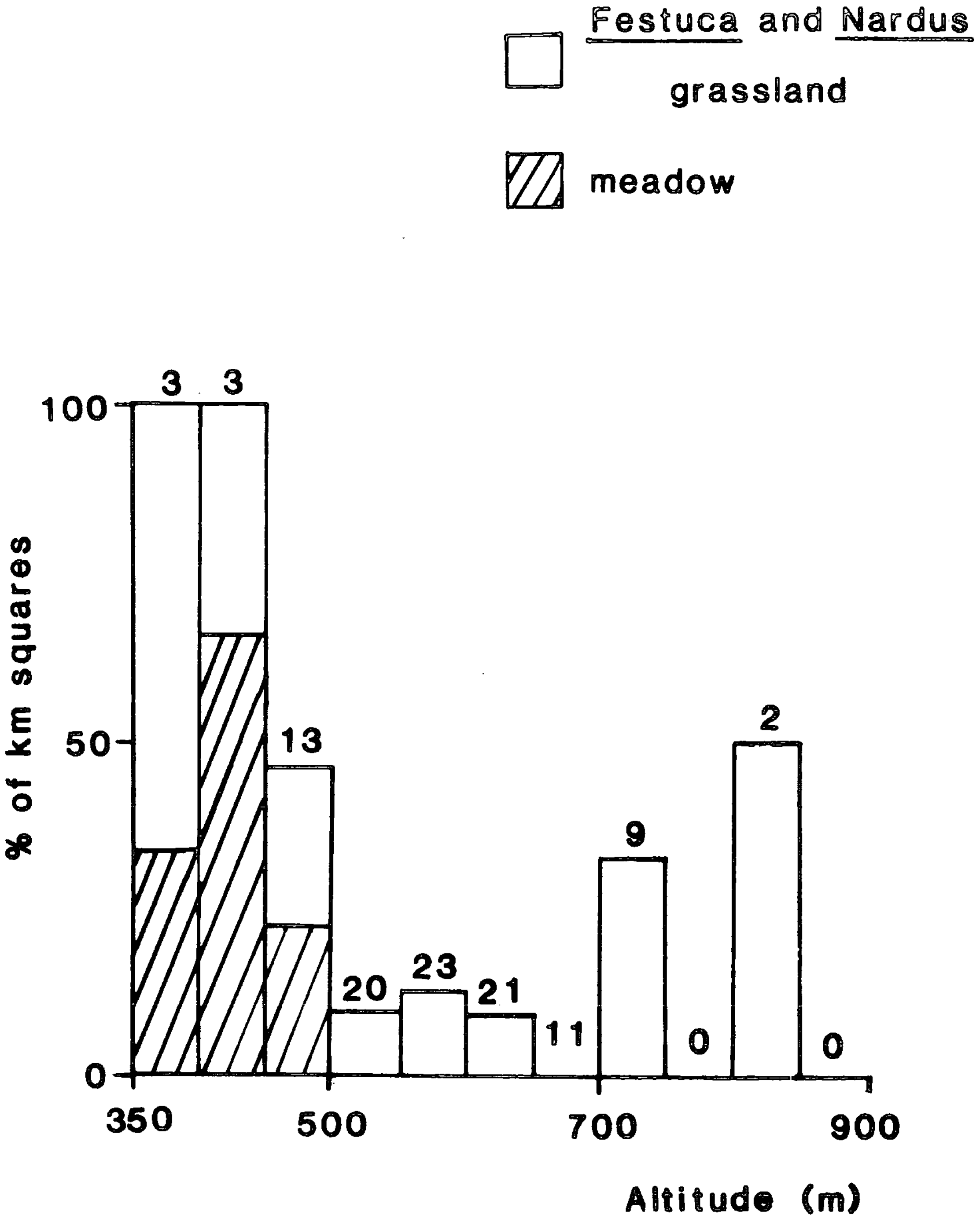

Festuca and Nardus grassland
meadow
% of km squares
100
50
0
3
3
13
20
23
21
11
9
0
2
0
350
500
700
900
Altitude (m)

Figure 14. Relationship between the number of species of wading birds and altitude on blanket bog and grassland sites in part of Upper Teesdale in 1978-80.

- Mean values and 95% confidence limits are plotted for 50m altitude intervals. Where sample sizes were less than 4 adjacent 50m altitude intervals have been grouped. Numbers above error bars indicate sample sizes (number of km squares).

Due to unequal sample sizes the regression lines have been fitted to the individual points.

Regression equations:

Blanket bog

$y = -0.051x + 4.64$

$r = -0.37$

d.f.= 80

$P < 0.01$

Grassland

$y = -0.092x + 7.61$

$r = -0.72$

d.f.= 21

$P < 0.001$

x = altitude (m) y = no. of species km^{-2}

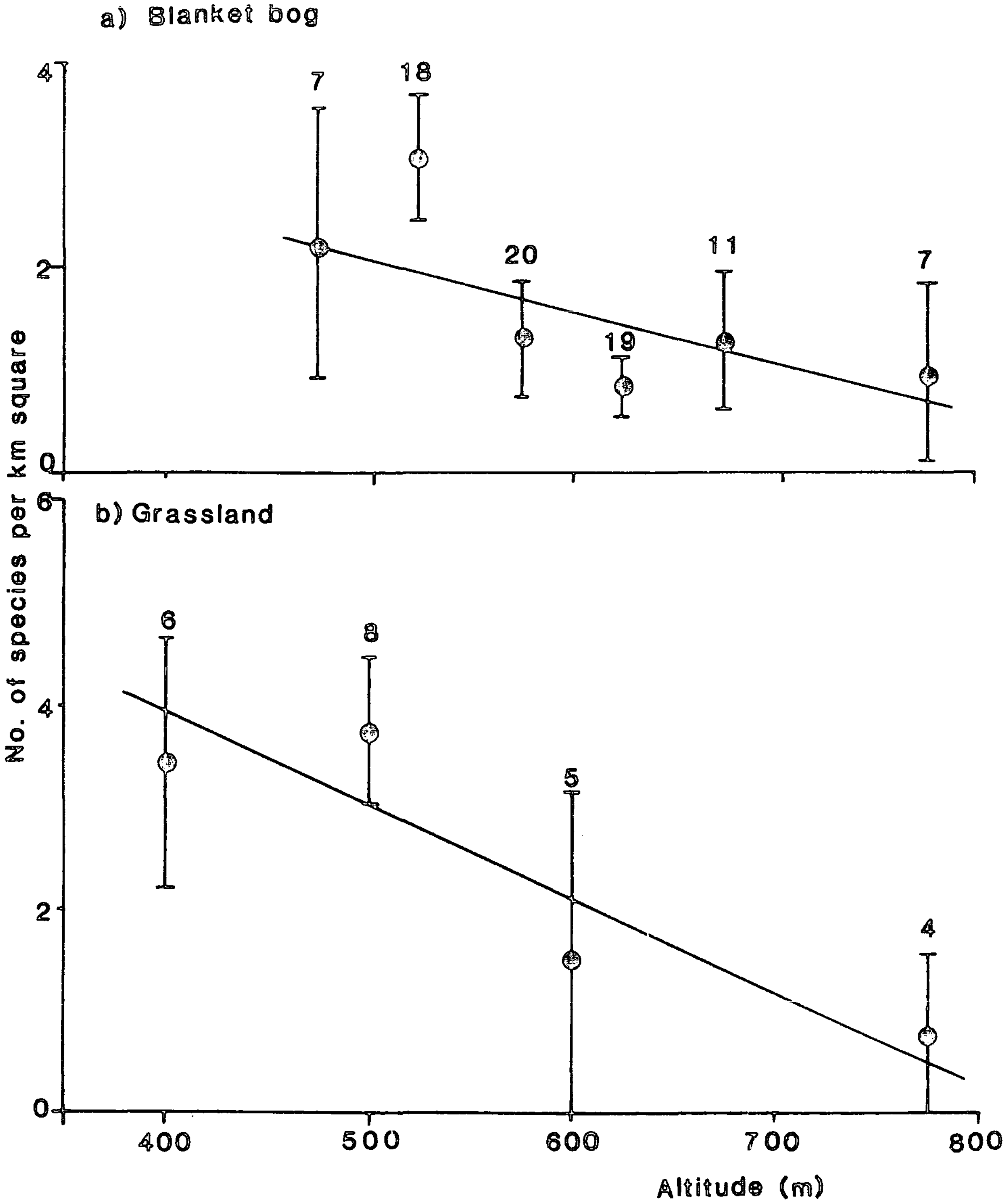

a) Blanket bog
b) Grassland
No. of species per km square
Altitude (m)
0
2
4
6
400
500
600
700
800
7
18
20
19
11
7
6
8
5
4

Figure 15. Relationship between the number of waders per km square and altitude for blanket bog and grassland sites in part of Upper Teesdale in 1978-80.

Mean values and 95% confidence limits are plotted for 50m altitude intervals. Where sample sizes were less than 4, adjacent 50m altitude intervals have been grouped. Numbers above error bars indicate sample sizes (number of km squares).

Due to unequal sample sizes the regression lines have been fitted to the individual points.

Regression equations for all altitudes up to 650m:-

a) Blanket bog

$r = -0.54$, d.f. $= 62$, $P < 0.001$

$y = -0.056x + 36.18$ where x = altitude (m)

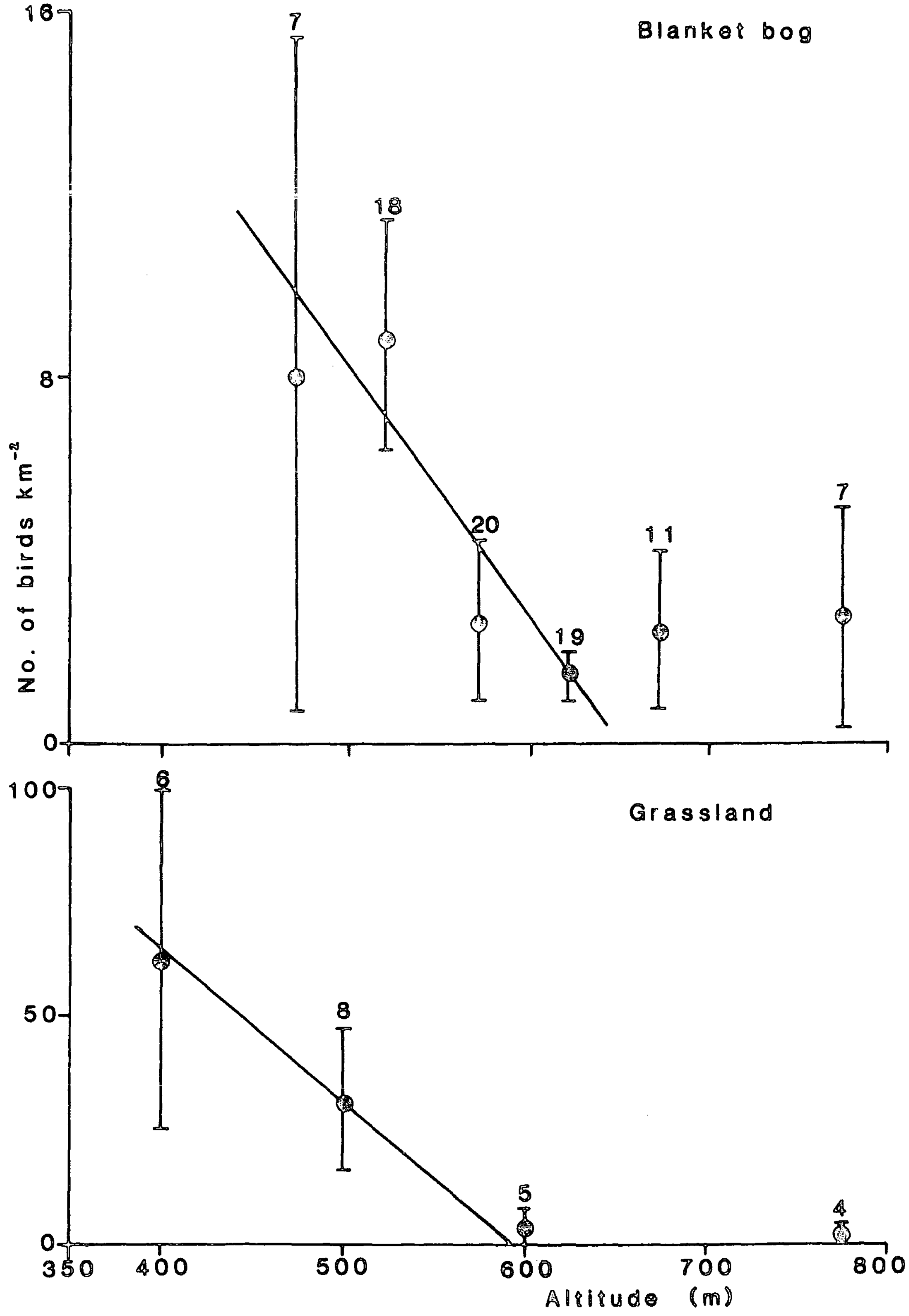
y = no. of birds km^{-2}

b) Grassland

$r = -0.75$, d.f. $= 17$, $P < 0.001$

$y = -0.33x + 197.71$ where x = altitude (m)

y = no. of birds km^{-2}



Blanket bog
16
8
0
No. of birds km^{-2}
7
18
20
19
11
7
Grassland
100
50
0
6
8
5
4
350
400
500
600
700
800
Altitude (m)

In terms of both species richness and number of birds the altitudinal decline was more rapid on grassland sites. Here the number of species decreased at almost two times the rate on blanket bog and the fall off in number of birds was nearly six times greater (Figs. 14 and 15).

Thus it appears that increasing altitude causes a decrease in both species richness and the number of individuals, the effect being independent of vegetation type. High altitudes may therefore be expected to hold both fewer species and fewer breeding pairs of waders than an area with similar vegetation at a lower altitude.

v) Overlap in wader species.

All the foregoing analyses only assess similarities in the distribution patterns of the waders and thus indicate where there is potential for direct overlap and the possibility of competition. They do not indicate which species are occurring together within the same km squares and make no attempt to quantify the actual degree of association. Two species may show identical distributions with respect to habitat type but if the area is extensive in relation to the number of birds present then the occurrence of each species could be mutually exclusive.

Considering first the presence or absence of species within the sample squares, the degree of association between pairs of species can be evaluated by Fager's index of affinity. This takes the same form as Sørensen's (1948) coefficient but is based on the number of occurrences of a species rather than the number of species present. It thus evaluates association between two species as opposed to the degree of similarity between two faunas in terms of species composition.

I_{AB} (Fager's index of affinity between species A and species B) $= \frac{2J}{nA+nB}$

where J = number of joint occurrences

and nA and nB = total number of occurrences of species A and B

The index has a range from 0 (no association, and the possibility of different selection patterns or the exclusion of one species by the other) to 1 (complete association). It does not consider negative association. Significance can be assessed by a one-tailed Student's 't' test (Southwood 1966):-

$$'t' = \left[\frac{(nA + nB)(2J-1)}{2nAnB} - 1 \right] \left[\sqrt{nA + nB - 1} \right]$$

The minimum significant ($P < 0.05$) value for 't' being 1.645.

Table 18 shows the joint occurrences of paired wader species in terms of the number of km squares in which both species were found in 1978 (the year for which the largest sample of km squares is available for analysis). Values for Fager's index of affinity based on these results suggest that there are significant associations ($P < 0.05$) between Lapwing and Redshank, Lapwing and Curlew, and Redshank and Curlew. All other pairs of species showed some overlap but the associations are not significant (Table 18). Unfortunately, using this index, rare and common species cannot be compared since the number of occurrences of one species must lie between half and one times the number of occurrences of the other species (Southwood 1966), otherwise too much emphasis is placed on the dominant species. Dunlin, therefore, have been excluded from the analysis.

Very few indices have been derived which will quantify direct overlap of species in terms of the actual number of individuals

Table 18. Overlap between wader species in part of Upper Teesdale in 1978.

The number of km squares which had joint occurrences of paired species

	Lapwing	Redshank	Snipe	Curlew	Golden Plover	Dunlin
Total no. of km squares occupied	30	31	24	42	54	12
Joint occurrences (No. of km squares)						
Lapwing	-	24	16	24	17	5
Redshank			12	25	19	7
Snipe				16	14	3
Curlew					26	8
Golden Plover						9
Dunlin						-

Fager's Index of Affinity and 't' values to assess association of paired wader species

	Lapwing	Redshank	Snipe	Curlew	Golden Plover	Dunlin
Lapwing		0.79	0.59	0.67	0.40	-
		*t=4.19	n.s.	*t=2.89	n.s.	
Redshank			0.44	0.68	0.45	-
			n.s.	*t=3.17	n.s.	
Snipe				0.48	-	-
				n.s.		
Curlew					0.54	-
					n.s.	
Golden Plover						-

\- indicates where joint occurrences cannot be used to calculate index of affinity because nA is not greater than ½nB

* $P < 0.05$

n.s. = not significant

occurring together. The vast majority consider only similarities in the spatial distributions of individuals or resource requirements (see e.g. Levins 1968, reviews by Southwood 1966 and Wolda 1981). Southwood (1966) modified the equation used by Whittaker and Fairbanks (1958) to give an index of association of individuals such that:-

$$Iai = 2\left[\frac{Ji}{A+B} - 0.5\right]$$

where Ji = number of individuals of A and B in samples
where both species are found
A+B = total number of individuals of A and B
in all samples.

This coefficient takes the normal range of -1 (no association) to +1 (complete association) and has been used satisfactorily by Anthony and Smith (1977) in an ecological study of two species of deer. For the present study where it was desirable to compare overlap between rare and common species this index was considered unsatisfactory as it was found to place too much emphasis on the most common species. A rare species may show total overlap with a more abundant species but from the point of view of the common species the degree of association may be negligible. To overcome such biases the data have been presented simply as the number, and percentage, of individuals of each species which occurred within the same sample squares as other species (Table 19). Thus, 82% of the total number of Dunlin found in 1978 occurred in km squares which also had Golden Plover present, whereas the percentage overlap from the point of view of the Golden Plover was only 23%. Golden Plover had the lowest degree of overlap with any other species and Lapwing the highest (Table 19). This is further reflected in the numbers of each species which occurred monospecifically in various km squares (Table 20).

Table 19. The number and percentage of individuals occurring within the same km squares for paired wader species in part of Upper Teesdale in 1978.

No. of birds

	Lapwing	Redshank	Snipe	Curlew	Golden Plover	Dunlin
Total no. of birds	505	116	49	118	130	17
Lapwing		103	37	84	47	6
Redshank	450		34	73	42	10
Snipe	394	54		58	35	3
Curlew	430	86	32		74	11
Golden Plover	254	67	25	60		14
Dunlin	27	16	2	18	30	

Percentage of birds

	Lapwing	Redshank	Snipe	Curlew	Golden Plover	Dunlin
Lapwing		89	76	71	36	35
Redshank	89		69	62	32	59
Snipe	78	47		49	27	18
Curlew	85	74	65		57	65
Golden Plover	50	58	51	51		82
Dunlin	5	14	4	15	23	

Table 20. The number and percentage of the total km squares occupied, and the number and percentage of individuals within those squares where each of six wader species occurred monospecifically in 1978.

	Km squares		Birds	
	No.	%	No.	%
Lapwing	0	0	0	0
Redshank	2	6.5	3	2.6
Snipe	2	8.3	3	6.1
Curlew	5	11.9	7	5.9
Golden Plover	19	35.2	39	30.0
Dunlin	2	16.7	2	11.8

Grassland sites were selected by more species and had higher densities of waders than blanket bog (Section 2, iii)). Therefore if grassland areas have limited availability, overlap between species is more likely and there is potential for competition. Table 21 indicates the extent to which individuals of each species occurred within the same km squares as other wader species in 1978, the sample being subdivided to illustrate overlap on km squares of different predominant vegetation type. Grassland sites had more overlap between species than the blanket bog areas (Table 19). On meadow the degree of overlap between Lapwing, Redshank, Snipe and Curlew was high. Only one pair of Golden Plover and no Dunlin were observed on that vegetation type in 1978 so there was little potential for interaction with these species. *Festuca* grasslands had high overlap between Lapwing, Redshank, Snipe, Curlew and Golden Plover.

Table 21. The number and percentage of individuals occurring within the same km squares of different predominant vegetation types for paired wader species in part of Upper Teesdale in 1978.

Meadow

No. of birds

	L	R	S	C	G	D
Total no.of birds	218	40	19	19	2	0
L		40	19	19	2	0
R	218		19	19	2	0
S	197	30		19	2	0
C	154	21	11		2	0
G	31	8	4	2		0
D	0	0	0	0	0	

% birds

	L	R	S	C	G	D
L		100	100	100	100	0
R	100		100	100	100	0
S	90	75		100	100	0
C	71	53	58		100	0
G	14	20	21	11		0
D	0	0	0	0	0	

Festuca

No. of birds

	L	R	S	C	G	D
Total no.of birds	208	30	13	25	28	1
L		30	13	24	19	0
R	169		12	23	16	0
S	169	15		19	19	0
C	202	29	13		19	0
G	179	21	12	21		0
D	0	0	0	0	0	

% birds

	L	R	S	C	G	D
L		100	100	96	68	0
R	81		92	92	57	0
S	81	50		76	68	0
C	97	97	100		68	0
G	86	70	92	84		0
D	0	0	0	0	0	

continued overleaf

Table 21 (continued)

Eriophorum

	No. of birds							% birds					
	L	R	S	C	G	D		L	R	S	C	G	D
Total no.of birds	53	21	9	41	38	13							
L		15	2	18	9	4	L		71	22	44	24	31
R	49		1	21	13	9	R	92		11	51	34	69
S	22	6		14	10	2	S	42	29		34	26	15
C	48	18	5		25	9	C	91	86	56		66	69
G	20	16	4	16		12	G	38	76	44	39		92
D	21	15	1	12	20		D	40	71	11	29	33	

Calluna/Eriophorum

	No. of birds							% birds					
	L	R	S	C	G	D		L	R	S	C	G	D
Total no.of birds	26	25	8	30	53	3							
L		18	3	23	17	2	L		72	38	77	32	67
R	20		2	10	12	1	R	77		25	33	23	33
S	6	3		6	15	2	S	23	12		20	28	67
C	26	18	3		22	2	C	100	72	38		42	67
G	24	22	7	18		2	G	92	88	88	60		67
D	6	1	3	6	10		D	23	4	38	20	19	

There was a greater availability of km squares with *Eriophorum* and *Calluna/Eriophorum* as the predominant vegetation types. Here the birds were more dispersed and there was less overlap between some species (Table 21). Lapwing and Redshank had a high degree of concurrence on the blanket bog sites as did Golden Plover and Dunlin on *Eriophorum*. Redshank, Snipe and Curlew occurred together less frequently than they did on the grassland sites.

vi) Habitat selection of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin on an area of moorland and marginal hill farmland.

Two multivariate statistical techniques (discriminant function analysis and stepwise multiple regression) were used to elucidate the relative importance of the habitat variables (Appendix 2) as predictors of both presence or absence and population densities of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin. As there was no evidence of any significant changes in selection or distribution patterns of the waders between years, the data have been presented to summarize the situation over the period 1978-80, counts of waders being averaged over the three breeding seasons (see Methods).

a) Lapwing.

A summary of the results of the discriminant analysis between areas in which Lapwing were recorded as present or absent is given in Table 22. The discrimination between km squares with and those without Lapwing was highly significant (final Wilk's Lambda = 0.43, $\chi^2_3 = 86.63$, $P < 0.001$). The predictive equation (formed from the unstandardized coefficients and the constant) gave correct classification for 90% of the cases. The significant discriminating variables were altitude,

Table 22. Summary of discriminant function analysis for areas (km squares) in which Lapwing were recorded as present or absent in part of Upper Teesdale in 1979-80.

		Discriminant function coefficients	
Step No.	Variable entered*	Standardized	Unstandardized
1	Altitude	-0.95	-0.014
2	Vegetation height	-0.55	-0.98
3	Grazed	0.29	0.81

Constant 9.56

Prediction results

	No. of cases	Predicted group membership Absent	Present
Actual group			
Lapwing absent	70	63	7
% classified		90	10
Lapwing present	35	4	31
% classified		11	89

Percentage of grouped cases correctly classified: 90%

Group centroids

Lapwing absent	-0.81
Lapwing present	1.63

*Altitude - median altitude, in metres.

Vegetation height - typical height of the predominant vegetation type grouped as < 10 cm, 10-20 cm and > 20 cm to give a score on an increasing scale of 1-3.

Grazed - scored cattle and sheep absent as 0, cattle and/or sheep present as

Table 23. Summary of discriminant function analysis, where the effects of altitude are excluded, for areas (km squares) in which Lapwing were recorded as present or absent in part of Upper Teesdale in 1978-80.

		Discriminant function coefficients	
Step No.	Variable entered*	Standardized	Unstandardized
1	% fields	0.67	0.03
2	Mines	0.40	0.14
3	*Nardus*	0.53	1.02
4	Disturbance	0.46	0.38
5	Peat hags	-0.34	-0.90

Constant -1.37

Prediction results

	No. of cases	Predicted group membership	
		Absent	Present
Actual group			
Lapwing absent	70	67	3
% classified		96	4
Lapwing present	35	12	23
% classified		34	66

Percentage of grouped cases correctly classified: 86%

Group centroids

Lapwing absent	-0.65
Lapwing present	1.30

* % fields - % of km square with enclosed land.

Mines - the number of disused mines, old shafts, old levels, hushes.

Nardus - *Nardus* grassland; scored absent as 0, present as 1, predominant as 2.

Disturbance - an increasing subjective scale of 1-6 (see Appendix 2).

Peat hags - scored absent as 0, present as 1.

vegetation height and the presence of grazing animals (cattle and sheep). Of these, altitude had nearly twice the discriminating power of vegetation height and approximately three times the discriminating power attributable to grazing (standardized discriminant function coefficients; Table 22). The four incorrectly classified km squares with Lapwing present were all at high altitudes for Lapwing.

The effect of altitude is likely to be due to a variety of interrelated factors rather than altitude *per se*. Therefore a second analysis was performed, altitude being excluded from the set of discriminating variables. The new variables selected still achieved significant group separation (final Wilk's Lambda = 0.54, $\chi^2_5 = 62.37$, $P < 0.001$). The percentage of a km square with enclosed land (% fields) now became the most important discriminating variable (i.e. had the highest standardized discriminant function coefficient). This variable was characteristic of low altitudes as was another discriminating variable, disturbance, a factor associated principally with the settled area of the Harwood Beck valley. Heavy road traffic, farm workers and pedestrians were found to have no repelling influence on Lapwing in the enquiries conducted by Nicholson (1938-39) and Lister (1964). However, in the Netherlands, van der Zande, ter Keurs and van der Weijden (1980) have demonstrated that roads may have a depressing effect on Lapwing breeding density up to a distance of 2000m, the relative intensity of disturbance increasing with traffic volume.

The only other discriminating variables were peat hags and past mining activity (Table 23). Peat hags are found only on blanket bog sites, areas avoided by Lapwing. Disused mine workings usually have patches of short grassland associated with them, thereby providing suitable sites for Lapwing even at higher altitudes.

Thus the effect of altitude on the presence or absence of Lapwing may, in part, be due to the availability of suitable habitats, the proportion of grassland sites being greater at lower altitudes (Fig. 13). However the fact that the discrimination achieved, without the inclusion of altitude, was slightly reduced suggests that other factors may be important. The overall accuracy of classification was reduced by only 4% when altitude was excluded but of those km squares where Lapwing were present only 66% were correctly classified compared with 89% when altitude was included (Tables 22 and 23).

A stepwise multiple regression analysis suggested that Lapwing density was also explained largely by the availability of suitable habitats which tended to occur at lower altitudes. A total of 70% of the variation in Lapwing density was explained by the percentage of fields, a further 4% being accounted for by altitude. Gradient was an additional significant factor, steeper gradients tending to detract Lapwings (Table 24). The avoidance of steep slopes may be due to the Lapwing's preference for a high water table and marshy areas with pools of either temporary or permanent standing water (e.g. Imboden 1971, Klomp 1953), factors linked to poorly drained, flat areas. Witherby *et al.* (1940), Spencer (1953) and Watson (1972) all comment that the Lapwing generally avoids steep slopes and Lister (1964) has shown that Lapwing breeding density is higher on poorly drained areas.

The Lapwing occupies a wide range of breeding habitats from salt marshes to high hill pastures and moorland, arable land to rushy fields, sewage farms and occasionally even colliery slag heaps (Nicholson 1938-9, Spencer 1953). Common to all breeding sites are the Lapwing's preferences for flat open, treeless areas with low, sparse or absent vegetation, often in the proximity of surface water

<u>Table 24</u>. Summary of stepwise multiple regression analysis to show the effect of habitat variables on Lapwing density in part of Upper Teesdale in 1978 80.

Dependent variable = Lapwing density (birds km^{-2})

Independent variables*	Slope	S.E. of Slope	F Value	% R^2 change
% fields	0.35	0.06	32.86	70
Gradient	-1.84	0.65	7.93	5
Altitude	-0.12	0.05	6.32	4

Constant = 73.18, N = 35, Multiple R = 0.89

Variables excluded from the analysis due to high intercorrelations ($r \geqslant 0.80$) with other habitat variables were:-

a) Aspect with respect to prevailing wind ($r > 0.80$ with aspect with respect to sun)

b) Hay, grazed meadow, % mineral soil, cattle ($r > 0.80$ with % fields)

'Grazed' was substituted for 'cattle'

* % fields - % of km square with enclosed land.
Gradient - gradient of main slope.
Altitude - median altitude, in metres.

or marshy ground (e.g. Venables 1937, Nicholson 1938-39, Klomp 1953, Lister, 1964, Imboden 1971). Newly ploughed land was the commonest breeding habitat recorded in Nicholson's (1938-39) survey and was found to be the preferred habitat by Robson and Williamson (1972). In Upper Teesdale there is no ploughed or tilled land available. Bare earth of any quantity is synonymous with eroded peat areas; peat hags were shown to discourage Lapwing. The discriminant and regression analyses demonstrated a preference for grassland areas of low vegetation height, particularly if grazed by sheep or cattle. In ungrazed areas Klomp (1953) found that the ultimate vegetation height determined whether Lapwing would breed in that locality, the differences in ultimate vegetation height probably being detected by the birds on the basis of field colour, grey-brown or grey-green areas being preferred. In Teesdale ground colour was closely linked to vegetation type. At the start of the breeding season most grassland sites were a greyish green colour, some hayfields being a slightly brighter green. Pale brown vegetation was usually indicative of *Eriophorum* and dark brown of *Calluna*, areas generally avoided by Lapwing. However, Seiskari (1956) gives an account of a breeding population of Lapwing on a raised bog in Finland amongst low (5-10cm), grey-brown vegetation. It may be that the Lapwing's response is to the vegetation type or structure rather than colour *per se*. Lapwings do not universally breed on ground of the same colour; however, a colour response may locally distinguish vegetation types.

The use of *Nardus* grassland (a significant discriminating variable; Table 23) as a breeding habitat has also been noted by Spencer (1953) who found that nesting quite often occurred on such areas, particularly if they had been burnt.

The selection of grazed areas of low vegetation height is of adaptive significance. The Lapwing is essentially a surface feeder and is guided by visual stimuli; short vegetation is therefore conducive to food location. Klomp (1953) has described how the mobility of adults and chicks is impeded in tall vegetation. While walking or running, the Lapwing does not raise its legs very high and its toes are hardly retracted so that the taller and denser the vegetation the more likely are they to become entangled. Moreover, the low flight display of the Lapwing and the scrape ceremony, during which the male displays the conspicuous chestnut feathers of the vent, would be inappropriate in tall vegetation.

The presence of grazing animals may be advantageous as both cattle and sheep droppings have a rich dung associated fauna (Laurence 1954, Papp 1971, Olechowicz 1974, Pisolkar 1980) providing an easily exploited food supply for both Lapwing adults and chicks. As well as enhancing food supply, grazing also maintains the low vegetation height essential to Lapwing.

High altitude acts as a barrier to Lapwing more strongly in winter than in summer. In the areas covered by Nicholson (1938-39), altitude preferences varied from area to area, but in general relatively few Lapwing bred above 370m. This is lower than the range of altitudes over which Lapwing occurred in the study area although within this they showed a distinct preference for the lower sites and none were found above 590m. However, in the past several breeding pairs have been recorded at 769m on Milburn Forest Fell (between Trout Beck and the River Tees; Fig. 1) and on the summit of Cross Fell (893m) (Brown 1974), which is the highest point of the study area. In the central Highlands of Scotland Lapwing breed up to 554m (Witherby *et al*. 1940) although Gordon (1939) has recorded two nesting pairs at 862m on Cairngorm and a bird, possibly with young, at 1077m. In the Swiss lowlands Lapwing show no preference for particular altitudes and breed up to 920m (Imboden 1971).

b) Redshank.

Redshank were found in approximately one third of the study area. Discrimination between km squares with and those without Redshank was highly significant (final Wilk's Lambda = 0.38, $\chi^2_5 = 97.48$, $P < 0.001$). Km squares with a discriminant score of less than -0.42 were classified as areas where Redshank were present whilst those having scores above this value were assigned as areas where Redshank were absent. A total of 89% of the cases was assigned to the correct group and the accuracy of classification was fairly equal between groups (Table 25).

The significant discriminating variables which appeared to discourage Redshank were high altitudes, tall vegetation and an uneven topography, whilst the presence of standing water or grazing animals contributed significantly to the presence of Redshank. Altitude was the most important variable having three times the discriminating power of the least important variables, ground roughness and grazing.

A discriminant analysis with altitude excluded is summarized in Table 26. This suggested that the altitude effect was partly due to the occurrence of enclosed pasture land and meadow (the percentage of fields) and the presence of larger streams and rivers, both of which were correlated with low altitudes. Standing water was retained as a significant variable, having almost equal discriminatory power to the percentage of fields. The discrimination achieved was still highly significant (final Wilk's Lambda = 0.50, $\chi^2_4 = 70.64$, $P < 0.001$)

Table 25. Summary of discriminant function analysis for areas (km squares) in which Redshank were recorded as present or absent in part of Upper Teesdale in 1978 - 80.

Step No.	Variable entered*	Discriminant function coefficients Standardized	 Unstandardized
1	Altitude	-0.92	-0.013
2	Vegetation height	-0.59	-1.06
3	Water	0.45	0.47
4	Ground roughness	-0.31	-0.40
5	Grazed	0.29	0.84
		Constant	9.35

Prediction results

	No. of cases	Predicted group membership Absent	 Present
Actual group			
Redshank absent	69	64	5
% classified		93	7
Redshank present	36	7	29
% classified		19	81

Percentage of grouped cases correctly classified: 89%

Group centroids

Redshank absent	-0.92
Redshank present	1.75

* Altitude - median altitude, in metres.
Vegetation height - typical height of the predominant vegetation type grouped as < 10 cm, 10-20 cm and > 20 cm to give score on an increasing scale of 1-3.
Water - standing surface of water. An increasing scale of 1-3 depending on the size of the water body. If no standing water, scored as 0.
Ground roughness - an increasing subjective scale from 0-2.
Grazed - scored cattle and sheep absent as 0, cattle and/or sheep present as 1.

Table 26. Summary of discriminant function analysis, where the effects of altitude are excluded, for areas (km squares) in which Redshank were recorded as present or absent in part of Upper Teesdale in 1978-80.

		Discriminant function coefficients	
Step No.	Variable entered*	Standardized	Unstandardized
1	% fields	0.84	0.036
2	Water	0.82	0.85
3	Mines	0.54	0.20
4	Streams	0.52	0.53

Constant -1.88

Prediction results

	No. of cases	Predicted group membership	
		Absent	Present
Actual group			
Redshank absent	69	61	8
% classified		88	12
Redshank present	36	9	27
% classified		25	75

Percentage of grouped cases correctly classified: 84%

Group centroids

Redshank absent	-0.72
Redshank present	1.38

* % fields - % of km square with enclosed land.

Water - standing surface water. An increasing scale of 1-3 depending on the size of the water body. If no standing water, scored as 0.

Mines - the number of disused mines, shafts, old levels, hushes.

Streams - an increasing scale of 1-3 depending on stream width. If no streams present, scored as 0.

and the predictive capabilities were only slightly lower than when altitude was included in the equation (c.f. Tables 25 and 26). Therefore, the effect of altitude on the presence or absence of Redshank is largely explained by the combination of variables in the second analysis (Table 26). Although Redshank tended to occur at the lower altitudes of the study area, altitude itself is no barrier provided the habitat is suitable; in central Asia, Redshank are found in marshes and along rivers flowing through high grass steppes to 462m in the subalpine and mountain zones of the Himalayas and Mongolia (Voous 1960). The Redshank was once typically a saltmarsh species but during the past century has spread inland (Thomas 1942) and into upland areas (Ratcliffe 1977b). In Britain the highest breeding site noted by Thomas was at 492m in Derbyshire, somewhat lower than the highest pairs in Teesdale at 590m.

The proportion of a km square with fields was also an important determinant of Redshank density, accounting for 52% of the variation in Redshank numbers (Table 27). The number of houses was also a significant factor indicating that human habitation, at least at the low levels of settlement within the study area, did not deter breeding Redshank. The correlation may also be due to the fact that the better quality pastures were close to the farms and more of these were cattle grazed, the poorer pastures being left to sheep. Many of those not left for hay had varying amounts of *Juncus effusus* present, rushy fields being the commonest Redshank breeding habitat recorded in Thomas' (1942) survey.

Grazing (a significant variable for discriminating between areas where Redshank are present or absent; Table 25) promotes tussock formation, tussocks providing the typical screened nest-sites

Table 27. Summary of stepwise multiple regression analysis to show the effect of habitat variables on Redshank density in part of Upper Teesdale in 1978-80.

Dependent variable = Redshank density (birds km^{-2})

Independent variables*	Slope	S.E. of Slope	F Value	% R^2 change
% fields	0.038	0.011	11.31	52
Houses	0.414	0.203	4.16	6

Constant = 1.794, N = 36, Multiple R = 0.76

Variables excluded from the analysis due to high intercorrelations ($r \geqslant 0.80$) with other habitat variables were:-

a) Aspect with respect to the prevailing wind ($r > 0.80$) with aspect with respect to the sun)

b) Hay, grazed meadow, % mineral soil, cattle ($r > 0.80$) with % fields)

'Grazed' was substituted for 'cattle'

* % fields - % of km square with enclosed land.

Houses - the number of houses or farms.

favoured by Redshank (e.g. Witherby *et al*. 1940, Thomas 1942, Greenhalgh 1969a) although open nests are sometimes made (Colthrup 1915, pers. obs.). Moreover, the deposition of dung by grazing animals may enhance food supply due to the attraction of dung-associated invertebrates. Rankin (1979) demonstrated that cowpat density was a proximate factor in Redshank nest-site selection on a salt marsh, this being linked to the increased food supply accorded by dung-associated invertebrates on the more heavily grazed areas.

Redshank typically breed on saltmarshes, wet, boggy or rushy pastures and the edges of moorland (Thomas 1942, Brown 1974) although they will nest in heather (Colthrup 1915, Thomas 1942, pers. obs.). Greenhalgh (1969a and 1971) noted a preference for thick, tall vegetation but Sharrock (1976) states that the usual habitat is generally without lush vegetation. In the present study, areas with short vegetation were associated with Redshank (Table 25). This may be partly due to a preference for grazed grassland sites. Dry, short pastures were amongst the commonest breeding habitats recorded by Thomas (1942) although he stressed the necessity of marshy ground, pools, rivers or lakes in close proximity. Standing water and streams were also demonstrated to be significantly associated with Redshank distribution in Teesdale (Tables 25 and 26). Nests, however, may sometimes be "a mile or more from water" (Bannerman 1961).

c) Snipe.

Snipe were recorded in just under one quarter of the km squares within the study area, most pairs occurring in the eastern half although some pairs extended right up to the western boundary (see Fig. 4 for their distribution in 1978). They therefore spread across a wide range of habitats. Nevertheless, on the basis of certain habitat variables, discrimination between areas where Snipe were present and absent was highly significant (final Wilk's Lambda = 0.58, $\chi^2_4 = 54.19$, $P < 0.001$). Km squares having a discriminant score of more than 0.54 were classified as areas where Snipe were present, scores below this value being designated as sites where Snipe were likely to be absent. The overall accuracy of classification by the predictive equation was 85% (Table 28). The significant discriminating variables were the percentage of enclosed land (percentage of fields), *Eriophorum*, an index of past mining activity (mines) and the number of houses, all except the latter being factors attracting Snipe. Fields had three to four times the discriminating power of any other variable (see standardized coefficients in Table 28).

The percentage of a km square with fields was the only factor found to significantly influence Snipe density, accounting for 40% of their variation in numbers (Table 29).

The Snipe is typically a bird of wet, marshy areas, being adapted to take most of its food by probing in soft substrates (see Tuck 1972), areas with ground compaction greater than 2.5kg cm^{-2} seldom being used as feeding areas (Johnson and Ryder 1977). Rushy fields, water meadows, washes, blanket bogs and the marshy edges of rivers and lakes are favoured breeding areas (e.g. Tuck 1972, Sharrock 1976), saltmarshes being used only occasionally as Snipe usually shun salt or brackish water (Walpole Bond 1938). They also use moist heaths and sometimes small, dry fields or heather areas on dry hillsides (Baxter and Rintoul 1953), or stony moorland (Sharrock 1976).

The index of past mining activity, a significant discriminating variable, reflects the presence of grassland sites at higher altitudes. *Juncus effusus*, often used by Snipe as nest-sites, was often found by

Table 28. Summary of discriminant function analysis for areas (km squares) in which Snipe were recorded as present or absent in part of Upper Teesdale in 1978 - 80.

Step No.	Variable entered*	Discriminant function coefficients Standardized	Unstandardized
1	% fields	1.26	0.057
2	*Eriophorum*	0.32	0.36
3	Houses	-0.46	-0.35
4	Mines	0.31	0.11
		Constant -0.92	

Prediction results

	No. of cases	Predicted group membership Absent	Present
Actual group			
Snipe absent	81	75	6
% classified		93	7
Snipe present	24	10	14
% classified		42	58

Percentage of grouped cases correctly classified: 85%

Group centroids

Snipe absent	-0.45
Snipe present	1.53

* % fields - % of km square with enclosed land.

Eriophorum - scored absent as 0, present as 1, predominant as 2.

Houses - the number of houses or farms.

Mines - the number of disused mines, shafts, old levels, hushes.

Table 29. Summary of stepwise multiple regression analysis to show the effect of habitat variables on Snipe density in part of Upper Teesdale in 1978 - 80.

Dependent variable = Snipe density (birds km^{-2})

Independent variables*	Slope	S.E. of slope	F Value	% R^2 Change
% fields	0.032	0.008	14.81	40

constant = 0.968, N = 24, Multiple R = 0.63

Variables excluded from the analysis due to high intercorrelations ($r \geqslant 0.80$) with other habitat variables were:-

a) Aspect with respect to the prevailing wind ($r > 0.80$ with aspect with respect to the sun)

b) Hay, grazed meadow, % mineral soil, cattle ($r > 0.80$) with % fields)

'Grazed' was substituted for 'cattle'

* % fields - % of km square with enclosed land.

old mines and "hushes" provided marshy patches suitable as Snipe feeding areas. The detracting influence of houses (Table 28) could be directly attributable to disturbance. However, it may also indicate that Snipe prefer the rougher, wetter, more tussocky pastures. These fields were further from human habitation and bordered the lower fell slopes. The higher numbers of farms/houses were associated with the better quality pastures and hayfields.

In an analysis of British Trust for Ornithology nest record cards, grass tussocks accounted for 58% of nest-sites, rushes nearly 34%, heather 5% and *Eriophorum* only 0.2% (Mason and Macdonald 1976). Some *Eriophorum* may have been wrongly classified as 'grass' tussocks; however, taking the results at face value they would suggest a very low preference for *Eriophorum*. In Teesdale, cotton grass was a significant discriminating variable and approximately 20% of the Snipe found in the study area were located in km squares where this vegetation type predominated.

d) Curlew.

Significant discrimination was obtained between areas with and without Curlew (final Wilk's Lambda = 0.73, $\chi^2_2 = 32.25$, $P < 0.001$), altitude and *Calluna/Eriophorum* being the only significant discriminating variables (Table 30). On the basis of their discriminant scores 76% of the cases were correctly classified.

The results of a second discriminant analysis, where altitude was excluded from the set of variables, is summarized in Table 31. This suggested that the importance of altitude as a discriminating variable was due partly to the preference of some Curlew for fields, these being available only at lower altitudes. *Eriophorum* was the only other significant discriminating variable although it had less than half the discriminating power of fields (see standardized coefficients; Table 31). These two variables gave significant separation between the groups (final Wilk's Lambda = 0.81, $\chi^2_2 = 20.93$, $P < 0.001$) and 68% of the km squares were correctly classified according to their discriminant scores, values greater than 0.105 being classified as areas with Curlew. The fact that more cases were assigned to the correct group when altitude was included as a discriminating variable (76% v. 67%; Tables 30 and 31) suggests that altitude may be having an effect not incorporated in any other habitat variable or combination of variables measured.

These analyses suggest, therefore, that in Teesdale the Curlew occupies two distinct habitats, blanket bog sites where *Eriophorum* predominates and the lower lying, enclosed pasture. This is in line with the increase of the Curlew during this century and its spread from damp, upland moors to rough, damp pastures at lower altitudes and even down to fields near sea level (e.g. Temperley 1951, Baxter and Rintoul 1952, Chislett 1954, Bannerman 1961, Sharrock 1976). Curlew nest in both grass and heather (e.g. Witherby *et al.* 1940, Bannerman 1961, pers. obs., Teesdale) but grass and sedge are preferred breeding sites to heather (Blair 1961) and areas with a complete cover of heather are avoided (Gordon 1915). In the present study Curlew were associated with pasture and cotton grass areas in preference to expanses of *Calluna/Eriophorum* (discriminant function coefficients; Tables 30 and 31).

In some areas arable land is also used for nesting and occasionally hayfields (Bannerman 1961, Robson and Williamson 1972, Brown 1974). In Teesdale, Curlew were observed feeding in hayfields but of those which bred in fields, nesting was restricted to the rough, damp pastures adjacent to the fell slopes. The breeding habitat

Table 30. Summary of discriminant function analysis for areas (km squares) in which Curlew were recorded as present or absent in part of Upper Teesdale in 1978 - 80.

Step No.	Variable entered*	Discriminant function coefficient Standardized	 Unstandardized
1	Altitude	-0.87	-0.11
2	*Calluna/Eriophorum*	-0.52	-0.57

Constant 6.97

Prediction results

	No. of cases	Predicted group membership Absent	 Present
Actual Group			
Curlew absent	64	50	14
% classified		78	22
Curlew present	41	11	30
% classified		27	73

Percentage of grouped cases correctly classified: 76%

Group centroids

Curlew absent	-0.48
Curlew present	0.75

* Altitude - median altitude, in metres.

Calluna/Eriophorum - scored absent as 0, present as 1, predominant as 2.

Table 31. Summary of discriminant function analysis, where the effects of altitude are excluded, for areas (km squares) in which Curlew were recorded as present or absent in parts of Upper Teesdale in 1978 - 80.

Step No.	Variable entered *	Discriminant function coefficients Standardized	 Unstandardized
1	% fields	1.00	0.040
2	*Eriophorum*	0.45	0.53
		Constant	-0.84

Prediction results

	No. of cases	Predicted group membership Absent	 Present
Actual group			
Curlew absent	64	46	18
% classified		72	28
Curlew present	41	16	25
% classified		39	61

Percentage of grouped cases correctly classified : 68%

Group centroids

Curlew absent	-0.38
Curlew present	0.59

* % fields - % of km square with enclosed land.

Eriophorum - scored absent as 0, present as 1, predominant as 2.

Table 32. Summary of stepwise multiple regression analysis to show the effect of habitat variables on Curlew density in part of upper Teesdale in 1978 - 80.

Dependent variable = Curlew density (birds km^{-2})

Independent variables*	Slope	S.E. of Slope	F Value	% R^2 Change
Vegetation height	-1.26	0.44	8.05	13
Ground roughness	0.95	0.37	6.67	13

Constant = 3.49, N = 41, Multiple R = 0.51

Variables excluded from the analysis due to high intercorrelations ($r \geqslant 0.80$) with other habitat variables were:-

hay, grazed meadow, % mineral soil ($r > 0.80$ with % fields)

* Vegetation height - typical height of the predominant vegetation type grouped as < 10 cm, 10-20 cm and > 20 cm to give a score on an increasing scale of 0-3.

Ground roughness - an increasing subjective scale of 0-2.

usually has frequent patches of peat moss and bog or marshy or waterlogged ground (e.g. Witherby *et al.*1940, Gordon 1915). since these provide suitable feeding sites.

Curlew breed in good numbers up to 550m (Sharrock 1976). Within the study area, over 70% of the Curlew were found below this level (Fig. 10) and altitude was a discriminating variable for predicting their presence or absence (Table 30). No Curlew were found breeding above 682m. Although fewer Curlew breed at higher altitudes, nests have been found up to 769m on the Skiddaw fells and up to 800m on the Pennine and Mallerstang fells (Brown 1974) and in Scotland breeding pairs are found on suitable mountain slopes up to 769m (Baxter and Rintoul 1954).

A stepwise multiple regression analysis suggested that Curlew density was best predicted by vegetation height and ground roughness, although together these variables accounted for only 26% of the variation in Curlew numbers (Table 32). The Curlew prefers rolling grassland hills and areas where the heather is not too rank, often nesting amongst young heather or on more open stretches which have been burnt (Baxter and Rintoul 1953, Blair 1961). Incubating Curlew usually leave their nests long before an intruder is near, therefore the selection of an area with low vegetation is advantageous as predators can be detected some distance away.

e) Golden Plover.

Although not the most abundant species, Golden Plover were more widely dispersed across the study area than any other wader (see Fig. 6 for their distribution in 1978). Between 1978 and 1980 they were present, on average, in nearly two thirds of the km squares.

Discrimination between these areas and those without Golden Plover was significant (final Wilk's Lambda = 0.89, $\chi^2_2 = 11.55$, $P < 0.01$), the presence of peat hags and *Festuca* grasslands being the only discriminating variables (Table 33). Km squares with a discriminant score of more than -0.095 were classified as areas where Golden Plover were present, those with scores below this value being designated as areas where Golden Plover were absent. However the prediction equation did not give equal accuracy for each group; of the km squares where Golden Plover were absent, 85% were assigned to the correct group, whereas of those in which Golden Plover were present, only 39% were correctly classified.

The set of habitat variables was also inadequate for explaining differences in Golden Plover density. *Festuca* grassland was the most important predictor although the inverse relationship of Golden Plover density with *Nardus* grassland also made a significant contribution. Together they accounted for only 15% of the variation in Golden Plover density (Table 34).

Golden Plover accept a wide range of plant communities provided that the general terrain is suitable, few birds nesting where gradients are in excess of 10° (Ratcliffe 1976). The typical breeding habitat is upland moors and peat mosses with stunted heather and often short grass, although undulating heaths at quite low altitudes are sometimes used (Witherby *et al.* 1940). The occurrence of Golden Plover in areas with peat hags, a significant discriminating variable (Table 33), has also been noted by Baxter and Rintoul (1953) and Nethersole-Thompson (1961).

Areas with short vegetation are preferred not only for feeding but also as nest sites. Golden Plover usually, but not invariably, select vegetation less than 15cm tall for nesting which gives the sitting bird good visibility and enables predators to be detected whilst still some distance away (Ratcliffe 1976). Thus in many locations Golden Plover favour patches of heather which have been recently burned as an integral part of Red Grouse management (e.g. Temperley 1951, Chislett 1954, Nethersole-Thompson 1961, Watson 1972, Ratcliffe 1976).

The overriding feature of the Golden Plover's breeding habitat is that the land is unenclosed, although occasional nests have been recorded in upland fields (Ratcliffe 1976). During the present study only three pairs bred in rough pasture fields bordering the fell slopes although other Golden Plover were often flushed from feeding sites in such areas. Only a small part of the study area had enclosed land, the rest largely consisting of blanket bog which Ratcliffe (1976) records as the most favoured of all nesting habitats. Interspersed with the blanket bog, outcrops of calcareous rock give rise to a base-rich soil and a species-rich *Festuca-Agrostis* grassland (see section on Vegetation). In northern England, high densities of Golden Plover are associated with the presence of substantial areas of base-rich soil where the limestone grasslands constitute an atypical habitat, Golden Plover usually being found on acidic moorland (Ratcliffe 1976). This association with upland grassland areas was apparent in the present study, *Festuca* grasslands being a significant variable for predicting both presence or absence and density of Golden Plover. These short, closely grazed grassland sites are important feeding areas, the short vegetation being conducive to prey location as Golden Plover are essentially visual feeders and take most of their food from the ground surface. Also, the supply of invertebrates on the grassland areas is richer than on the neighbouring blanket bog (see section on 'Invertebrates'). It appears, therefore, that much of the study area

Table 33. Summary of discriminant function analysis for areas (km squares) in which Golden Plover were recorded as present or absent in part of Upper Teesdale in 1978-80.

Step No.	Variable entered*	Discriminant function coefficients Standardized	Unstandardized
1	Peat hags	0.84	2.20
2	*Festuca*	0.58	0.84
		Constant -0.94	

Prediction results

	No. of cases	Predicted group membership Absent	Present
Actual group			
Golden Plover absent	39	33	6
% classified		85	15
Golden Plover present	66	40	26
% classified		61	39

Percentage of grouped cases correctly classified : 56%

Group centroids

Golden Plover absent	-0.45
Golden Plover present	0.26

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* Peat hags - scored absent as 0, present as 1.

Festuca - *Festuca* grassland; scored absent as 0, present as 1, predominant as 2.

Table 34. Summary of stepwise multiple regression analysis to show the effect of habitat variables on Golden Plover density in part of Upper Teesdale in 1978 - 80.

Dependent variable = Golden Plover density (birds km^{-2})

Independent variables*	Slope	S.E.of Slope	F Value	% R^2 Change
Festuca	0.69	0.26	7.11	9
Nardus	-0.85	0.38	5.02	6

Constant = 2.47, N = 66, Multiple R = 0.39

Variables excluded from the analysis due to high intercorrelations ($r \geqslant 0.80$) with other habitat variables were:-

a)	Crags	($r > 0.80$ with outcrops)
b)	Cattle	($r > 0.80$ with hay and grazed meadow)
c)	Houses	($r > 0.80$ with grazed meadow

'Grazed' was substituted for cattle

* *Festuca* - *Festuca* grassland; scored absent as 0, present as 1, predominant as 2.

Nardus - *Nardus* grassland; scored absent as 0, present as 1, predominant as 2.

is suitable Golden Plover habitat, this accounting for their wide distribution. The blanket bog provides suitable nest sites and if the vegetation here is too tall and dense for easy feeding, patches of grassland are usually close by. The strips of alluvial grassland by the larger streams are apparently important to some pairs, birds often moving their broods from blanket bog areas to the streamsides later in the season, presumably to take advantage of the richer food supply.

f) Dunlin.

Between 1978 and 1980 Dunlin occurred, on average, in only 19 km squares within the study area. A highly significant discrimination was achieved (final Wilk's Lambda = 0.58, $\chi^2_2 = 56.11$, $P < 0.001$) between these sites and areas with no Dunlin by which 92% of sites without Dunlin and 68% of sites with Dunlin were correctly classified (Table 35). For each case, discriminant scores of more than 0.70 were classified as areas in which Dunlin were likely to be present, those below this score being designated as sites without Dunlin.

In Britain the Dunlin's typical breeding habitat is poorly drained upland moors with scattered small pools (Sharrock 1976) although they also breed near sea level on saltmarshes (e.g. Greenhalgh 1969, Rankin 1979) and on the machair grasslands of the Outer Hebrides (Fuller 1978 and 1981, Wilson 1978). The breeding areas are almost always damp or marshy, poorly drained areas (e.g. Yalden 1974, Fuller 1978) although in Finland Dunlin breed on coastal meadows with short vegetation and comparatively dry, often stony and sandy soil (Soikelli 1964). In arctic Alaska Dunlin select relatively well drained tundra because these provide the first snow-free areas and the lower marshes are flooded with meltwater. However, after the eggs hatch the adults and young move to feed in the marshes which by then are drained of the floodwaters (Holmes 1966a).

In Teesdale, Dunlin selected areas with standing water and tended to avoid sites with relatively large amounts of *Calluna/ Eriophorum* (see discriminant function coefficients; Table 35). The dislike of larger expanses of *Calluna/Eriophorum* may relate to the Dunlin's preference for more waterlogged sites with pools. The typical *Calluna/Eriophorum* blanket bog community has few pools or hollows (Ratcliffe 1977a) and therefore does not constitute suitable Dunlin breeding habitat. The accessibility of water has been stressed by Brown 1938, Witherby *et al.* 1940, Bannerman 1961 and Watson 1972 . In the Peak District Yalden (1974) found Dunlin breeding distribution was correlated with the distribution of *Eriophorum vaginatum* but that pairs were absent where the cover of cotton grass was not broken up by small pools. Nests are often situated next to small pools or creeks (Brown 1938 and 1974).

Waterlogged areas and pools are of importance since they provide suitable feeding grounds where the main prey of Dunlin, Chironomidae and Tipulidae larvae occur (Holmes 1966b). The Pennine areas with drier peat have fewer Tipulidae (Coulson (1962). Dunlin become more reliant on the margins of open water as feeding areas as the surrounding ground dries out (Maclean 1969). Therefore in selecting areas with standing water, particularly when these are larger bodies such as the moorland tarns or Cow Green reservoir, Dunlin have wet sites available for feeding even during dry weather.

In a stepwise multiple regression analysis none of the habitat variables had a significant effect on Dunlin breeding density. Holmes (1970) has suggested that the density of breeding Dunlin is related to the abundance and availability of their food supply. No data are available to test whether Dunlin density is food related in Teesdale.

Table 35. Summary of discriminant function analysis for areas (km squares) in which Dunlin were recorded as present or absent in part of Upper Teesdale in 1978 - 80.

Step No.	Variable entered*	Discriminant function coefficient Standardized	 Unstandardized
1	Water	0.96	1.21
2	*Calluna/Eriophorum*	-0.39	-0.43

Constant -0.15

Prediction results

	No. of cases	Predicted group membership Absent	 Present
Actual group			
Dunlin absent	86	79	7
% classified		92	8
Dunlin present	19	6	13
% classified		32	68

Percentage of grouped cases correctly classified : 88%

Group centroids

Dunlin absent	-0.40
Dunlin present	1.80

---

* Water - standing water; scored 1-3 according to the size of the water body.

Calluna/Eriophorum - scored absent as 0, present as 1, predominant as 2.

Discussion

The study area as a whole is presumably attractive to waders because it is a large, relatively undisturbed, open area, having few trees and for the most part being flat or only gently sloping. The song flights and displays of waders are well adapted for presentation in such habitats (Dabelsteen 1978) and their defence against predators is better (Klomp 1953) probably because the greater visibility afforded by the open nature of the terrain makes early detection of predators possible and aerial mobbing more effective. However, within the study area, Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin all exhibited aggregated distributions (Table 7) suggesting that selection of specific habitats was occurring.

The multivariate analyses suggested which habitat variables were implicated in eliciting the settling reaction of the different wader species. Factors affecting presence or absence were satisfactorily determined by discriminant analysis for all wader species except Golden Plover, 78-90% of the cases being correctly classified (Tables 22, 23, 25, 26, 28, 30, 31, 35). The poor discrimination for Golden Plover (only 56% of the cases correctly classified; Table 33) suggests that the variables measured were inadequate to explain their distribution; also, it is possible that since Golden Plover were recorded in a wide range of habitats throughout the study area, their selection within this may have been quite weak. The multiple regression analyses showed that some of the habitat variables were also important, to varying degrees, as factors influencing breeding density for all species except Dunlin (Tables 24, 27, 29, 32 and 34). Miller (1942) and Tinbergen (1948) considered that habitat selection was mediated by only a few environmental stimuli. The maximum number of significant variables in any of the multivariate analyses was five.

The main characteristics of the distributions of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin are summarized in Table 36. Dunlin was the only species to show a distinct preference for blanket bog, most waders being attracted to grassland sites in spite of their lower availability (23 km squares grassland v. 82 km squares blanket bog). The preferences for grassland were apparent in that:-

a) a higher percentage of km squares with grassland had waders present than the km squares where blanket bog predominated (Table 9);

b) species richness and species diversity was higher than on blanket bog sites (Tables 16 and 17);

c) densities of Lapwing, Redshank and Snipe were all significantly higher on grassland as opposed to blanket bog (Table 15). The same trend was apparent for Curlew and Golden Plover although the differences in density were not significant.

As a result of b) and c) there was more inter- and intra-specific overlap on grassland (Table 21). This may partly be due to the fact that more species selected grassland sites but it may also be that, over the breeding season as a whole, the poorer food supply on blanket bog results in it having a lower carrying capacity than grassland areas where high prey levels are sustained throughout the season (see 'Invertebrates'), thereby supporting a greater number of breeding pairs.

Of the six vegetation types having the largest extent within the study area (Table 1) most species were found on four or five types whilst Golden Plover was recorded on all six (Fig. 8). However,

Table 36. A summary of the main features of the distributions of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin in Upper Teesdale.

	Altitude	Pasture	Upland Grassland	*Eriophorum*	*Calluna/ Eriophorum*	Water
Lapwing	Low altitude.	Highest densities.	Scattered pairs where vegetation is short.	-	-	May attract pairs into predominantly blanket bog areas - usually on alluvial grassland in river valleys; some pairs round reservoir.
Redshank	Low altitude.	Highest densities.	-	-	-	
Snipe	Most of population at low altitude. Scattered pairs higher up.	Highest densities.	Scattered pairs near marshy areas or flushes.	Low densities.	Few pairs.	Marshy areas in river valleys and around reservoir. Wet drainage channels.
Curlew	Intermediate altitudes - lower fell slopes and river valleys.	Scattered pairs; high densities in parts. Flocks at beginning and end of season.	Wetter sites. Tussocky areas.	Carries almost 50% of the population.	Few pairs. Low density.	No particular attraction to water but often found at the lower altitudes of river valleys.
Golden Plover	Present throughout altitude range but mainly on higher fells.	Very few nesting pairs. Sometimes used for feeding. Flocks at beginning and end of season.	Short dry limestone grasslands most favoured habitat. Highest densities.	Carries 33% of population.	Carries 40% of population.	-
Dunlin	Fell tops; also lower down by large bodies of standing water.	Small flocks occasionally present during bad weather early in season.	-	Most of the population. Highest densities.	Few pairs. Low density.	Pools and tarns on fell tops. Especially favour large bodies of standing water; highest densities around reservoir.

the actual preferences as demonstrated by selection ratios (Table 14), were much narrower than this spread across several plant communities would suggest. For each species there was significant evidence of selection of only one or two vegetation types. Thus Lapwing, Redshank and Snipe selected both meadow and *Festuca*, Curlew selected meadow and *Eriophorum* , whilst Dunlin selected only *Eriophorum*, a preference also noted by Yalden (1974) in the Peak District of Derbyshire. A selection of *Festuca* grassland was the only significant preference demonstrated for Golden Plover. These preferences coincided with the vegetation types having the highest densities of each species (Fig. 9). There was no evidence that *Nardus* grassland, *Calluna/Eriophorum* or *Calluna* was preferentially selected by any of the waders.

The waders also showed some separation with respect to altitude (Figs. 10 and 11), the main features of their distributions parallelling the trends shown by the total avifauna. The avifauna of upland areas shows some degree of altitudinal zonation but the main trend is a reduction in species diversity with increasing altitude, only eight species being characteristic of ground above 763m (Ratcliffe 1977b). In the Moor House and Cross fell region several wader species have been found nesting at record elevations in Britain; Lapwing 880m, Curlew 790m , Snipe 790m and Redshank 730m (Ratcliffe 1977a). However, the incidence of these species breeding at such high altitudes in the study area is presumably low since these records by far exceed the highest breeding sites observed between 1978 and 1980 (see Fig. 10). Only Golden Plover and Dunlin were observed within a short distance of the summit of Cross Fell (893m), the highest point of the study area. Lapwing, Redshank and Snipe all occurred predominantly at the lower altitudes (Figs. 10 and 11) probably because of their selection for grassland areas (Table 14) which had greater availability lower down (Fig.13).

The main effects of altitude on the distributions of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin were:-

a) a decrease in the mean number of species per km square with increasing altitude, the loss being about one species for every 100m rise in altitude (Fig. 12);

b) a decrease in the mean number of birds per km square (Figs. 15 and 16).

Thus a km square at high altitude has, on average, both fewer wader species and fewer breeding pairs than a corresponding square at lower altitude. The relationships were not consistent with the change from grassland to predominantly blanket bog as altitude increased (Fig. 13), the effect being apparent within both grassland and blanket bog sites (Figs. 14, 15 and 16). Also, it seems unlikely that any climatic differences associated with the range of altitudes in the study area could be responsible for the decline in wader abundance and species richness. Dunlin, the smallest of the six wader species and hence the one likely to be most susceptible to chilling, particularly the chicks, breeds on the highest and most exposed part of the study area, Cross Fell.

As several interesting changes have been noted in the invertebrate fauna at higher altitudes it is possible that the altitudinal decline in the waders may be related to their food supply. Although there is some replacement of characteristically lowland species by upland and montane species, the general trend is a fall in the number of insect species with increasing elevation (Greenslade 1968, Mani 1968 and Houston 1970). Coulson and Butterfield (pers. comm.) in a study of a variety of upland sites in northern England also found a negative linear correlation with altitude for both invertebrate abundance and species richness but only on peat sites; there was no such significant relationship on mineral sites. The decrease applied to all groups except Tipulidae which increased with altitude.

Mani (1962 and 1968) considered that the most obvious effects of altitude on insects were a tendency to melanism and a reduced wing size and mean body length, the latter being of most consequence to birds. Not only is there a progressive reduction in the mean body size of most orders of insects with increasing elevation, but the smaller-sized orders such as Diptera and Collembola gain dominance (Mani 1968). A decrease in the mean body size of Coleoptera was noted by Theile and Kirchner (1958) Mani (1962) and Houston (1970). Considering changes within the same species, Butterfield (1973) found no indication that the size of individuals of two dipterans, *Tipula subnodicornis* and *Molophilus ater*, decreased with altitude but, for beetles, Houston (1970) demonstrated that both males and females of *Patrobus assimilis* showed a significant reduction in body length between 550m and 850m. Since beetles are an important dietary component of many inland feeding waders (see e.g. Collinge 1924-27, Witherby *et al.* 1940, Hibbert-Ware and Ruttledge 1945, Kumari 1958, Dement'ev *et al.* 1969, Ratcliffe 1976) such changes may be of some consequence, particularly as it has been shown that Lapwing chicks prefer Coleoptera of a modal length greater than 5mm (Potts 1970). Presumably adult Lapwing and other waders would preferentially take still larger prey. Byrkjedal (1980) suggests that Golden Plover may select adult Coleoptera, particularly the larger species, in preference to other prey since they were more common in the diet than would be expected from their relative abundance.

Lapwing, Curlew and Golden Plover are all recorded as taking fairly large quantities of berries (*Empetrum* and *Oxycoccus* spp.) (Kumari 1958, Byrkjedal 1978 and 1980) but these would not be available throughout the breeding season and therefore do not constitute a consistent, alternative food supply to invertebrates. Peat is too acidic to support lumbricids, which are often an important contributor to many wader diets, therefore these cannot account for the observed decreases in the wader populations on blanket bog. Also, there is no indication that the supply of earthworms is inadequate on upland grasslands. Svendsen (1957) found a diverse lumbricid fauna on the mineral soils of the Moor House N.N.R., with densities comparable to, and in some instances much higher than, those found on lowland grassland sites.

On balance, therefore, the fact that increasing elevation is associated with a reduction in invertebrate species-richness and abundance of individuals, an increase in the proportion of small sized species and a tendency for the individuals of some species to be smaller, suggests that the higher altitudes may have an inadequate food supply for some waders and that they may be able to support fewer breeding pairs than lowland sites. This is, however, speculative and a detailed study of the energetic requirements of the different wader species is required alongside data on availability of their main prey species at different altitudes to assess whether these requirements can be met.

Of the six wader species studied there was, therefore, some separation with respect to vegetation type and altitude and the variables selected by the multivariate analyses indicated that, for each species, at least some of the factors important in determining their distributions were different and that they were tending to select separate habitats.

However, the similarities in the distributions of Lapwing, Redshank and Snipe, and to a lesser extent Curlew, and their high degree of co-occurrence necessitated further investigation to establish their niche differences more fully (Section 3).

SECTION 3

WADERS OF MARGINAL HILL FARMLAND

The survey carried out in 1978 over an area of 105 km^2 indicated similar patterns of distribution for Lapwing, Redshank, Snipe and Curlew (Section 2). Most of the overlap between these species and the highest densities of breeding pairs, occurred in the km squares centered on the agricultural land in the east of the study area (Fig. 1). To determine the degree of similarity in the distribution patterns of Lapwing, Redshank, Snipe and Curlew at a finer level, and to assess factors influencing their selection of fields as breeding sites, 200 fields within the hill farmland of the Harwood Beck Valley were studied in 1979 and 1980. In addition to the physical characteristics of the fields, aspects of land management practices, as factors potentially affecting the distribution of the waders, were considered for those fields where it was possible to obtain management histories. A sampling programme was undertaken to examine the food supply available to the waders and the growth of Lapwing chicks raised on different habitats was investigated.

1. History and land management practices of the Harwood Beck Valley.

Parts of Upper Teesdale have been under the influence of man since Mesolithic hunters first came in search of the deer which haunted the forest glades and streamside clearings (Roberts 1978). Within the study area, the land affected most today exists as a strip of marginal hill pasture along the Harwood Beck Valley. Here, the environmental changes wraught by man have created a habitat well suited to the waders, namely Lapwing, Redshank, Snipe and, to a lesser extent, Curlew, which are now characteristic of the area.

The study of pollen deposits indicates that the first major vegetation change occurred between 7000-6000 B.C. when the woodland was replaced by grassland on the better drained limestone soils and blanket bog over areas of boulder clay (Turner 1978). The deterioration of the climate to cooler, wetter conditions at this time was unfavourable for tree growth. Man felling the trees for timber or to create pasture for his herds may also have been a factor and the browsing of domesticated cattle and sheep helped prevent regeneration. The disappearance of much of the woodland created a habitat suitable for waders, their displays being well adapted for delivery in open situations (Dabelsteen 1978).

There is however little evidence of permanent settlement in the upper dale before 1100 A.D., the higher altitudes being used mainly as summer pastures (Roberts 1978). Small unscattered farmsteads were later established and then in the second half of the 18th and the 19th century extensive lead mining throughout the dale caused a rise in the human population. Since mining declined in the final decades of the 19th century, the population has fallen and today the picture is of small groups or isolated farms each surrounded by an area of "inby" land, the enclosed, managed land around the farms, beyond which lies the "outby" or fells, the rough, unimproved areas used for summer grazing.

Sheep have been, and still are, the dominant grazing animal in Upper Teesdale. They graze the lower, improved pastures only during the winter and at lambing time, being turned out onto the fells in the summer when cattle replace them on the pasture of the valley bottom. Grazing maintains the low vegetation essential to Lapwing, walking being impeded in tall vegetation (Klomp 1953). It can also promote tussock formation (Wein 1973) thereby providing sites for the typically screened nests of Redshank and Snipe.

The high rainfall (1523 mm yr^{-1} on Widdybank rising to over 2000 mm yr^{-}

on Cross Fell (Pigott 1978a)) leaches the soil of nutrients and increases its acidity. To prevent the pasture created in the east of the study area reverting to heather, coarse grasses and rushes (habitat more favourable to Golden Plover, Dunlin and Curlew) drainage and applications of fertilizer are necessary. In the mid 19th century many fields were provided with underdrains and the process continued throughout the whole of Lord Barnard's estate in the second half of the 19th century (Roberts 1978). Thus all fields close to the farms in the Harwood Beck Valley which required drainage would at this time have had tile drains inserted. Although some of these still function, today this type of drainage has been superceded by less expensive open drains ("grips") which are used in many marginal pastures where rush infestation is heavy. Since drainage discourages the germination and growth of rushes it may be expected to decrease the availability of suitable nesting habitat for Redshank and Snipe and reduce the amount of soft, marshy ground essential as Snipe feeding localities. Conversely, it has helped create the better quality pastures with less tussocky vegetation more suited to Lapwing.

Applications of lime and basic slag are used to counteract the leaching effect of rainfall. Liming raises the pH of the soil thereby favouring the establishment of earthworms and enhancing the waders' food supply.

Although some grain has been grown in the past, hay is the main crop and today there is no arable land. Most fields are therefore little disturbed by machinery during the breeding season. The hay meadows and better quality pastures are treated with both organic and inorganic fertilizers. Fortunately there has been little use of herbicides thereby helping preserve the herb-rich vegetation of the hay meadows and consequently maintaining a diverse invertebrate fauna. Lapwing nest in the hayfields and these are used extensively as feeding areas for flocks of Lapwing, Golden Plover and Curlew at both the beginning of the breeding season and again after the hay has been cut.

The meadows existing in Upper Teesdale are the product of at least 125 years of intensive management and many have been cultivated two to three times longer (Roberts 1978). The long standing management practices have created and maintained a landscape favourable to the waders which now breed there and have resulted in the formation of several field types. Some fields have been allowed to revert to rough pasture with a high cover of rushes, while others have probably never been improved.

2. Invertebrates.

The differences in the invertebrate faunas found on the peat and mineral soils of the study area, and the implications these have for breeding waders, have been discussed previously (Section 1). Mineral soils provide the agricultural land at the lower altitudes of the study area and at higher altitudes occur only alongside the main streams and rivers and on areas where limestone and sandstone outcrop. Most of the invertebrates of these upland grasslands are also typical of lowland grasslands in Britain. However, many lowland species are not represented having failed to penetrate the higher altitudes. Thus the fauna of the Teesdale grasslands is essentially a species-poor, lowland grassland community restricted to those species able to tolerate the harsh climate (Coulson & Whittaker 1978).

Within the Harwood Beck Valley a variety of vegetation types were distinguished (Section 3, 3)). As these were found to have varying densities of breeding waders it was desirable to investigate whether these differences were food-related. Several authors have attributed variations in prey levels to differences in the breeding densities of certain avian species (Holmes 1970, van Balan 1973, Rankin 1979) and Seastedt & Maclean (1979) found that territory size was correlated with food availability in Lapland Longspurs. Thus in 1979 and 1980 pitfall traps and soil cores were used to investigate invertebrate populations on different field types in the

Harwood Beck Valley to try and establish whether variations in prey levels could be influencing the distribution of waders breeding there.

Methods

a) Pitfall traps

Pitfall traps have been used extensively to sample surface dwelling invertebrates such as Araneida, Collembola, Coleoptera and especially Carabidae (e.g. Williams 1959, Duffey 1962 & Pearson & White 1964). Their ease of use commends them as a potentially valuable means of sampling certain animal populations (Luff 1975). However, pitfall trapping must be used with discretion; it is of little value for the direct estimation of populations or the comparison of communities (Briggs 1961, Greenslade 1964) but it is adequate to assess the relative numbers of a species in different vegetation types (Greenslade 1964). For the present study the method was considered suitable since it was only necessary to obtain a relative rather than absolute measure of wader prey availability on the different field types. The number of animals caught in pitfall traps is partly dependent on activity (Greenslade 1961). This was desirable as it incorporates a measu of the availability of the invertebrates to the birds. The active species are likely to be more readily available as prey since they will be detected with greater ease by waders, such as Lapwing, which feed by visual cues. As all traps were in the same general locality any climatic effect on the activity of the invertebrates would be the same for each site.

Pitfall traps were placed on representative areas of different field types in 1979 and 1980. Each trap had a neck diameter of 45mm. and was set so that the rim was flush with the ground surface as this ensures maximum catches (Greenslade 1964). Specimens were quickly killed, so preventing their escape and predation of other invertebrates caught, by the addition of 50ml. of a 2% formalin-detergent solution to each trap.

All traps were emptied, cleaned (a clear, smooth surface being necessary to maintain retaining efficiency (Luff 1975)) and reset at fortnightly intervals. Ten traps were used at all sites except for two sites in 1980 where five traps were used. (An analysis of the 1979 data at these two sites suggested that the last five traps produced the same prey levels and pattern of seasonal abundance as the first five traps.) The traps were set in a straight line with an inter-trap distance of 5m., catches being reduced if the traps are too closely spaced relative to the distance moved by the animals (Luff 1975). As most of the sampling areas were grazed plastic traps were used in preference to glass, despite their lower catching efficiency (Luff 1975), so that if damaged they would not be harmful to the stock.

b) Soil sampling.

For sampling earthworms Zicsi (1962) recommended a minimum core size of $1/16m^2$ but Svendsen (1955) found that $1/35m^2$ and $1/25m^2$ cores gave satisfactory population estimates on the upland soils of the Moor House N.N.R. although he obtained more damaged specimens from the smaller of his two core sizes. Samples this size are too large to hand sort quickly and efficiently in the field. A preliminary survey indicated that estimates of invertebrate density obtained from $1/100m^2$ cores were not significantly different to those obtained from $1/30\ m^2$ cores (15 x $1/100m^2$ soil cores:- 93±26 invertebrates m^{-2}; 15 x $1/30m^2$ soil cores:- 110±20 invertebrates m^{-2}). Therefore, for all further samples a core size of $1/100m^2$ was used to a depth of 15cm.

Samples were taken on representative areas of different field types within the Harwood Beck Valley in 1979 and 1980. To extract the larger invertebrates samples were either hand sorted in the field in a white enamel tray or carried back to the laboratory and sorted within two days, any samples stored overnight being kept at 5°C.

Soil wetness was determined for all sites sampled in 1979 and 1980, and organic content was assessed for the samples taken in August 1980. In each field four small cores were taken to a depth of 15cm. The vegetation was clipped from the surface and the cores bulked together to form one sample before weighing. To determine the moisture content the samples were dried in an oven at 105°C until constant weight was reached. Small weighed sub-samples of the dried soil were placed in a muffle oven at 450°C for four hours, cooled in a dessicator and reweighed to assess organic content.

Results

i) Invertebrate abundance and seasonal variation in numbers on different field types.

a) Surface-active invertebrates.

Pitfall traps were used to sample surface active invertebrates on representative areas of different field types, the sampling sites being characterized as follows.

1. Dry, heavily grazed meadow. Grazed for the whole year by cattle and sheep. Treated annually with compound fertilizer at the rate of 252kg.ha^{-1} and applications of farmyard manure.

2. Hay meadow. Grazed by sheep from August to April and by cattle for about two weeks only each year. Treated annually with compound fertilizer at the rate of 377kg.ha^{-1} and applications of farmyard manure.

3. Two grazed meadow sites with a cover of *Juncus effusus* exceeding 5% were sampled. The first site chosen was so heavily grazed during 1979 that the *Juncus* was vastly reduced in height, thus a second site was also sampl in 1980 in case the heavy grazing and reduction in sward height had made the former site atypical.

J1:- Grazed by sheep and cattle all year apart from the winter months. Farmyard manure spread on the drier areas. Limed every five years.

J2:- Grazed by cattle at the rate of 5.93 cows ha^{-1} for three months during the summer and one horse in winter. Treated with compound fertilizer at the rate of $252kg.ha^{-1}$ every two years and applications of farmyard manure but only on the dry areas.

5. Wet, rough pasture. Grazed by cattle and sheep. Not fertilized.

6. Damp, lightly grazed meadow. Horses were grazed all year at an intensity of $0.57ha^{-1}$ and cattle grazed at the rate of $1.14ha^{-1}$ for 2-3 months in the summer. Not fertilized.

Fig. 16 shows the mean number of invertebrates caught per pitfall trap per day between 15 April and 8 July in 1979 and 1980 on the different field types, this period covering the laying and fledging periods for the majority of the waders. (Sampling continued up to 5 August on all sites but hay meadow, catches here being terminated on 8 July due to haymaking. Data has, therefore, been included only up to 8 July so that all sites are directly comparable). Numbers of invertebrates were highest on hay meadow in both 1979 and 1980 and lowest on wet, rough pasture. The lightly grazed meadow sampled in 1979 had lower invertebrate catches than the heavily grazed site for all groups except spiders. Similar levels of invertebrates were found on both the *Juncus* sites in 1980 for all groups except Diptera which were more abundant on J1, possibly as a result of farmyard manure being spread on part of the site.

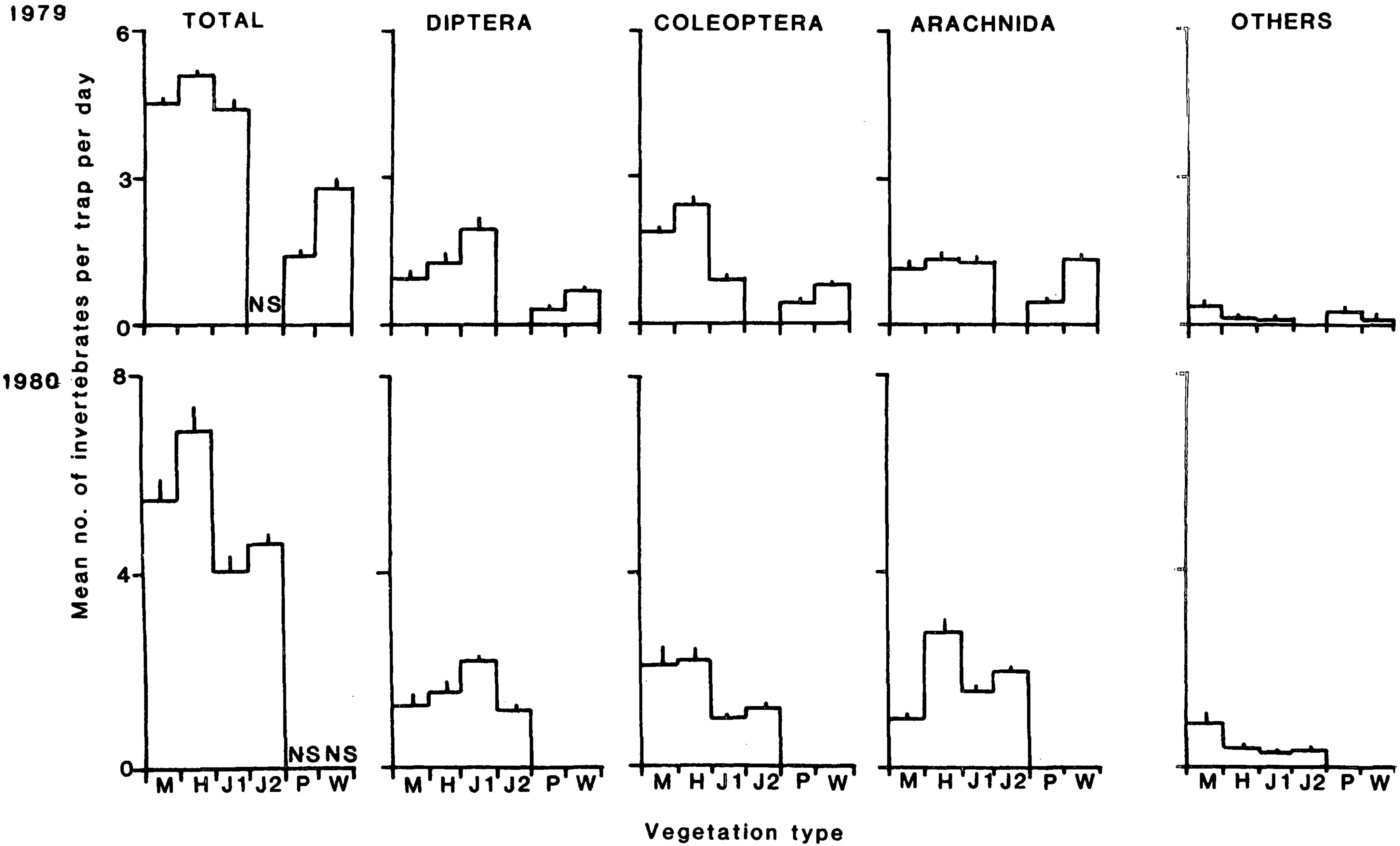
Traps were emptied at fortnightly intervals from 15 April to 5 August on all areas except hay meadow where catches were terminated on 8 July due to haymaking. The seasonal variation in the number of invertebrates caught at the different sites is shown in Figs. 17 to 21. The period of prey abundance has been taken as the time when catches exceeded four invertebrates per trap per day, this incorporating the most obvious peaks in the seasonal abundance of invertebrates on the different sites. The peak invertebrate levels attained and the periods of prey abundance are

Figure 16

Mean numbers of invertebrates (total, Diptera, Coleoptera, Arachnida and "others") caught per pitfall trap per day from 15 April to 8 July 1979 and 1980 on different field types in the Harwood Beck Valley.

Error bars indicate one S.E. of mean

M = dry, heavily grazed meadow, no *Juncus effusus*.
H = hay
J1 & J2 = grazed meadow, *Juncus effusus* cover >5%.
P = wet, rough pasture.
W = lightly grazed meadow, no *Juncus effusus*.
N.S. = not sampled.


1979
1980
TOTAL
DIPTERA
COLEOPTERA
ARACHNIDA
OTHERS
6
3
0
8
4
0
NS
NS
NS
M
H
J1
J2
P
W
Mean no. of invertebrates per trap per day
Vegetation type

tabulated for each area in Table 36 to facilitate comparison between sites. Each site showed a gradual build up of invertebrate numbers to a peak in late May or June followed by a decline. However, a number of differences between sites were apparent which can be summarized as follows:-

(a) on heavily grazed meadow peak invertebrate levels were significantly higher than those on the lightly grazed site in 1979 ($t = 2.4$, d.f. = 18, $P<0.05$; Table 36) and the period of abundance was twice as long;

(b) wet rough pasture had the lowest invertebrate levels of any of the sites sampled and there was no period when catches exceeded four invertebrates per trap per day although a slight peak in numbers was evident between 10 June and 22 July (Table 36, Fig.20);

(c) on both *Juncus* sites the period of invertebrate abundance started on 13 May in both 1979 and 1980. This was 2-4 weeks earlier, for both years, than any other site except for the hay meadow (Table 36). In 1979, J1 showed two peaks of invertebrate abundance (Fig. 19). The first short peak, 13-27 May, may have been a result of large quantities of farmyard manure being spread on part of the site in early May since large numbers of dung associated invertebrates (especially *Scathophaga stercoraria*) appeared in the pitfall catches at this time.

(d) On hay meadow invertebrate levels early in the season were at least 40% higher than on all other sites in 1980; there was also a peak evident at this time in the 1979 catches (Fig. 18).

For sites sampled in both 1979 and 1980 the main difference between years was the timing of peak invertebrate levels, these being reached 2-6 weeks earlier in 1980 (Table 36). The earlier peak in 1980 may be attributable to the mild, dry spring; by contrast the hard winter of 1978-79 was followed by a particularly cold spring with snow blizzards occurring

Table 36.

The timing and magnitude of peak prey levels and the period of invertebrate abundance as shown by pitfall catches made on different field types in the Harwood Beck Valley in 1979 and 1980.

The period of abundance refers to the interval where pitfall catches exceeded 4 invertebrates per trap per day.

	Peak invertebrate levels (mean no. invertebrates per trap per day ± S.E.)	Date of peak invertebrate levels	Period of abundance
Heavily grazed meadow:			
1979	8.3 ± 0.9	10 - 24 June	8 weeks: 27 May - 22 July
1980	10.8 ± 1.5	27 May - 10 June	8 weeks: 27 May - 22 July
Hay meadow:			
1979	9.0 ± 1.0	24 June - 8 July	6 weeks +: 15-29 April, 10 June - 8 July +
1980	9.2 ± 1.0	27 May - 10 June	12 weeks +: 15 April - 8 July +
Juncus: Site 1			
1979	7.5 ± 0.6	8 - 22 July	8 weeks: 13-27 May, 10 June - 22 July
1980	6.0 ± 0.6	27 May - 10 June	6 weeks: 13 May - 24 June
Juncus: Site 2			
1980	6.8 ± 0.4	27 May - 10 June	6 weeks: 13 May - 24 June
Lightly grazed meadow:			
1979	5.6 ± 0.7	10 - 24 June	4 weeks: 10 June - 8 July
Wet rough pasture:			
1979	2.8 ± 0.3	24 June - 8 July	No period of abundance. Slight peak evident 10 June - 22 July but invertebrate numbers never reach those recorded on other sites.

Figure 17

Mean numbers of invertebrates (total, Diptera, Coleoptera, Arachnida and "others") caught per pitfall trap per day on a dry, heavily grazed meadow in the Harwood Beck Valley between 15 April and 5 August 1979 and 1980.

Error bars indicate one S.E. of mean. Catches based on 10 pitfall traps.

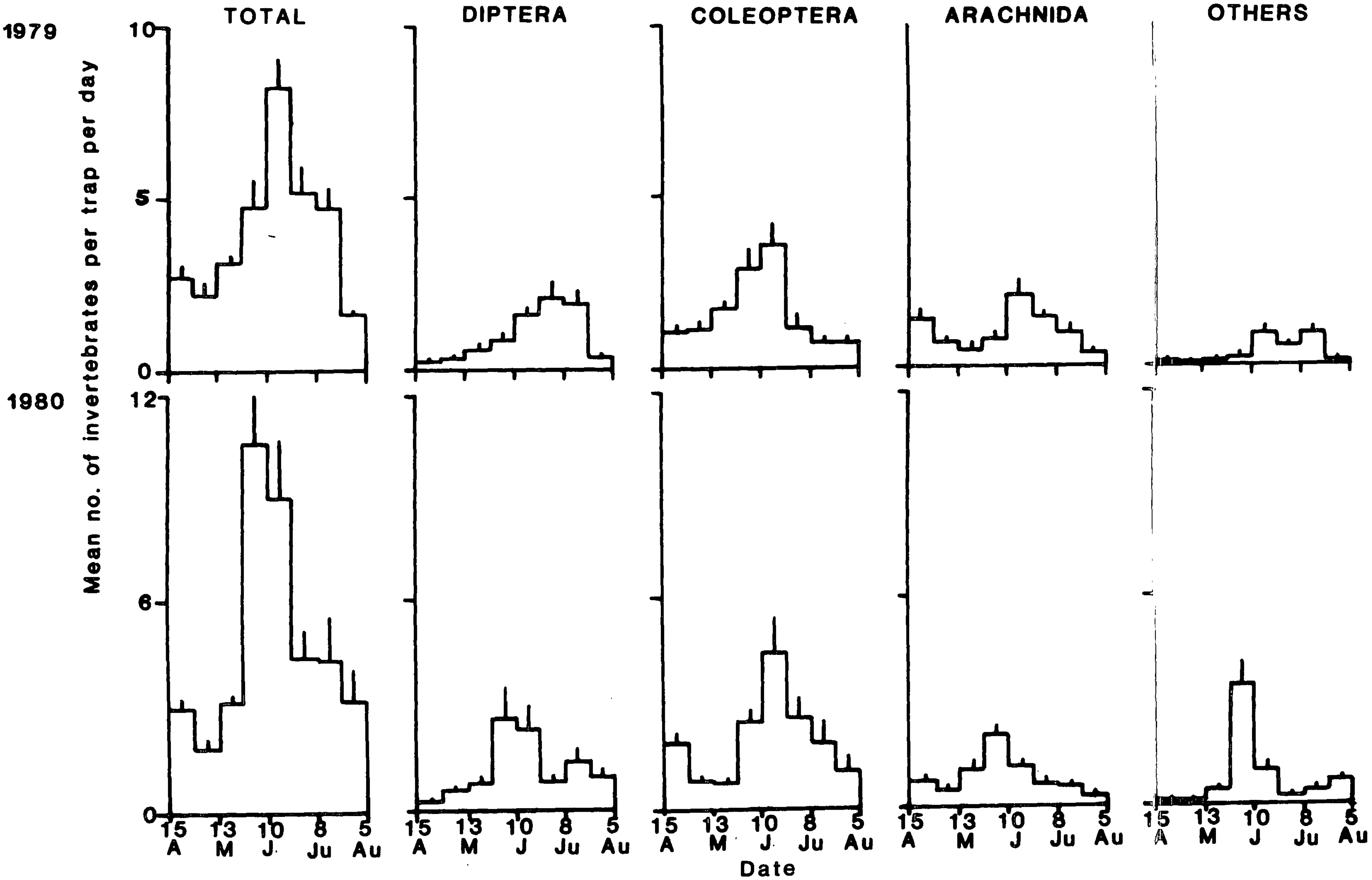

TOTAL
DIPTERA
COLEOPTERA
ARACHNIDA
OTHERS
1979
1980
Mean no. of invertebrates per trap per day
10
5
0
12
6
0
15
A
13
M
10
J
8
Ju
5
Au
Date

Figure 18

Mean numbers of invertebrates (total, Diptera, Coleoptera, Arachnida and "others") caught per pitfall trap per day on a hay meadow in the Harwood Beck Valley between 15 April and 8 July 1979 and 1980.

Error bars indicate one S.E. of mean. Catches based on 10 traps in 1979 and 5 traps in 1980.

Catches were terminated on 8 July each year due to hay-making.

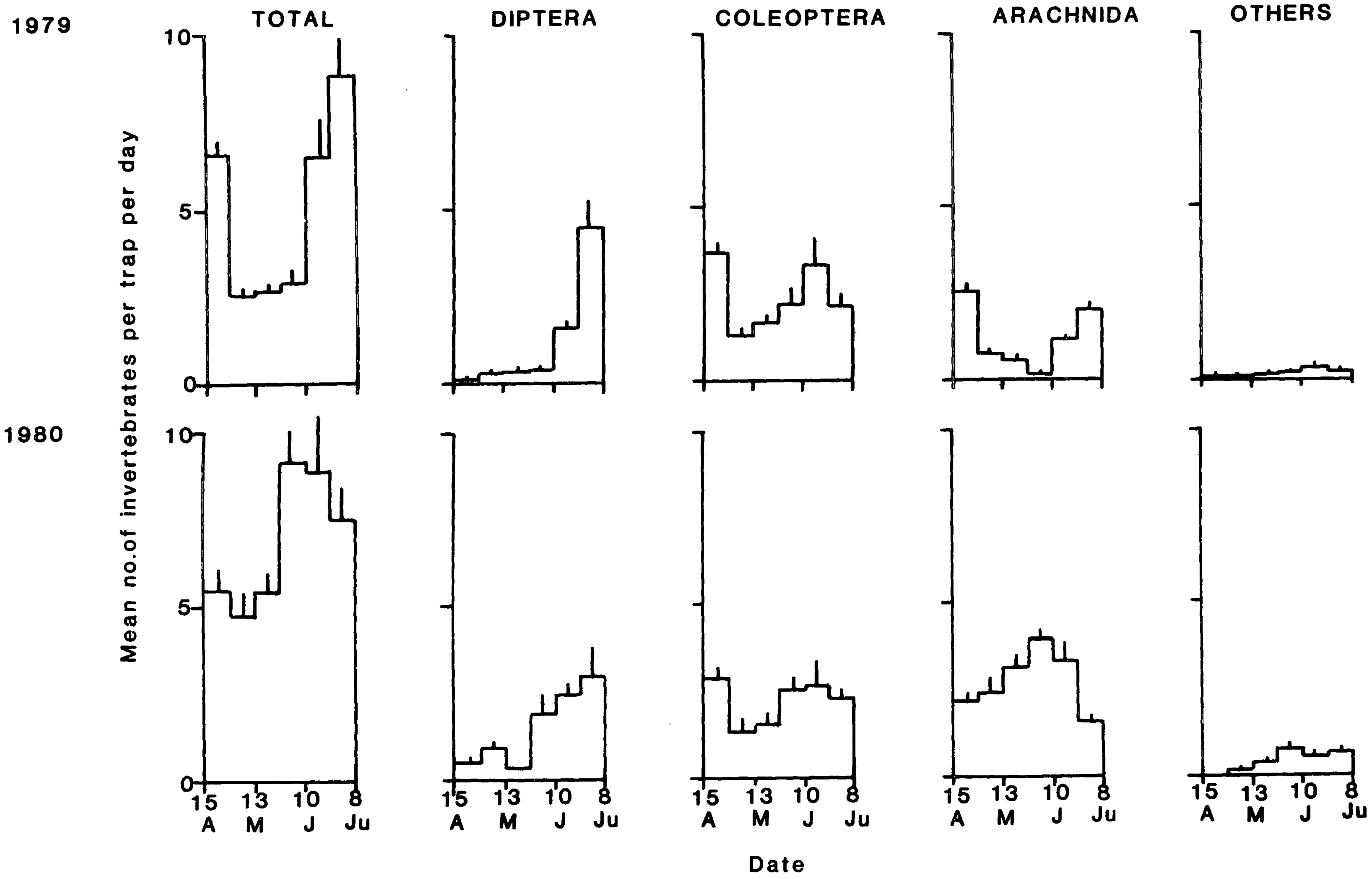

1979
1980
TOTAL
DIPTERA
COLEOPTERA
ARACHNIDA
OTHERS
10
5
0
Mean no.of invertebrates per trap per day
15
13
10
8
A
M
J
Ju
Date

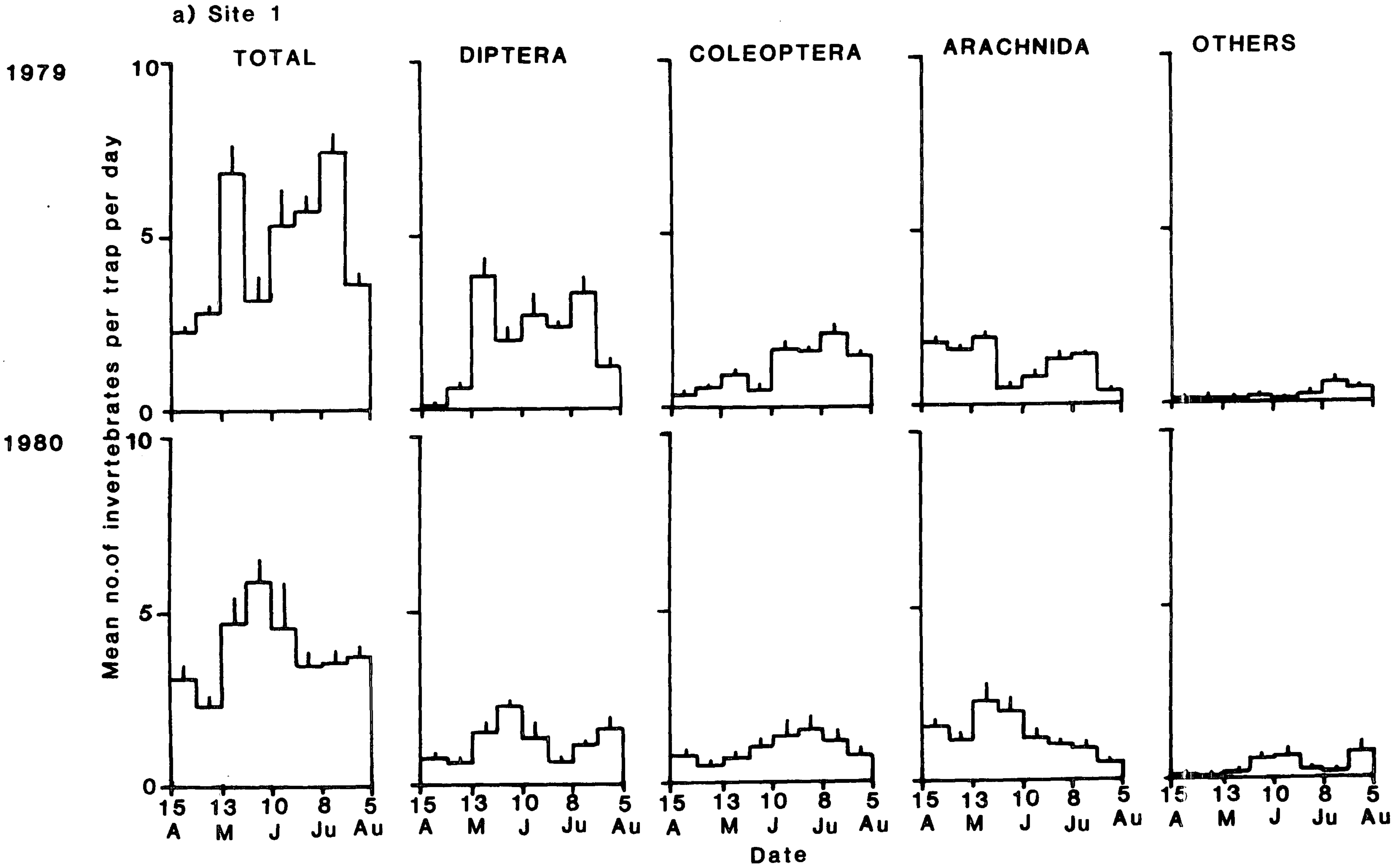
Figure 19

Mean numbers of invertebrates (total, Diptera, Coleoptera, Arachnida and "others") caught per pitfall trap per day on grazed meadow with *Juncus effusus* cover greater than 5% in the Harwood Beck Valley between 15 April and 5 August 1979 and 1980.

a) Site 1 - sampled 1979 and 1980

b) Site 2 - sampled 1980

Error bars indicate one S.E. of mean. Catches based on 10 traps for site 1 in 1979 and Site 2 in 1980, and 5 traps for Site 1 in 1980.


a) Site 1
TOTAL
DIPTERA
COLEOPTERA
ARACHNIDA
OTHERS
1979
1980
10
5
0
Mean no.of invertebrates per trap per day
15 A
13 M
10 J
8 Ju
5 Au
Date

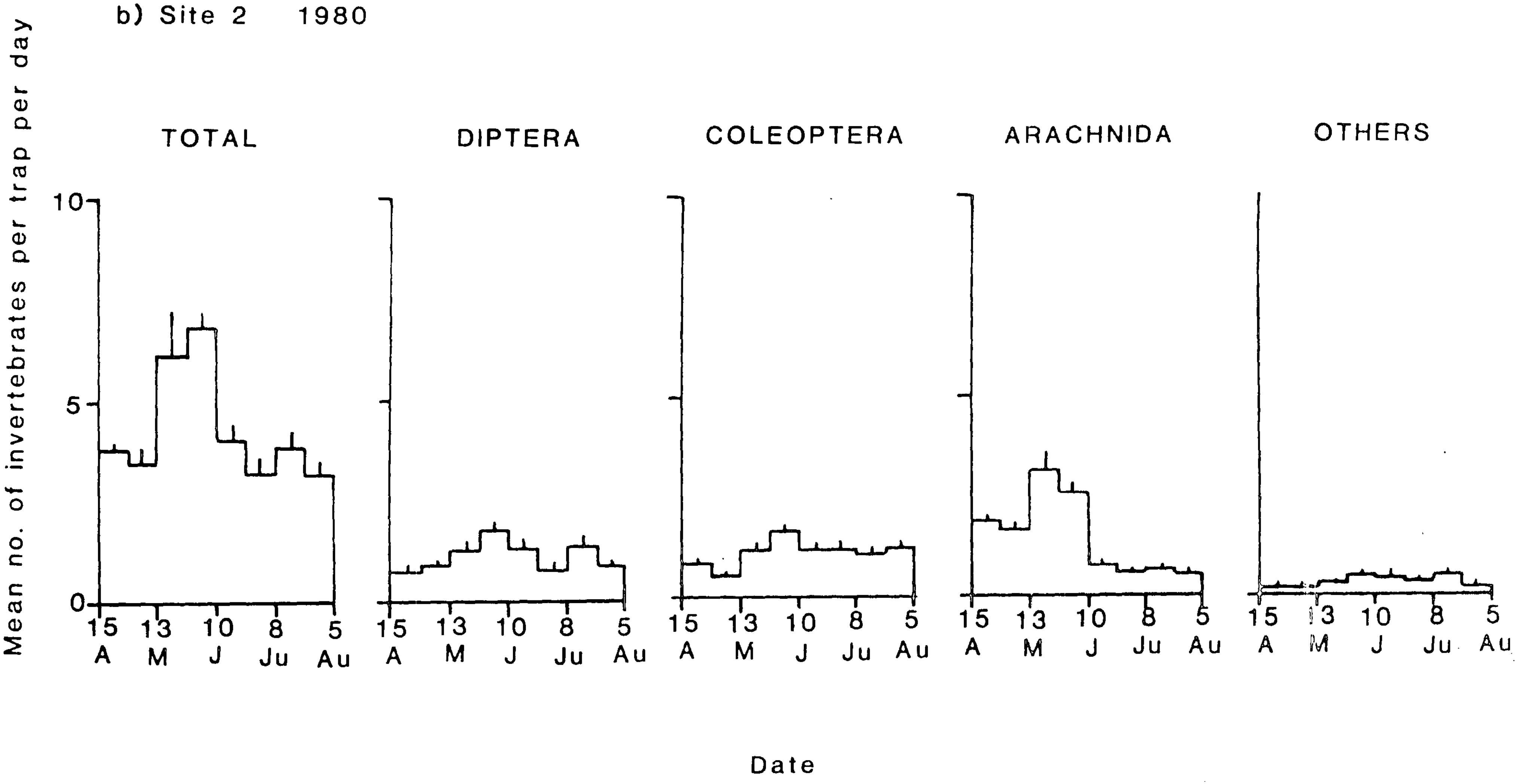

b) Site 2 1980
Mean no. of invertebrates per trap per day
TOTAL
DIPTERA
COLEOPTERA
ARACHNIDA
OTHERS
10
5
0
15 A
13 M
10 J
8 Ju
5 Au
Date

Figure 20

Mean numbers of invertebrates (total, Diptera, Coleoptera, Arachnida and "others") caught per pitfall trap per day on wet, rough pasture in the Harwood Beck Valley between 15 April and 5 August 1979.

Error bars indicate one S.E. of mean. Catches based on 10 traps.

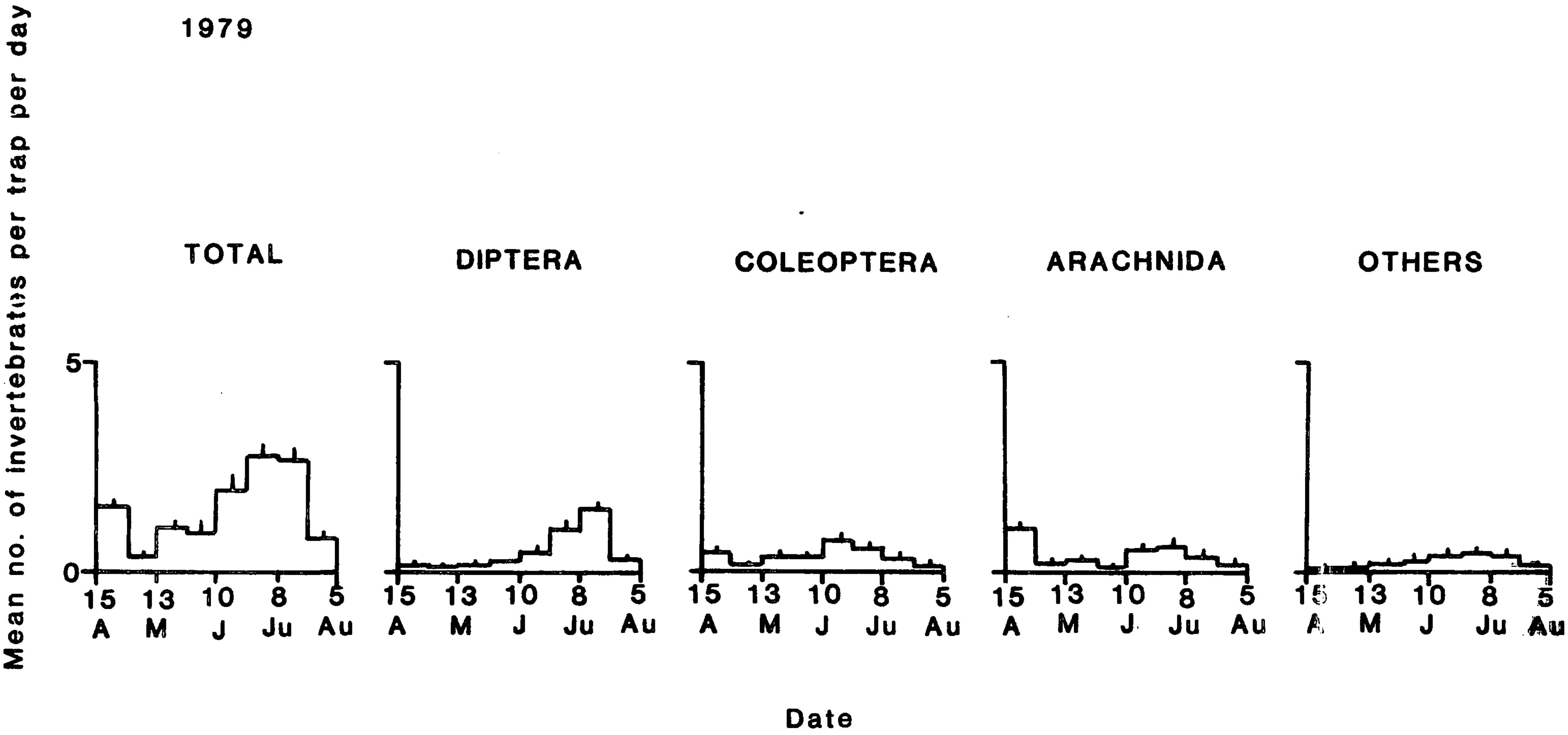
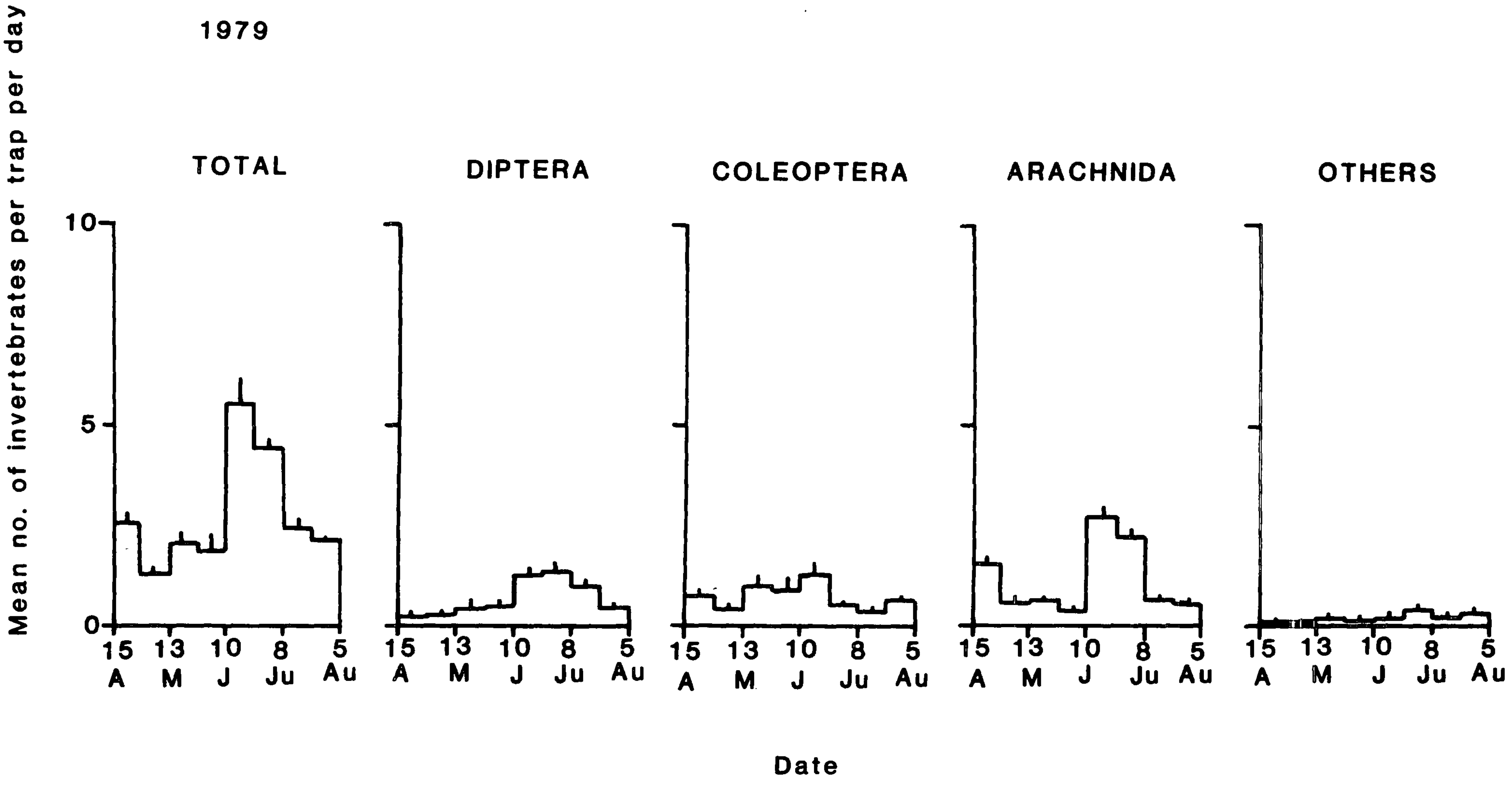

1979
Mean no. of invertebrates per trap per day
TOTAL
DIPTERA
COLEOPTERA
ARACHNIDA
OTHERS
5
0
15 A
13 M
10 J
8 Ju
5 Au
Date

Figure 21

Mean numbers of invertebrates (total, Diptera, Coleoptera, Arachnida and "others") caught per pitfall trap per day on a lightly grazed meadow in the Harwood Beck Valley between 15 April and 5 August 1979.

Error bars indicate one S.E. of mean. Catches based on 10 pitfall traps.


1979
Mean no. of invertebrates per trap per day
TOTAL
DIPTERA
COLEOPTERA
ARACHNIDA
OTHERS
10
5
0
15 A
13 M
10 J
8 Ju
5 Au
Date

almost daily until 19 May.

The periods of prey abundance on all field types except rough pasture coincide with time when most of the waders have young and hence food is abundant at a time when pressure on the feeding sites is greatest. As regards feeding sites for waders, hay meadow has the highest prey levels but is inaccessible for much of the season when the vegetation is long. However, the high density of invertebrates early in the season relative to the other field types make hayfields valuable feeding sites at this time. The low invertebrate abundance on rough pasture suggests that it may be a poor feeding area for waders compared to the other sites available. Thus, considering the season as a whole, grazed meadow and grazed meadow with *Juncus* appear to be the most favourable sites for food, esepcially when heavily grazed since this appeared to enhance invertebrate levels.

(b) Soil invertebrates

Of the total invertebrates retrieved from soil cores in June 1979 and Apri 1980 82% were lumbricids and 12% tipulid larvae (mainly *Tipula paludosa*), the remainder being other dipteran larvae, beetle larvae and slugs. Table 37 gives the densities of earthworms, tipulid larvae and total invertebrates found on representative areas of different field types in 1979. There were no significant differences in invertebrate abundance on grazed meadow, grazed meadow with *Juncus*, hay meadow, rough pasture or rough pasture with *Juncus*.

Most Lapwing bred on grazed meadow, grazed meadow with *Juncus* and hay meadow but the breeding densities of birds on these sites differed (Section 3 3)). Also, hay meadows were particularly favoured as feeding sites especially at the beginning of the season when the vegetation was short and again after the hay was cut when it was used by flocks of Lapwing, Golden Plover and Curlew. To investigate whether such differences were attributable to the soil fauna these sites were sampled further in 1980. Two sets of

Table 37.

Densities of earthworms, tipulid larvae and total invertebrates obtained from soil cores taken on different field types in the Harwood Beck Valley in June 1979.

Densities are expressed as mean numbers m^{-2} ± one S.E. The density estimate for each field was based on 5 x 1/100 m^2 soil cores.

Field type	Earthworms m^{-2}	Tipulids m^{-2}	Total invertebrates m^{-2}	No. of fields sampled
Grazed meadow	257 ± 86	83 ± 19	349 ± 105	7
Grazed meadow, *Juncus effusus* cover >5%	377 ± 115	51 ± 13	449 ± 116	7
Hay	343 ± 39	36 ± 7	398 ± 40	19
Rough pasture	235 ± 140	120 ± 14	375 ± 158	4
Rough pasture, *Juncus effusus* cover >5%	316 ± 162	48 ± 25	388 ± 172	5

Table 38.

Densities of earthworms, tipulid larvae and total invertebrates obtained from soil cores taken on different field types in the Harwood Beck Valley in April and August 1980.
Densities are expressed as mean numbers m^{-2} ± one S.E. Density estimates for each field were based on 5 x 1/100 m^{2} soil cores for the April samples and 1 x 1/100 m^{2} soil cores in August.

	No. of earthworms m^{-2}		No. of tipulid larvae m^{-2}		Total invertebrates m^{-2}	
Field type	April	August	April	August	April	August
Grazed meadow	304 ± 162 (N = 5)	650 ± 69 (N = 10)	32 ± 18 (N = 5)	10 ± 10 (N = 10)	364 ± 162 (N = 5)	810 ± 119 (N = 10)
Grazed meadow *Juncus effusus* cover >5%	350 ± 65 (N = 8)	433 ± 88 (N = 15)	40 ± 26 (N = 8)	0 (N = 15)	420 ± 79 (N = 8)	453 ± 98 (N = 15)
Hay	374 ± 40 (N = 7)	500 ± 79 (N = 22)	40 ± 14 (N = 7)	14 ± 7 (N = 22)	443 ± 37 (N = 7)	550 ± 80 (N = 22)

* Estimates for tipulid larvae are low in August as adults had started to emerge.

Table 39

Soil water content and organic content of different field types in the Harwood Beck Valley in 1979 and 1980.

N = number of fields sampled.

Field type	Percent water content of soil ± 1 S.E. 1979	 1980	Percent organic content ± 1 S.E. (dry weight); 1980
Grazed meadow	52.0 ± 2.4 (N = 7)	44.1 ± 2.2 (N = 10)	15.9 ± 1.8 (N = 10)
Grazed meadow, *Juncus effusus* cover >5%	58.8 ± 3.1 (N = 7)	60.5 ± 2.2 (N = 15)	31.1 ± 4.3 (N = 15)
Hay	45.7 ± 2.0 (N = 19)	42.0 ± 1.2 (N = 22)	13.9 ± 0.6 (N = 22)
Rough pasture	60.1 ± 6.2 (N = 4)		
Rough pasture, *Juncus effusus* cover >5%	61.1 ± 6.3 (N = 5)		

samples were taken, one in April during a dry spell and one at the beginning of August after a period of heavy rain. Table 38 gives the densities of invertebrates obtained from these samples. Again there were no significant differences between the densities of invertebrates on the different field types either in April or August. Earthworm abundance and therefore total invertebrate numbers, was greater during the wet weather in August than during the dry spell in April on all field types sampled although the differences were not significant except for the increase in total invertebrates on grazed meadow ($t = 2.22$, d.f. = 13, $P<0.05$). However, there was no indication that the proportion of earthworms occurring in the top 5cm of the cores had increased, therefore their availability to the waders was probably unchanged. Tipulid densities were low on all sites in August due to the emergence of adults which started to appear in the pitfall traps at this time. Compared to an increase in soil invertebrates of 123% on grazed meadow and 24% on hay meadow, the variation in numbers of invertebrates between the dry and wet periods was only 8% on the grazed meadow with *Juncus* sites which suggests that there may be a more constant supply of food to waders feeding on these wetter areas.

Sectioning of the cores immediately they were taken showed that 85% of the invertebrates were present in the top 5cm. of soil. There were no apparent differences in the proportion of invertebrates present in the top zone of the core on the different field types and therefore no suggestion of a greater availability of prey on certain areas.

Table 39 gives the values for soil water content and organic content for the different field types in 1979 and 1980. Hay meadow was significantly drier than all other field types in 1979 but was no different to grazed meadow in 1980. There was a trend of increasing soil wetness from grazed meadow and hay meadow through grazed meadow with *Juncus* to rough pasture. Organic content was significantly higher on the *Juncus* sites sampled than grazed meadow ($t = 3.26$, d.f. = 23, $P<0.01$) or hay meadow ($t = 3.96$, d.f. = 35, $P<0.001$). The effect of these factors on invertebrate abundance and the distribution of Lapwing is discussed in the following section.

ii) Soil conditions and the abundance of soil invertebrates as factors affecting the distribution of Lapwing.

Of the wader species breeding in the Harwood Beck Valley Lapwing were numerically dominant and occurred on all field types but at varying densities. It was therefore possible to evaluate their distribution statistically with respect to the prey levels and soil conditions determined in 1979 and 1980.

There was no correlation between the density of lumbricids, tipulid larvae or total soil invertebrates and Lapwing breeding density in either 1979 or 1980. Also, in both years, there were no significant differences in prey densities on fields with and without breeding Lapwing (Tables 40 and 41).

Soil water content and organic content had no relationship with the abundance of soil invertebrates but was related to the distribution of Lapwing. Organic content is correlated with soil water content since organic material can hold more water than the mineral constituents of the soil. Also, wherever there is impeded draining organic material will build up as decay processes are inhibited in the anaerobic conditions caused by waterlogging. There was a logarithmic relationship between soil wetness and organic content ($r = 0.86$, d.f. = 45, $P<0.001$; Fig. 22) therefore any effect of water content on Lapwing distribution is also apparent for organic content. It is unlikely that the birds respond directly to organic content whereas water content of the soil reflects the ease with which the substrate can be probed by a feeding bird. The proportion of fields with breeding Lapwing was higher where soil water content exceeded 50% (1979

Table 40.

Densities of earthworms, tipulid larvae and total invertebrates on fields with and without breeding Lapwing in the Harwood Beck Valley in June 1979.

Densities are expressed as mean numbers m^{-2} ± one S.E. The density estimate for each field was based on 5 x 1/100 m^2 soil cores.

	Lapwing present	Lapwing absent
Earthworms	299 ± 43	369 ± 65
Tipulids	54 ± 7	62 ± 15
Total invertebrates	372 ± 46	446 ± 69
No. of fields sampled	29	13

Table 41

Densities of earthworms, tipulid larvae and total invertebrates in a) April and b) August on fields with and without breeding Lapwing in the Harwood Beck Valley in 1980.

Densities are expressed as mean numbers m^{-2} ± one S.E. The density estimates for each field were based on 5 x 1/100 m^2 soil cores in April and 1 x 1/100 m^2 soil cores in August.

	Lapwing present		Lapwing absent	
	a)	b)	a)	b)
Earthworms	327 ± 64	460 ± 61	393 ± 57	568 ± 78
Tipulids	37 ± 16	4 ± 4	40 ± 16	14 ± 7
Total invertebrates	393 ± 66	500 ± 66	463 ± 67	668 ± 95
No. of fields sampled	14	25	6	22

The estimate for tipulid larvae in August is low as some adults had started to emerge.

Table 42.

The proportion of fields with Lapwing, together with their breeding densities, on wet and dry fields in the Harwood Beck Valley in 1979 and 1980.

Wet and dry fields were determined by a soil water content of greater than or less than 50%.

1979

	Soil water content		
	< 50%	> 50%	
No. of fields with Lapwing	10	19	
No. of fields without Lapwing	10	3	$\chi_1^2 = 6.48$ $P < 0.05$
Breeding density (pairs ha^{-1} ± 1 SE)	0.16±0.045	0.43±0.080	

$t = 2.94$, d.f. $= 40$, $P < 0.01$

1980

	Soil water content		
	< 50%	> 50%	
No. of fields with Lapwing	11	14	
No. of fields without Lapwing	17	5	$\chi_1^2 = 5.38$ $P < 0.05$
Breeding density (pairs ha^{-1} ± 1 SE)	0.18±0.050	0.57±0.125	

$t = 2.90$, d.f. $= 45$, $P < 0.01$

Figure 22.

Relationship between soil water and organic content for fields in the Harwood Beck Valley in 1980.

Regression equation:-

$\log y = 2.03 \log x - 2.16$

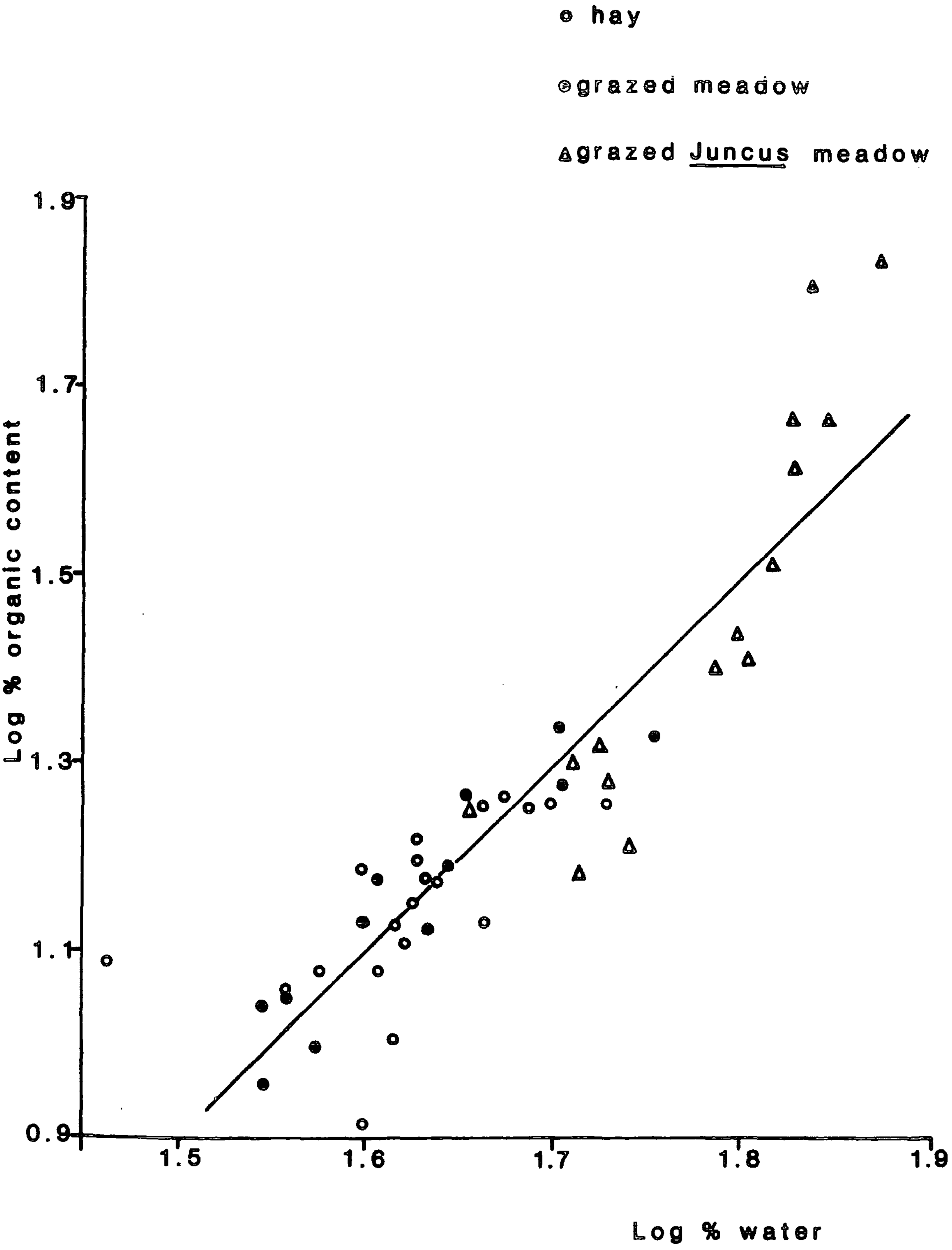
where y = % organic content

and x = % water

$r = 0.86$

d.f. = 45

$P < 0.001$


● hay
⊙ grazed meadow
△ grazed Juncus meadow
Log % organic content
1.9
1.7
1.5
1.3
1.1
0.9
1.5
1.6
1.7
1.8
1.9
Log % water

$\chi_1^2 = 6.48$, $P<0.05$; 1980 $\chi_1^2 = 5.38$, $P<0.05$; Table 42). The wetter fields also had higher breeding densities of Lapwing (1979 $t = 2.94$, d.f. = 40, $P<0.01$; 1980 $t = 2.86$, d.f. = 45, $P<0.01$; Table 42). By selecting the wetter localities as breeding areas Lapwing not only obtain sites where the substrate is easier to probe for prey but may also gain more reliable feeding areas as the wet fields had a more constant food supply than the drier fields (see (i)(b)).

3. The distribution and densities of wading birds within the Harwood Beck Valley.

Lapwing, Redshank, Snipe, Curlew and Golden Plover were all recorded breeding within the enclosed land of the Harwood Beck Valley. However of these, the first four species were numerically dominant and only three pairs of Golden Plover were recorded breeding in any one year, each of these having nest sites in rough pasture fields bordering the lower fell slopes.

In addition to their importance as a breeding ground for waders the fields around Harwood Beck were also used extensively as feeding areas by both pre- and post-breeding flocks of waders. Waders start to move back into Teesdale after the winter in February/March, the pre-breeding flocks feeding mainly on hay meadows and grazed meadow fields, grazed meadow fields with a high cover of *Juncus effusus* being more favoured for roosting. Post-breeding flocks also make extensive use of the hay meadows as feeding sites as soon as the hay is cut in July/August. Lapwing and Curlew flocks are often quite large (up to 200 and 60 birds respectively) whereas Redshank and Snipe usually occur in small numbers (less than five) in association with flocks of other species. Although Golden Plover did not favour fields as breeding sites sizeable pre-and post-breeding flocks (up to 120 birds in any one field) use the hay meadows as feeding sites. Small numbers of Dunlin (up to 10 birds) occasionally accompany flocks of Golden

Plover if cold, snowy conditions persist at the beginning of the season.

Methods

The 200 fields used in the survey incorporated the majority of the enclosed land in the Harwood Beck Valley. Counts of breeding waders were made from the middle of April, when pairs were established on territories, to the end of the first week in June when the first post-breeding flocks of Lapwing began to form. Each field was visited a minimum of three times during this period. Birds which were apparently using fields as feeding sites only and readily moved off to adjacent areas have been excluded from the counts of breeding pairs. Observations of displaying or incubating birds, nests and broods of young chicks confirmed which fields were used for nesting. Field areas were measured from 6" : 1 mile Ordnance Survey maps with a planimeter to evaluate the densities of breeding waders in each field.

Five distinct field types occurred in the Harwood Beck Valley. These were distinguished as follows:-

1. Grazed meadow. - A relatively herb-rich *Agrostis* - *Festuca* grassland forming the better quality pasture of the dale. Usually dry and well drained hence *Juncus effusus* occurs in only small amounts or is absent. The turf is usually short and even with few tussocks. Cattle and/or sheep graze the fields for a large part of the year. Inorganic fertilizers are applied every 1-2 years at the rate of 125-250kg.ha^{-1} and farmyard manure is spread on the fields as available. Lime and basic slag are usually applied every five years.

2. Grazed *Juncus* meadow.- Similar to grazed meadow but more poorly drained, the higher water table allowing germination and growth of *Juncus effusus*. Grazed meadow fields were placed in this category if *Juncus* cover exceeded 5%. Generally less heavily grazed than 1. and if fertilized treated on the dry areas only.

3. Hay meadow. - Herb-rich vegetation with predominantly broad-leaved grasses (e.g. *Agrostis* sp., *Anthoxanthum odoratum*, *Dactylis glomerata*, *Cynosurus cristatus*, *Holcus lanatus*). The fields are generally well drained and have an even topography. They are grazed by cattle and sheep for only short periods in early spring and autumn allowing hay to be cropped in July or August. Inorganic fertilizers (c. 250kg.ha^{-1}) and large quantities of farmyard manure are applied annually.

4. Rough pasture. - Poor quality mainly undrained pasture usually bordering the lower fell slopes. Relatively few herbaceous plants although *Galium saxatile* and *Potentilla erecta* commonly occur. Narrow roll-leaved grasses (e.g. *Festuca ovina*, *Deschampsia flexuosa* and *Nardus stricta*) predominate, usually forming tussocks. The fields are sheep grazed for a large part of the year and sometimes cattle grazed in summer. Inorganic or organic fertilizers are rarely applied. Lime and basic slag are used occasionally on some fields.

5. Rough *Juncus* pasture. - As for rough pasture but wetter and with a cover of *Juncus effusus* exceeding 5%. No applications of fertilizers, lime or basic slag.

Results

i) Distribution and densities of breeding pairs.

Table 43 gives the number and percentage of each field type in which breeding pairs of Lapwing, Redshank, Snipe and Curlew respectively occurred in 1979 and 1980. More grazed *Juncus* meadow fields were occupied than any other field type only 10 and 15% of these fields being without waders in 1979 and 1980 respectively. Lapwing, being the most numerous and widespread wader in the valley, occupied the greatest proportion of fields in each category.

Fig. 23 shows the distribution of breeding pairs of Lapwing, Redshank, Snipe and Curlew on the five field types in 1979 and 1980 and the relative availability of those sites in the Harwood Beck Valley. Kendall's rank

Table 43.

The number and percentage of fields of different vegetation type in the Harwood Beck Valley in which each species of breeding wader was located, and the number and percentage of fields without waders, in 1979 and 1980.
Based on the presence or absence of Lapwing, Redshank, Snipe and Curlew in each field. Percentages given in brackets.

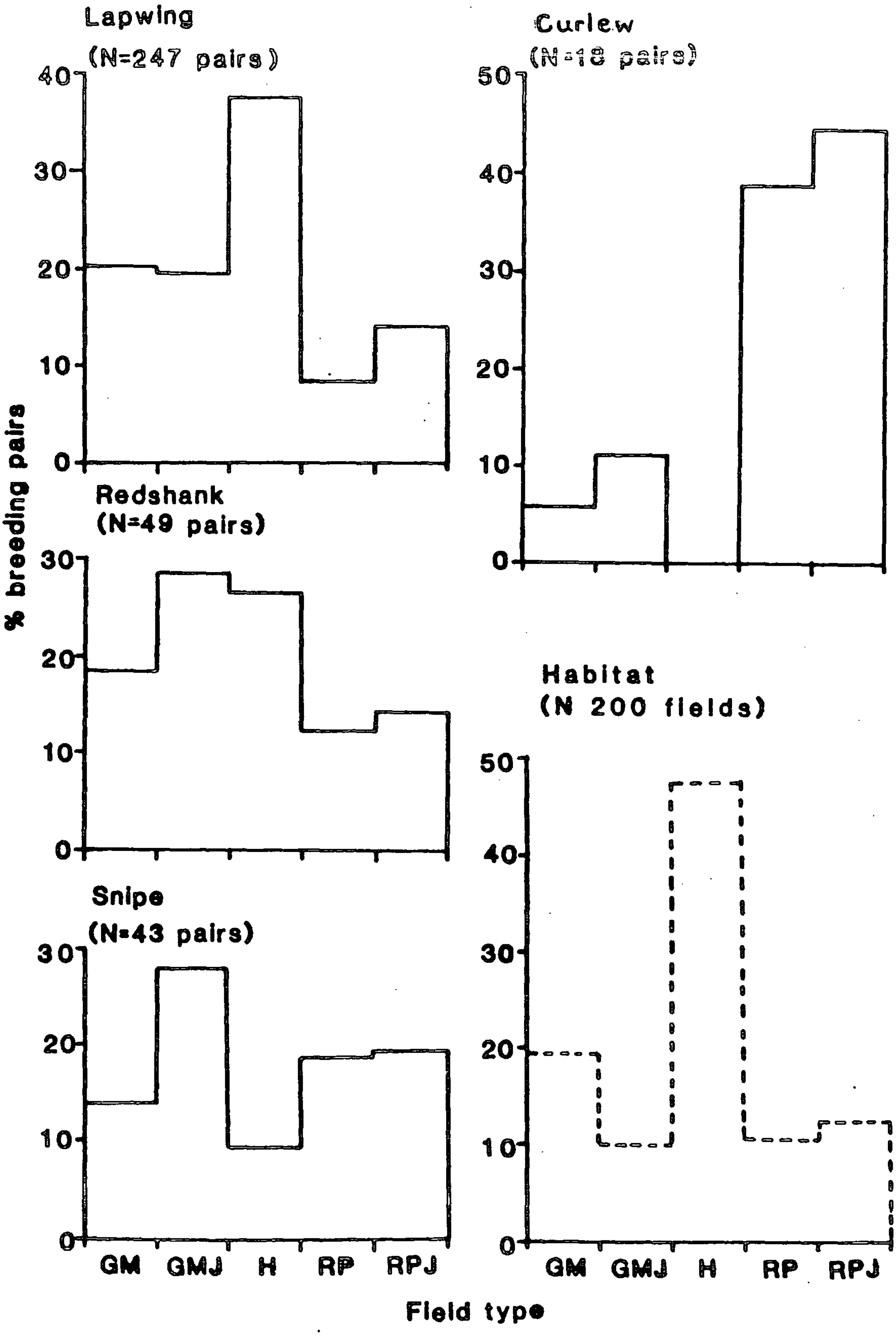
	Grazed meadow (N = 39 fields)	Grazed *Juncus* meadow (N = 20 fields)	Hay (N = 95 fields)	Rough pasture (N = 21 fields)	Rough *Juncus* pasture (N = 25 fields)	TOTAL (N = 200 fields)
1979						
Lapwing	27 (69.2)	18 (90.0)	72 (75.8)	16 (76.2)	22 (88.0)	155 (77.5)
Redshank	9 (23.1)	11 (55.0)	13 (13.7)	5 (23.8)	7 (28.0)	45 (22.5)
Snipe	5 (12.8)	9 (45.0)	4 (4.2)	6 (28.6)	12 (48.0)	36 (18.5)
Curlew	1 (2.6)	2 (10.0)	0	6 (28.6)	5 (20.0)	14 (7.0)
No waders	11 (28.2)	2 (10.0)	22 (23.2)	5 (23.8)	3 (12.0)	43 (21.5)
1980						
Lapwing	25 (64.1)	17 (85.0)	77 (81.1)	18 (85.7)	17 (68.0)	154 (77.0)
Redshank	7 (17.9)	7 (35.0)	9 (9.5)	4 (19.0)	6 (24.0)	33 (16.5)
Snipe	0	8 (40.0)	3 (3.2)	2 (9.5)	11 (44.0)	24 (12.0)
Curlew	0	0	0	3 (14.3)	6 (24.0)	9 (4.5)
No waders	14 (35.9)	3 (15.0)	18 (18.9)	2 (9.5)	7 (28.0)	44 (22.0)

Figure 23.

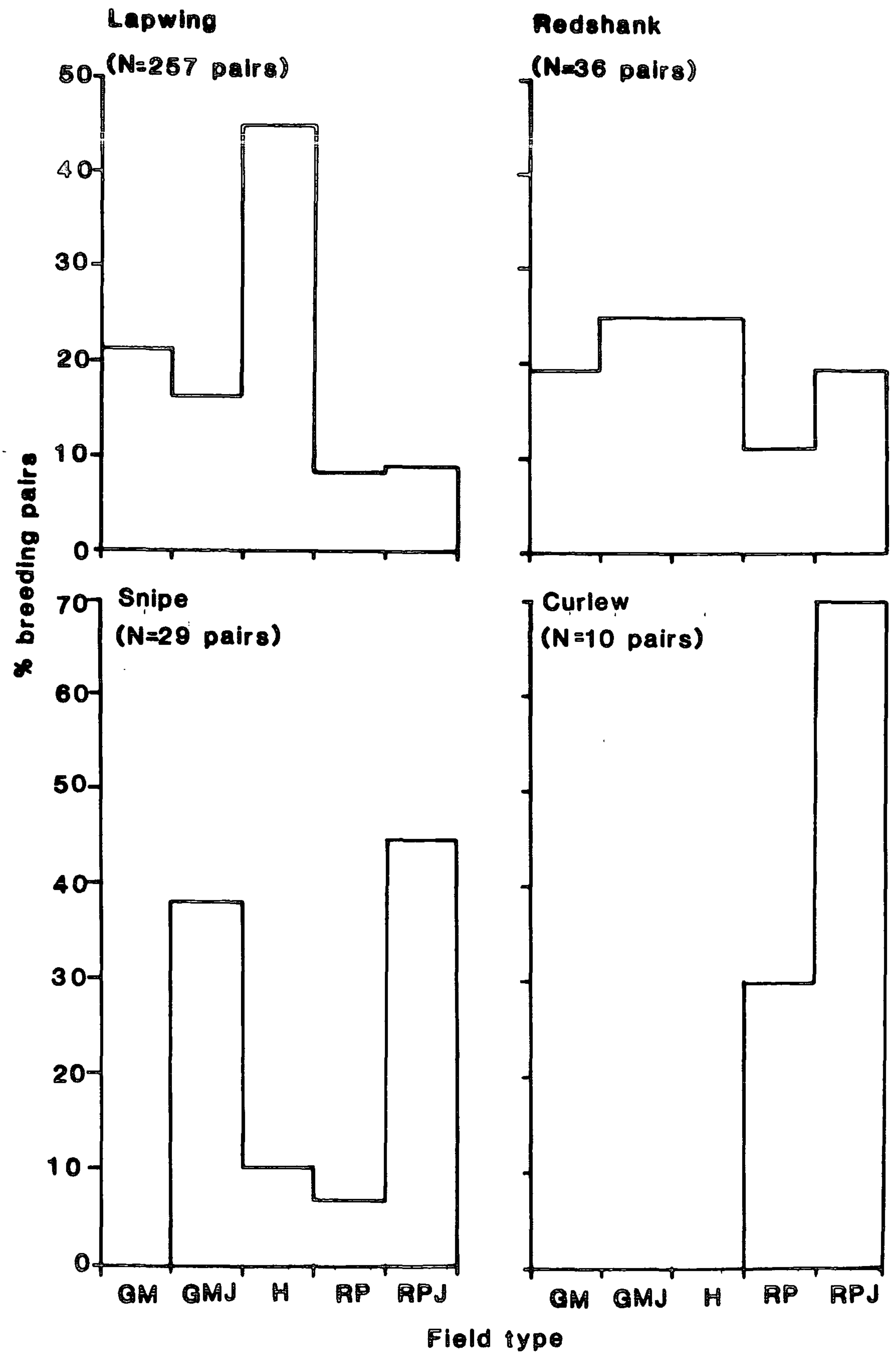
Percentage of the population of each of four wader species found on different field types in the Harwood Beck Valley in 1979 and 1980. Hatched line indicates the percentage of fields classified in each vegetation type (same in 1979 and 1980).

GM = grazed meadow
GMJ = grazed *Juncus* meadow
H = hay meadow
RP = rough pasture
RPJ = rough *Juncus* pasture

1979


Lapwing
(N=247 pairs)
40
30
20
10
0
Curlew
(N=18 pairs)
50
40
30
20
10
0
% breeding pairs
Redshank
(N=49 pairs)
30
20
10
0
Habitat
(N 200 fields)
50
40
30
20
10
0
Snipe
(N=43 pairs)
30
20
10
0
GM
GMJ
H
RP
RPJ
GM
GMJ
H
RP
RPJ
Field type

1980



Lapwing
(N=257 pairs)
Redshank
(N=36 pairs)
Snipe
(N=29 pairs)
Curlew
(N=10 pairs)
% breeding pairs
0
10
20
30
40
50
60
70
GM
GMJ
H
RP
RPJ
Field type

correlation coefficients comparing the distributions of pairs of species indicated significantly similar patterns of distribution only for Snipe and Curlew in 1979 ($\tau = 0.8$, $P < 0.5$) whilst Lapwing and Curlew showed significantly disimilar distributions in 1979 ($\tau = -0.8$, $P < 0.05$). No other associations were significant. Rank correlation coefficients comparing wader distribution with the distribution of habitats indicated that none of the wader species were distributed in accordance with the availability of field types. Therefore, breeding pairs of waders were not dispersed at random throughout the valley but were selecting certain habitats.

The selection ratios (Section 2) calculated from the data shown in Fig. 23 are given in Table 44. These indicate that the wetter *Juncus* sites are the preferred habitats; grazed *Juncus* meadow was selected by Lapwing, Redshank and Snipe in 1979 and 1980, Snipe in addition selecting rough *Juncus* pasture sites in both years. Curlew also showed selectivity for *Juncus* sites but preferred the less well managed rough pasture areas bordering the lower fell slopes and also selected the drier rough pasture fields without *Juncus*. Although high percentages of the Lapwing and Redshank populations occurred on hay meadow (Fig. 23) there was no indication that these areas were being preferentially selected. The high number of breeding pairs present on hayfields is probably in part attributable to the extensive availability of that particular habitat throughout the valley.

The field types selected by Lapwing, Redshank, Snipe and Curlew also had the highest densities of those species (Fig. 24). Thus, grazed *Juncus* meadow supported the highest densities of Lapwing, Redshank and Snipe. Rough *Juncus* pasture, which was also selected by Snipe, had the second highest breeding density of that species although densities were 60% lower than those on grazed *Juncus* meadow. Similarly the selection of rough *Juncus* pasture fields by Curlew was reflected in the higher densities found on these sites. Rough

Table 44.

Selection ratios and standard errors for wader species located on different field types in the Harwood Beck Valley in 1979 and 1980.

	Grazed meadow	Grazed *Juncus* meadow	Hay	Rough pasture	Rough *Juncus* pasture
1979					
Lapwing	1.04±0.13	*1.94±0.25	0.79±0.065	0.81±0.17	1.14±0.18
Redshank	0.94±0.28	*2.86±0.65	0.56±0.13	1.16±0.45	1.14±0.40
Snipe	0.72±0.27	*2.79±0.68	0.20±0.09	1.77±0.57	*2.42±0.56
Curlew	0.29±0.28	1.11±0.74	0	*3.70±1.09	*3.55±0.94
1980					
Lapwing	1.10±0.13	*1.63±0.23	0.95±0.065	0.78±0.16	0.71±0.14
Redshank	0.99±0.34	*2.50±0.72	0.53±0.15	1.06±0.50	1.55±0.53
Snipe	0	*3.79±0.90	0.22±0.12	0.66±0.45	*3.58±0.74
Curlew	0	0	0	2.86±1.38	*5.60±1.16

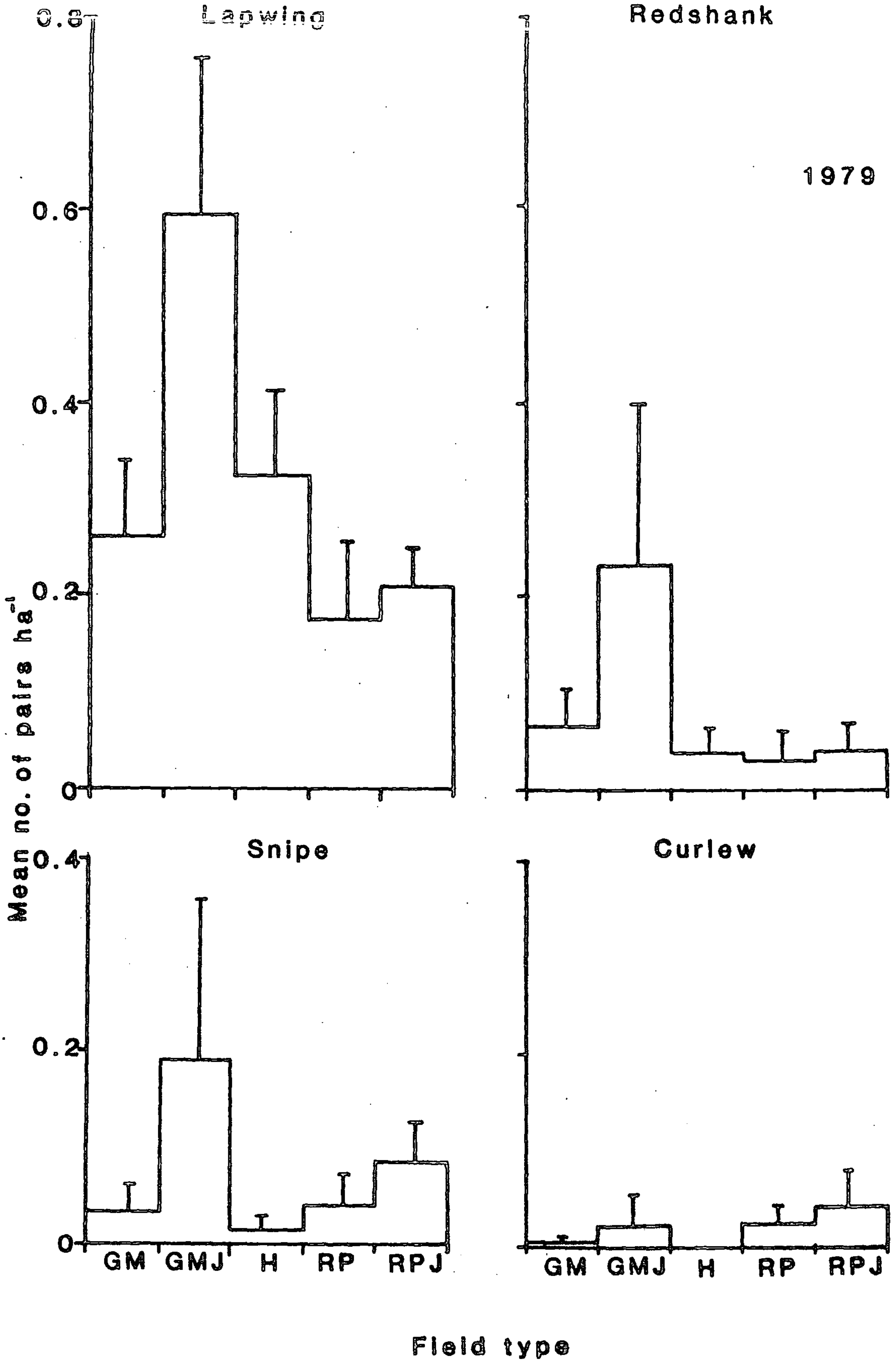
*indicates where there is significant evidence of selection i.e. Selection ratio - 2.SE > 1.

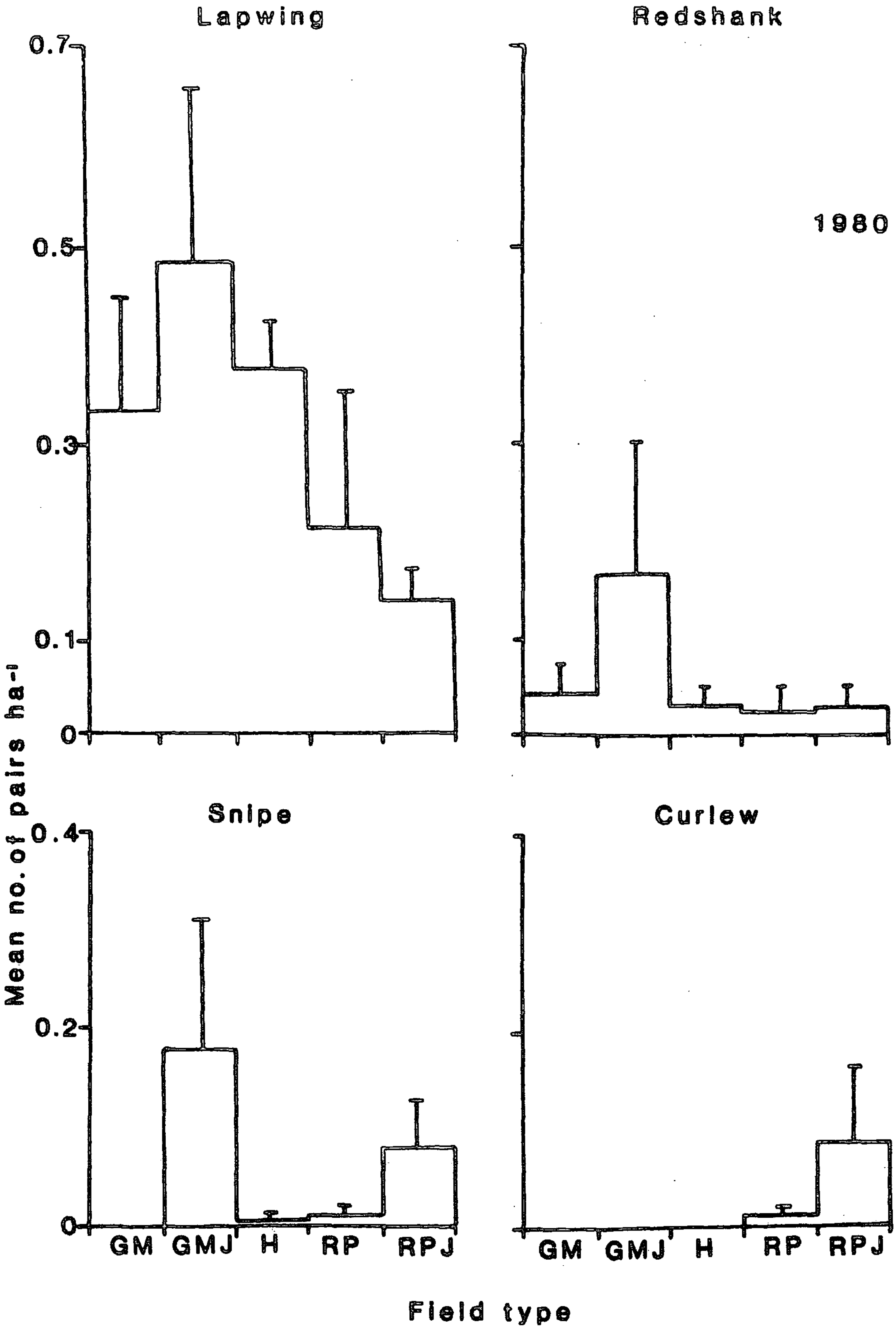
Figure 24.

Breeding densities (mean number of pairs ha^{-1}) of four wader species on different field types in the Harwood Beck Valley in 1979 and 1980.

Error bars indicate 95% confidence limits.

GM = grazed meadow (N = 39 fields)
GMJ = grazed *Juncus* meadow (N = 20 fields)
H = hay meadow (N = 95 fields)
RP = rough pasture (N = 21 fields)
RPJ = rough *Juncus* pasture (N = 25 fields)


0.8
Lapwing
Redshank
1979
0.6
0.4
0.2
0
Mean no. of pairs ha-1
0.4
Snipe
Curlew
0.2
0
GM
GMJ
H
RP
RPJ
GM
GMJ
H
RP
RPJ
Field type


Lapwing
Redshank
1980
0.7
0.5
0.3
0.1
0
Mean no. of pairs ha-l
Snipe
Curlew
0.4
0.2
0
GM
GMJ
H
RP
RPJ
GM
GMJ
H
RP
RPJ
Field type

pasture areas were apparently not favoured by the waders and had low breeding densities. The driest fields, grazed meadow and hay meadow, had relatively low densities of Redshank, Snipe and Curlew (all less than 0.1 pairs ha^{-1}) but supported densities of Lapwing between 50 and 70% of that on grazed *Juncus* meadow.

ii) Overlap of species

The overlap between wader species breeding in the Harwood Beck Valley in terms of the number of fields jointly occupied is presented in Table 45. This indicates that almost all fields with breeding pairs of Redshank, Snipe or Curlew also had Lapwing present. By contrast, joint occupancy by all other pairs of species was much less common.

All indices of association between species overemphasize the common species and lend insufficient weight to rare species (Sørensen 1948, Fager 1957, Whittaker & Fairbanks 1958, Southwood 1966). They cannot therefore be usefully applied to these data since Lapwing numbers far outweighed those of the other wader species. Therefore in order to assess the overlap of wader species the data has been presented simply as the percentage of pairs breeding together in the same fields (Table 46). Again this shows that in both 1979 and 1980 the majority of Redshank, Snipe and Curlew bred in association with Lapwing. However, these overlaps involved comparatively small percentages of the Lapwing population. More than half the Redshank and Snipe populations bred in the same fields but were associated with small percentages of the Curlew population.

The numbers of wader species breeding together on the different field types are given in Table 47. These indicate that there was more overlap between species on the *Juncus* sites; 30% of grazed *Juncus* meadow fields had three species present in both years whilst on rough *Juncus* pasture 32% and

Table 45.

Overlap between wader species on fields in the Harwood Beck Valley in 1979 and 1980.

Figures refer to the number of fields which had joint occurrences of paired species.

1979	Lapwing	Redshank	Snipe	Curlew
Total no. of fields occupied	155	45	36	14
Joint occurrences (No. of fields):-				
Lapwing	-	43	35	14
Redshank			21	7
Snipe				10
Curlew				-

1980	Lapwing	Redshank	Snipe	Curlew
Total no. of fields occupied	154	33	24	9
Joint occurrences (No. of fields):-				
Lapwing	-	33	24	7
Redshank			16	3
Snipe				2
Curlew				-

Table 46 .

The percentage of breeding pairs of each wader species occurring within the same fields in the Harwood Beck Valley as other species in 1979 and 1980.

a) 1979

	% pairs			
	Lapwing	Redshank	Snipe	Curlew
occurring with:				
Lapwing	-	96	98	100
Redshank	43	-	65	33
Snipe	28	49	-	61
Curlew	15	16	35	-
Total pairs	247	49	43	18

b) 1980

	% pairs			
	Lapwing	Redshank	Snipe	Curlew
occurring with:-				
Lapwing	-	100	100	70
Redshank	39	-	72	20
Snipe	26	50	-	30
Curlew	4	6	10	-
Total pairs	257	36	29	10

Table 47.

The number and percentage of fields having different numbers of breeding wader species for each field type in the Harwood Beck Valley in 1979 and 1980.
Percentages given in brackets.

	Grazed meadow (39 fields)		Grazed *Juncus* meadow (20 fields)		Hay (95 fields)		Rough pasture (21 fields)		Rough *Juncus* pasture (25 fields)	
	1979	1980	1979	1980	1979	1980	1979	1980	1979	1980
No. of wader species										
0	11 (28.2)	14 (35.9)	2 (10.0)	3 (15.0)	22 (23.2)	18 (18.9)	5 (23.8)	2 (9.5)	3 (12.0)	7 (28.0)
1	18 (46.2)	18 (46.2)	4 (20.0)	8 (40.0)	58 (61.1)	68 (71.6)	7 (33.3)	14 (66.7)	8 (32.0)	5 (20.0)
2	7 (17.9)	6 (15.4)	7 (35.0)	3 (15.0)	14 (14.7)	7 (7.4)	4 (19.0)	3 (14.3)	5 (20.0)	7 (28.0)
3	3 (7.7)	1 (2.6)	6 (30.0)	6 (30.0)	1 (1.1)	2 (2.1)	1 (4.8)	1 (4.8)	8 (32.0)	5 (20.0)
4	0	0	1 (5.0)	0	0	0	4 (19.0)	1 (4.8)	1 (4.0)	1 (4.0)

20% of the fields had three species present in 1979 and 1980 respectively. Waders more often bred monospecifically on hay meadows than any other site, 61.1% of fields in 1979 and 71.6% in 1980 having only one breeding species present. However, a high proportion (66.7%) of rough pasture fields also had only one wader species present in 1980. Except for one grazed *Juncus* meadow field in 1979, Lapwing, Redshank, Snipe and Curlew only occurred together on rough pasture sites, particularly the drier *Juncus* free areas.

Discussion.

Lapwing, Redshank, Snipe and Curlew all exhibited selection of at least one of the field types distinguished within the Harwood Beck Valley. Selection ratios (Table 44) indicated that grazed *Juncus* meadow was preferentially selected to other field types by all species but Curlew. Since grazed *Juncus* meadow fields only accounted for 10% of the total number of fields available in the valley, it is possible that there is competition for territories on these areas. Although Lapwing and Redshank occurred on other field types grazed *Juncus* meadow was the only vegetation type for which selection was demonstrated; Snipe however also selected rough *Juncus* pasture. The few Curlew breeding on the enclosed land in the valley did not compete for the fields preferred by Lapwing and Redshank since they selected breeding territories only on rough pasture areas, sites largely devoid of Lapwing and Redshank (Fig. 23). Potentially they could, however, be in competition with Snipe for territories on the rough *Juncus* pasture fields. The densities of waders observed on the various field types reflected the preferences indicated by the selection ratios. Those fields selected by each species also had the highest breeding densities. Grazed *Juncus* meadow supported the highest overall density of waders. Although

Snipe also selected breeding territories on rough *Juncus* pasture their densities on the grazed *Juncus* meadow areas were twice as high as those on the rough pasture sites.

The breeding pairs of Redshank, Snipe and Curlew bred largely in association with Lapwing. Lapwing were generally the first wader species to disassociate from flocks and take up territories on the fields, therefore other waders had the opportunity of selecting sites on which Lapwing were already settled. Redshank nests in particular have often been recorded in close proximity to Lapwing nests (Nicholson 1938-9, Thomas 1942, von Frisch 1957, Campbell 1974), nesting close to other species no doubt being facilitated by their apparent lack of territoriality (Hale 1956). Such behaviour may be an anti-predator strategy (Bub 1957, Lack 1968) and is analagous to the nesting of anatids and shorebirds in gulleries and tern colonies (Koskimies 1957, Bengston 1972, Newton & Campbell 1975), waders nesting close to other wader species (Dyrcz *et al.* 1981) and passerines nesting in Lapwing territories (Eriksson & Götmark 1982). Using artificial nests, Göransson *et al.* (1975) have shown experimentally that the anti-predator behaviour of Lapwing results in a reduction of predation on nearby nests. Both the Redshank and Lapwing are known to sometimes breed sub-colonially (Rinkel 1940, Thomas 1942, Williamson 1951). Lapwing in particular show mutual anti-predatory behaviour, collectively "mobbing" approaching predators. Such behaviour is no doubt more effective than the efforts of a single individual. Redshank will also react communally against potential predators (Grosskopf 1959) but their tendency to attack is lower than that of larger waders, such as Lapwing, who attack readily and strongly (Simmons 1955). Snipe and Curlew may also gain advantages from the Lapwing's anti-predatory behaviour. Although both species readily gave alarm calls they were never observed directly attacking predators in Teesdale. In mixed species associations of ground nesting birds the predation rate on one species' eggs may be reduced if predators form a specific search image for those of another species. Rankin (1979) demonstrated that the breeding success of Redshank nesting less than 50 m from Lapwing or other Redshank nests was almost twice that of nests situated further away.

Of the five field types distinguished in the Harwood Beck Valley, only fields having a cover of *Juncus effusus* exceeding 5% tended to have more than one wader species present within the same field (Table 47). For such vegetation types more than 50% of the fields had more than one wader species. There was therefore likely to be more inter-specific competition for food on these sites. However, as Lapwing are essentially visual feeders and take most of their food from the ground surface they may not be competing for food with the longer-billed species. Redshank, Snipe and Curlew are much more likely to compete as although they will take food from the ground surface, they typically forage by probing for invertebrates in soft, wet substrates. For the most part, however, these three species were in association with Lapwing and by comparison there was relatively little direct overlap between the long-billed species (Table 46).

4. The selection of fields as breeding sites by Lapwing, Redshank, Snipe and Curlew.

Management practices within the enclosed marginal hill pasture of the Harwood Beck Valley have given rise to a variety of field types. Therefore the wading birds have a choice of breeding habitat. Within any one field type, a number of fields may be superficially similar. However, while some fields are used for nesting, adjacent fields which appear almost identical may have no breeding waders. Therefore, in order to evaluate the suitability of fields as breeding sites for waders, multivariate techniques were used to assess the importance of various proximate factors which may influence the selection process.

Methods

Measurements of habitat variables were made to describe fields in the Harwood Beck Valley in 1979. Details of these are given in Appendix 5 . From questionnaires answered by farmers, it was possible to obtain information regarding land management practices for 177 of the 200 fields examined. Together, these variables were used in multivariate analyses to evaluate their effect on the distributions of Lapwing, Redshank, Snipe and Curlew as observed within the field system of the Harwood Beck Valley in 1979 and 1980. Counts of waders were made as described in Section 3 (3).

Fields favoured by waders one year were usually favoured in the following year. This is reflected in the correlations between the numbers of each species between years (see Appendix 6). It is probable that surviving adults return to the same fields in successive years. Moreover, it is unlikely that the birds respond to different habitat factors between years. If, for example, short vegetation is preferred by Lapwing one year because tall grass impedes walking, then short vegetation is likely to be preferred in subsequent years. Therefore counts of waders made in 1979 and 1980 have been combined. For the discriminant analyses the set of fields with a particular species present was taken to be those in which that species was recorded in either 1979 or 1980 or in both years. The dependent variable for the multiple regression analyses was taken as the mean density of pairs per field over the two breeding seasons 1979 and 1980. By combining the counts for the two years data one set of factors was obtained from the multivariate analyses. The predictive equations can then be used to test the suitability of other areas for these wader species.

Discriminant function analysis was used to investigate factors predicting the presence or absence of a species whilst stepwise multiple regressions gave an insight into factors involved in determining the density of breeding pairs in a particular field. The number of fields with no breeding pairs was large for most species, therefore characteristics denoting absence weight heavily in any regression analysis. To avoid this, only those fields with birds present were used in the multiple regressions, ensuring that only the effect of habitat variables on density was considered. The use of both discriminant function analysis and stepwise multiple regression has been discussed in Section 2.

As data on field management policies could not be obtained for all fields, the addition of these variables to the other field characteristics measured reduced the sample size in any multivariate analysis. Therefore, for each species in each year, two sets of analyses were performed. One group of analyses used data for all 200 fields in the discriminant analyses, and all fields with each species present for the regression analyses, but incorporated only the general field characteristics as discriminating or independent variables. Second analyses used both the field and management variables on the reduced sample of fields for which management data was available. In the results, data are presented for the analysis on the full complement of fields wherever the second analysis including the management variables indicated that these exerted no significant effect. For those species shown to be effected by land management practices, data is presented for the reduced sample of fields incorporating the management variables.

Results

a) i) Lapwing

A summary of the results of the discriminant analysis between fields in which Lapwing were recorded as present or absent in 1979-80 is presented in Table 48. The discrimination between fields with and those without Lapwing was significant (final Wilk's Lambda = 0.92, $\chi^2_2 = 17.24$, $P < 0.001$) and the predictive equation, formed from the unstandardized discriminant function coefficients and the constant, classified 74% of cases correctly.

From the range of variables offered (Appendix 5), the presence of marshy patches was the most important discriminating variable (highest standardized discriminant function coefficient; Table 48). This is in line with the Lapwing's preference for breeding sites with a high water table (Klomp 1953, Imboden 1971). Fields with an irregular gradient were also attractive to Lapwing (significant discriminating variable; Table 48). Irregular gradients were characteristic of the wet pastures, their uneven terrain making the use of farm machinery difficult and thereby rendering them unsuitable for improvement and use as hay meadows. Also, gradient changes may allow patches of wet ground to develop, particularly where there are large depressions in the ground, or steep slopes draining onto flat areas.

The results of the multiple regression analysis investigating the effect of the habitat variables on Lapwing breeding density are given in Table 49. Sites largely covered with tussocky vegetation were negatively correlated with Lapwing density, possibly because they would impede locomotion, the Lapwing's method of walking being suited to a short sward (Klomp 1953). Fields with steep gradients were also negatively correlated with the number of breeding pairs. This may be linked to the preference for marshy areas (Table 48) where the water table is high, flatter areas tending to be more poorly drained. Lister (1964) showed that Lapwing density was higher on poorly drained areas and Nicholson (1938-9), Witherby *et al.* (1940), Spencer (1953) and Watson (1972) all state that Lapwing generally avoid steep slopes. Grazed *Juncus* meadow was attractive

Table 48.

Summary of discriminant function analysis for fields in which Lapwing were recorded as present or absent in the Harwood Beck Valley in 1979 80.

Step No.	Variable entered*	Discriminant function coefficients: Standardized	Unstandardized
1	Marshy patches	0.87	1.79
2	Irregular gradient	0.52	1.04
		constant:	- 1.30

Prediction results

Actual group	No. of cases	Predicted group membership: Absent	Present
Lapwing absent	22	14	8
% classified		64	36
Lapwing present	178	44	134
% classified		25	75

Percentage of grouped cases correctly classified: 74%

Group centroids

Lapwing absent	-0.86
Lapwing present	0.11

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* Marshy patches - scored absent as 0, present as 1.

Irregular gradient - break in slope; scored even as 0, irregular as 1.

Table 49.

Summary of stepwise multiple regression analysis to show the effect of habitat variables on the breeding density of Lapwing in fields of the Harwood Beck Valley in 1979-80.

Dependent variable = Breeding density of Lapwing; no. of pairs ha^{-1}

Independent variables*	Slope	SE of slope	F value	% R^2 change
Tussocks	-0.15	0.034	18.59	8
Gradient	-0.018	0.0060	9.51	6
Grazed *Juncus* meadow	0.28	0.084	10.72	4
Telegraph poles	-0.029	0.012	6.05	3
% bare ground	0.071	0.030	5.55	2

constant = 0.53, N (no. of fields with Lapwing) = 178, Multiple R = 0.48

* Tussocks - relative abundance of tussocks; scored 0 - 2.

Gradient - gradient of main slope.

Grazed *Juncus* meadow - vegetation type; scored absent as 0, present as 1.

Telegraph poles - number of telegraph poles in the field or round perimeter.

% bare ground - estimated as % ground without vegetation.

to Lapwing and a significant influence on density. Fields of this type invariably had marshy patches present and the high cover of *Juncus effusus* is indicative of the high water table preferred by Lapwing. Grazed *Juncus* meadow was preferentially selected by Lapwing (Table 44), carried the highest percentage of the breeding population (Fig. 23) and had the highest breeding densities (Fig. 24).

The number of telegraph poles in or around the perimeter of the field had negative effects on Lapwing density. These may be likened to the presence of trees as both telegraph wires and poles may be used as perches by avian predators. Telegraph poles are present throughout the valley and as trees are relatively uncommon they provide some of the few perches available. The avoidance of trees by nesting Lapwing was noted by Klomp (1953) and Taylor (1974). Klomp defined the ultimate cause of this response in terms of the greater offensive powers of enemies, such as Carrion Crows, in areas with trees. In an open situation, with no perches available, the crows are much more conspicuous, require a longer flying time per attack and alight on the ground less frequently than in wooded localities. As Lapwing "mob" predators using strong aerial attacks these are likely to be more efficient in an open situation.

Fields with higher percentages of bare ground had higher Lapwing densities (significant independent variable; Table 49) than those with a more complete vegetation cover. Bare ground provides an easily friable substrate for nest sites and, prey location in the absence of vegetation may be easier on such areas, for a bird feeding primarily by visual cues like the Lapwing.

Considered together, all the independent variables found to be significant, only accounted for 23% of the variability in Lapwing density. Management variables were found to have no direct influence on the presence or absence of Lapwing, neither did they explain a significant proportion of the variation in Lapwing breeding density between fields.

ii) Redshank

Table 50 gives the results of the discriminant function analysis for fields in which Redshank were recorded as present or absent during the breeding seasons of 1979 and 1980. The discrimination between fields with and those without Redshank was highly significant (final Wilk's Lambda = 0.76, $\chi^2_6 = 53.33$, $P < 0.001$). Using the predictive equation 75% of cases were assigned to the correct group.

The presence of trees in the field was the only significant variable which appeared to discourage Redshank. A tendency to nest in treeless areas has also been observed in the Lapwing (Klomp 1953, Taylor 1974) and explained in terms of predator avoidance, attacks by, for example, Carrion Crows, being driven off more easily in open situations. Although Black-headed Gulls are a major avian predator in Upper Teesdale, Carrion Crows and Rooks also take wader eggs and as these often hunt from the vantage points of trees wader nests situated in treeless areas may escape the attention of these predators. Since Redshank do not readily attack potential predators (Simmons 1955) any adaption to predator avoidance is likely to be selective.

Several of the variables attracting Redshank to fields were associated with a high water table, the presence of marshy patches and grazed *Juncus* meadow vegetation being favoured. A greeny brown field colour was also attractive. This was associated with grassland areas interspersed with patches of *Juncus effusus*. The attraction of Redshank to grazed *Juncus* meadow was also apparent in the high breeding densities occurring on these fields (Fig. 24) and selection ratios indicated that this was the only field type to be preferentially selected (Table 44). Redshank usually breed in dense ground vegetation in or near marshy areas (Venables 1937, Larsson 1976). Tussock nest sites, screening the eggs well, are usually selected (Thomas 1942, Squires 1978) although exposed nest sites occasionally occur (Colthrup 1915, Rooke 1950, pers. obs.). Clumps of *Juncus effusus* provide ideal screened nest sites and also good hiding places for chicks. Rushy fields were the commonest habitat recorded in the Redshank Inquiry (Thomas 1942) although wet pastures and marshes were also frequently used. Thomas (1942) considered that some kind of wet land was essential for the Redshank breeding site and where nesting occurred on dry ground access to the margins of pools or patches of marshy ground is required, the latter being a feature which was selected in Teesdale. The soft substrate afforded by such habitats allows this long-billed species to probe deeply for earthworms.

Redshank tended to occur in the large fields (Table 50), a characteristic also noted by Taylor (1974) in Weardale. However, although large fields were attractive to Redshank, regression analysis indicated that they did not support high densities of birds for their size, field area being negatively correlated with the density of breeding pairs (Table 51). The multiple regression analysis investigating the effects of the habitat variables on breeding density, summarized in Table 51, was otherwise largely in agreement with the factors determining presence or absence selected by the discriminant analysis. Thus greeny brown fields with grazed *Juncus* meadow vegetation was associated with higher densities of Redshank. The number of telegraph poles in or around the field was negatively correlated with breeding density, a factor that may be considered equivalent to the avoidance of trees (Table 50) since avian predators may also use these as vantage points from which to look for nests.

During the breeding season Redshank are associated with grazed habitats, tolerating a wide range of grazing intensity (Bergman 1946,

Table 50.

Summary of discriminant function analysis for fields in which Redshank were recorded as present or absent in the Harwood Beck Valley in 1979-80.

Step No.	Variable entered*	Discriminant function coefficients: Standardized	Unstandardized
1	Field area	0.47	0.075
2	Greeny brown field colour	0.34	2.82
3	Marshy patches	0.48	1.00
4	Irregular gradient	0.41	0.83
5	Grazed *Juncus* meadow	0.34	1.18
6	Trees in field	-0.30	-0.75
		constant:	- 1.25

Prediction results

Actual group	No. of cases	Predicted group membership: Absent	Present
Redshank absent	138	113	25
% classified		82	18
Redshank present	62	26	36
% classified		42	58

Percentage of grouped cases correctly classified: 75%

Group centroids

Redshank absent	-0.37
Redshank present	0.83

* Field area - in hectares.
Greeny brown field colour - scored absent as 0, present as 1.
Marshy patches - scored absent as 0, present as 1.
Irregular gradient - break in slope; scored even as 0, irregular as 1.
Grazed *Juncus* meadow - vegetation type; scored absent as 0, present as 1.
Trees in field - scored trees absent as 0, clump of trees as 1, row of trees as 2.

Table 51.

Summary of stepwise multiple regression analysis to show the effect of habitat variables on the breeding density of Redshank in fields of the Harwood Beck Valley in 1979-80.

Dependent variable = Breeding density of Redshank; no. of pairs ha^{-1}.

Independent variables*	Slope	SE of slope	F value	% R^2 change
Grazed *Juncus* meadow	0.25	0.050	24.63	25
Greeny brown field colour	0.45	0.090	24.54	15
Field area	-0.0059	0.0017	11.16	12
No. of months grazed in breeding season	-0.028	0.011	6.38	5
Telegraph poles	-0.026	0.011	5.78	4

constant = 0.27, N (no. of fields with Redshank) = 53, Multiple R = 0.78

Sample size was reduced to incorporate management variables as the analysis with these included indicated that some management factors had a significant influence on Redshank breeding density.

* Grazed *Juncus* meadow - vegetation type; scored absent as 0, present as 1.

Greeny brown field colour - scored absent as 0, present as 1.

Field area - in hectares.

Number of months grazed in breeding season - number of months grazed between March and July; 1-5.

Telegraph poles - number of telegraph poles in the field or round perimeter.

Larsson 1969). Grazing promotes tussock formation and hence provides suitable nest sites for the Redshank. In Teesdale, Redshank favoured rushy fields which were habitually grazed from year to year but preferred those sites which were grazed for short periods only, or not at all, during the breeding season, possibly to avoid nests and chicks being trampled by livestock. There was a negative correlation between the number of months for which a field was grazed during the breeding season and the density of Redshank (Table 51).

Grazed *Juncus* meadow had a higher correlation with Redshank breeding density than any other variable measured, accounting for 25% of the variability in Redshank numbers. An equation formed by the addition of all significant factors explained 61% of the variation in Redshank density between fields.

iii) Snipe

The results of the discriminant analysis to isolate factors affecting the presence or absence of Snipe are summarized in Table 52. General field characteristics were the only variables having a significant effect, aspects of field management apparently being unimportant. On the basis of the variables selected significant discrimination between fields with and those without Snipe was obtained (final Wilk's Lambda = 0.65, $X_4^2 = 84.99$, $P < 0.001$). The predictive equation, formed from the discriminating variables, gave correct classification of whether Snipe were present or absent for 81% of the fields. The distribution of *Juncus effusus* was the most powerful discriminating variable (highest standardized discriminant function coefficient; Table 52). Rushy fields are amongst the Snipe's most favoured breeding habitats (Witherby *et al.* 1940, Sharrock 1976); both grazed *Juncus* meadow and rough *Juncus* pasture were attractive to Snipe

Table 52

Summary of discriminant function analysis for fields in which Snipe were recorded as present or absent in the Harwood Beck Valley in 1979-80.

		Discriminant function coefficients:	
Step No.	Variable entered*	Standardized	Unstandardized
1	Distribution of *Juncus*	0.56	0.17
2	Field area	0.35	0.056
3	Grazed *Juncus* meadow	0.43	1.52
4	Rough *Juncus* pasture	0.38	1.24
		constant:	- 1.22

Prediction results

	No. of cases	Predicted group membership: Absent	Present
Actual group			
Snipe absent	154	126	28
% classified		82	18
Snipe present	46	10	36
% classified		22	78

Percentage of grouped cases correctly classified: 81%

Group centroids

Snipe absent	-0.40
Snipe present	1.34

* Distribution of *Juncus* - scored according to the number of sections of the field in which *Juncus effusus* was found; 1-10.

Field area - in hectares.

Grazed *Juncus* meadow & Rough *Juncus* pasture - vegetation type; scored absent as 0, present as 1.

Table 53.

Summary of stepwise multiple regression analysis to show the effect of habitat variables on the breeding density of Snipe in fields of the Harwood Beck Valley in 1979-80.

Dependent variable = Breeding density of Snipe; no. of pairs ha^{-1}

Independent variables*	Slope	SE of slope	F value	% R^2 change
Greeny brown field colour	0.89	0.075	139.12	37
No. of months grazed by ponies	-0.058	0.0081	52.01	16
Grazed *Juncus* meadow	0.23	0.034	43.65	17
Field area	-0.0053	0.0011	21.53	8
No. of months grazed by sheep	-0.014	0.0038	13.33	6
Trees adjacent to field	-0.053	0.018	8.51	2
Trees in field	-0.082	0.038	4.63	2

constant = 0.24, N (no. of fields with Snipe) = 40, Multiple R = 0.94

Sample size was reduced to incorporate management variables as the analysis with these included indicated that some management factors had a significant influence on Snipe breeding density.

* Greeny brown field colour - scored absent as 0, present as 1.

Number of months grazed by ponies - 1-12 months.

Grazed *Juncus* meadow - vegetation type; scored absent as 0, present as 1.

Field area - in hectares.

Number of months grazed by sheep - 1-12 months.

Trees adjacent to field, trees in field - scored trees absent as 0, clump of trees as 1, row of trees as 2.

breeding in Teesdale (discriminating variables; Table 52). Wet areas are essential for Snipe feeding sites as these long-billed waders feed by tactile methods, probing deep into the substrate to obtain invertebrates.

A large field was more likely to have Snipe present (positive discriminating variable; Table 52) but the largest fields did not support the highest breeding densities and field area was negatively correlated with density in the regression analysis (Table 53).

Other significant effects on Snipe breeding density, isolated by multiple regression analysis, are shown in Table 53. A greeny brown field colour and grazed *Juncus* meadow were positive factors affecting the density of Snipe. Although rough *Juncus* pasture was used by Snipe (discriminating variable, Table 52 and Table 43), such fields did not support a high number of pairs for their size and hence were inversely correlated with density. Trees in or around the field were unattractive to Snipe and negatively correlated with breeding density. The link between avian predators and trees has already been discussed for Lapwing and Redshank.

The only management variables which accounted for significant amounts of the variation in Snipe density were negative correlations with the number of months a field was grazed by ponies or sheep. This may be because Snipe prefer longer vegetation than, for example, Lapwing, and therefore tend to avoid the more intensively grazed swards. As Snipe do not leave the nest readily when incubating, flushing only at the last possible moment, nesting in longer vegetation with good cover is likely to make this behaviour more successful.

All factors found to have significant effects on Snipe density together accounted for 88% of the variability in numbers between fields (Table 53).

iv) Curlew

Within the study area relatively few Curlew bred in fields, most preferring the unenclosed fell slopes. However, since some fields in the Harwood Beck Valley were used, and there was an apparent overlap with Lapwing, Redshank and Snipe, the Curlew's habitat preferences in this area were investigated more closely. The results of the discriminant analysis between fields with and those without Curlew are summarized in Table 54. Although there was only a small sample of fields with Curlew, discrimination between the groups was highly significant (final Wilk's Lambda = 0.68, $\chi^2_3 = 74.75$, $P < 0.001$). The predictive equation formed from the discriminating variables correctly classified 89% of the fields.

Field area was the most powerful discriminating variable, large fields being the preferred sites. Braaksma (1960) considered that solitude was one of the most important aspects for Curlew breeding habitat, areas visited too frequently by man being avoided. In the Harwood Beck Valley Curlew were associated with those fields further away from houses or farms, the distance from houses being a positive discriminating variable (Table 54).

Fields with *Juncus effusus* scattered throughout were favoured (discriminating variable, Table 54). Since the increase and spread of Curlew this century, breeding on wet, rough pasture and rushy fields has become common (Witherby *et al.* 1940, Sharrock 1976). The selection of areas with *Juncus effusus* ensures that the habitat has a high water level. Braaksma (1960) has reported a correlation between ground water level and the number of breeding pairs of Curlew in the Netherlands. As it was the large fields with *Juncus* furthest away from houses that were selected in Teesdale, this indicates that it was the rough *Juncus*

Table 54.

Summary of discriminant function analysis for fields in which Curlew were recorded as present or absent in the Harwood Beck Valley in 1979-80.

		Discriminant function coefficients	
Step No.	Variable entered*	Standardized	Unstandardized
1	Field area	0.75	0.13
2	Distribution of *Juncus*	0.44	0.12
3	Distance from houses	0.26	0.0013
		constant:	- 1.30

Prediction results

		Predicted group membership:	
Actual group	No. of cases	Absent	Present
Curlew absent	183	164	19
% classified		90	10
Curlew present	17	4	13
% classified		23.5	76.5

Percentage of grouped cases correctly classified: 89%

Group centroids

Curlew absent	-0.21
Curlew present	2.22

* Field area - in hectares.

Distribution of *Juncus* - scored according to the number of sections of the field in which *Juncus effusus* was found; 1-10.

Distance from houses - distance to nearest house in metres.

Table 55.

Summary of stepwise multiple regression analysis to show the effect of habitat variables on the breeding density of Curlew in the Harwood Beck Valley in 1979-80.

Dependent variable = Breeding density of Curlew; no. of pairs ha^{-1}

Independent variables*	Slope	SE of slope	F value	% R^2 change
Distance from houses	0.00053	0.00014	14.37	35
Lime	-0.20	0.073	7.54	25

constant = 0.026, N (no. of fields with Curlew) = 15, Multiple R = 0.78

- Sample size was reduced to incorporate management variables as the analysis with these indicated that some management factors had a significant influence on Curlew breeding density.

* Distance from houses - distance to nearest house in metres.

Lime - lime applied to field; scored as 0/1.

pasture that was the preferred field type as these fields were invariably large and since they were at the limit of the inby land, bordering the fell slopes, they were furthest from habitation. Rough *Juncus* pasture was used by most of the field breeding Curlew (Fig. 23), it was preferentially selected (Table 44) and had the highest density of breeding pairs (Fig. 24). The preference for this vegetation is more likely to bring Curlew into competition with Snipe than either Lapwing or Redshank since this field type was also selected by Snipe (Table 44 and Table 54).

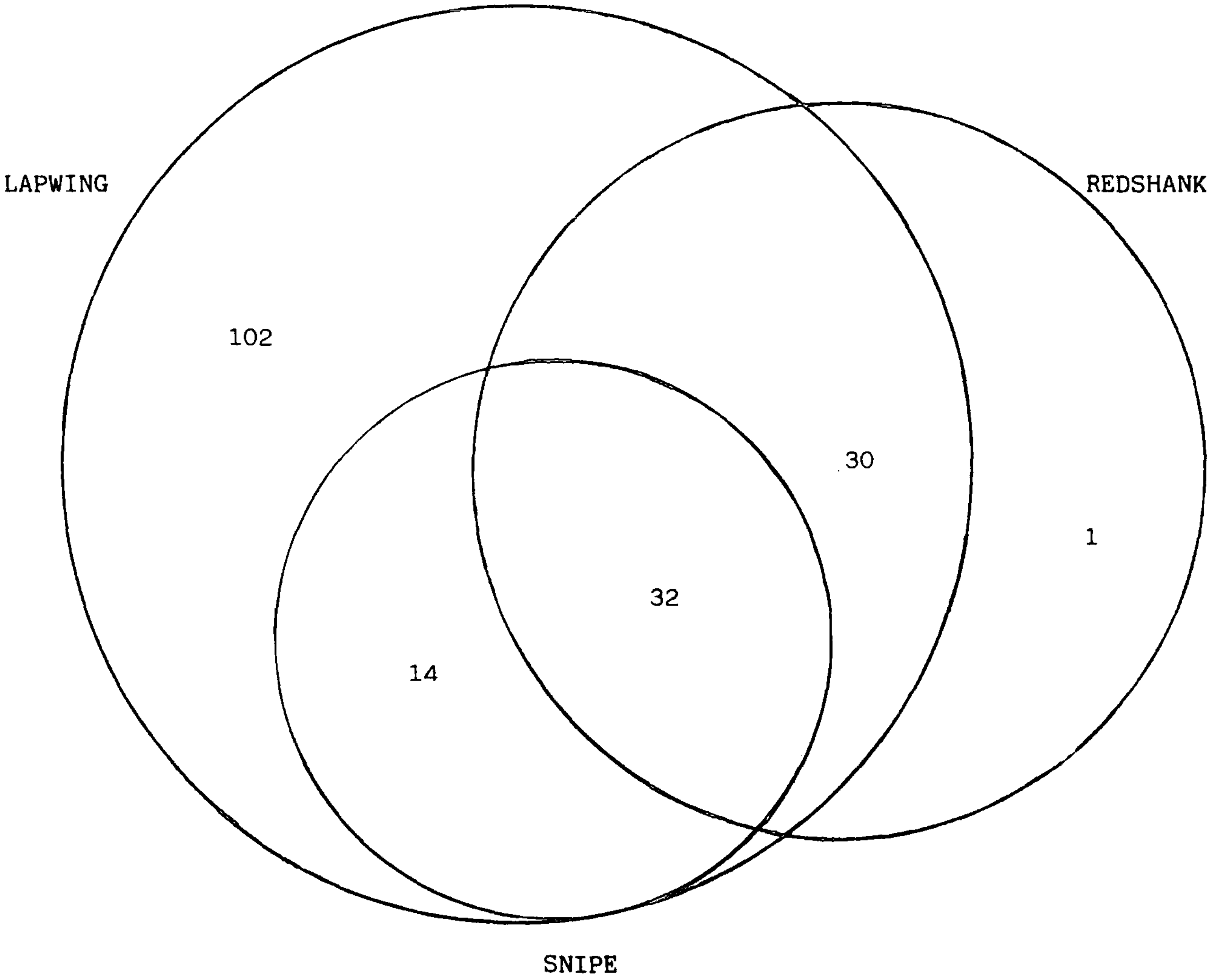
The multiple regression analysis investigating the effect of habitat variables on Curlew breeding density is summarized in Table 55. Only two factors were found to exert a significant effect on Curlew density, although together they explained more than half the variation in Curlew numbers. Increasing Curlew densities were associated with fields further from habitation; the proximity of houses was therefore an important determinant of both presence and absence and density of Curlew. The only management variable having a significant influence was the avoidance of fields which were limed. The wetter, rough pasture fields preferred by Curlew received neither applications of lime or fertilizer.

b) Characteristics of fields shared by different associations of wading birds.

Of the 200 fields surveyed in the Harwood Beck Valley about half had only one breeding wader species present in both 1979 and 1980, this usually being Lapwing. However, certain fields were used by more than one species. Discriminant function analysis was used to characterize the type of field used by different associations of breeding waders. Only overlaps between Lapwing, Redshank and Snipe were considered; Curlew were excluded as the

Figure 25

Schematic representation of the number of fields occupied by different associations of wader species in the Harwood Beck Valley in 1979-80.


LAPWING
REDSHANK
102
30
1
32
14
SNIPE

number of fields they occupied in association with other species were too few for a meaningful analysis.

The number of fields occupied by different associations of waders is shown in the Venn diagram in Fig. 25. Associations were decided on the basis of a species' presence in either 1979 or 1980 or in both years. Thus fields with, for example, Lapwing and Redshank were taken to be those in which these species were recorded in either 1979 or 1980 or in both years but had no breeding pairs of Snipe. Redshank and Snipe occurred largely in association with Lapwing. Where Redshank and Snipe bred together in the same field, Lapwing were also invariably present. Only one field was recorded where Redshank bred alone. No fields were occupied solely by Snipe. Over 50% of the fields where Lapwing bred had neither Redshank or Snipe present. All three wader species were recorded in 16% of the fields surveyed.

i) Lapwing.

The result of the discriminant analysis characterizing fields in which only Lapwing bred in 1979 or 1980 are presented in Table 56. There was significant discrimination between fields with only Lapwing and all other fields (final Wilk's Lambda = 0.85, $\chi^2_2 = 32.34$, $P < 0.001$) and 68% of cases were classified correctly by the predictive equation.

Hay meadow and sites with little or no *Juncus* were typical of areas where only Lapwing bred, these factors being the only significant discriminating variables (Table 56). Of the field types available in the Harwood Beck Valley, grazed meadow, hay meadow and rough pasture were all free of *Juncus*. However, less than 10% of Lapwing bred on rough pasture whereas grazed meadow had 20% and hay meadow about 40% of breeding pairs (Fig. 23). Although grazed *Juncus* meadow had the highest Lapwing densities

Table 56.

Summary of discriminant function analysis for fields in the Harwood Beck Valley where Lapwing were recorded as the only breeding wader in 1979-80.

Step No.	Variable entered*	Discriminant function coefficients: Standardized	Unstandardized
1	Distribution of *Juncus*	-0.72	-0.20
2	Hay meadow	0.44	0.92
		constant:	0.33

Prediction results

Actual group	No. of cases	Predicted group membership: Absent	Present
Lapwing absent	96	64	34
% classified		65	35
Only Lapwing present	102	31	71
% classified		30	70

Percentage of grouped cases correctly classified: 68%

Group centroids

Lapwing absent	-0.43
Only Lapwing present	0.41

* Distribution of *Juncus* - scored according to the number of sections of the field in which *Juncus effusus* occurred; 1-10.

Hay meadow - vegetation type; scored absent as 0, present as 1.

(Fig. 24), and was preferentially selected (Table 44), its low availability (10% of the fields surveyed) meant that many pairs of Lapwing breeding in the valley had to select other habitats. The smaller populations of the other wader species breeding in this area permitted a narrower choice of habitat. The discriminant analysis (Table 56) suggests that other waders largely avoided the drier, *Juncus*-free areas, particularly hay meadows, leaving Lapwing as the only wader breeding extensively on these sites.

ii) Lapwing and Redshank.

The discriminant analysis between fields with Lapwing and Redshank present and all other fields is summarized in Table 57. On the basis of the discriminating variables significant group separation was achieved (final Wilk's Lambda = 0.94, $\chi^2_2 = 11.10$, $P < 0.005$) and 68% of cases were correctly classified.

The only variables which appeared to distinguish fields with both Lapwing and Redshank were associated with grazing. Areas grazed for a large part of the year by sheep were favoured whilst sites grazed by ponies were avoided. In Upper Teesdale the rough pasture fields were sheep grazed during the summer months and early autumn (usually June to October). Grazed meadow and grazed *Juncus* meadow would typically have sheep present throughout the winter and spring (October to May), three months longer than the grazing duration on rough pasture. Hay meadow is the least intensively grazed having sheep present only at lambing time and occasionally during bad weather in the winter.

Table 57.

Summary of discriminant function analysis for fields in the Harwood Beck Valley in which both Lapwing and Redshank were recorded breeding and Snipe were absent in 1979-80.

		Discriminant function coefficients:	
Step No.	Variable entered*	Standardized	Unstandardized
1	No. of months grazed by sheep	0.87	0.23
2	No. of ponies	-0.64	-0.036
		constant:	-0.76

Prediction results

Actual group	No. of cases	Predicted group membership: Absent	Present
Lapwing and/or Redshank absent	170	118	52
% classified		69	31
Lapwing and Redshank present, Snipe absent	30	13	17
% classified		43	57

Percentage of grouped cases correctly classified: 68%

Group centroids

Lapwing and/or Redshank absent	-0.10
Lapwing and Redshank present, Snipe absent	0.63

The original sample size of 200 fields was reduced to include management variables as the analysis with these incorporated suggested that some management factors were important discriminating variables.

* Number of months grazed by sheep - 1-12 months.

Number of ponies - number of ponies grazing in field.

iii) Lapwing and Snipe.

The discriminant analysis indicating factors associated with fields which had both Lapwing and Snipe present, but which lacked breeding Redshank, is summarized in Table 58. Significant group separation was obtained (final Wilk's Lambda = 0.87, $\chi^2_2 = 26.37$, $P < 0.001$) and 76% of cases were correctly classified by the predictive equation formed from the discriminating variables.

The variables selected suggested that Lapwing and Snipe tended to occur together on fields where *Juncus effusus* was plentiful and well distributed. Typically, the fields were away from human habitation. The selection of sites further from houses indicates that rough *Juncus* pasture would be preferred to grazed *Juncus* meadow fields since the latter were partially managed and usually situated closer to the farms than the rough pasture sites.

iv) Lapwing, Redshank and Snipe.

All three wader species occurred in 16% of the sites surveyed. The results of the discriminant analysis isolating the significant features of these fields are summarized in Table 59. The variables selected gave significant discrimination between fields where Lapwing, Redshank and Snipe bred and all other fields (final Wilk's Lambda = 0.69, $\chi^2_4 = 71.71$, $P < 0.001$). The predictive equation derived from these variables classified 84% of cases correctly.

The discriminating variables indicated that the fields occupied jointly by Lapwing, Redshank and Snipe were the larger grazed *Juncus* meadow or rough *Juncus* pasture fields, often having an irregular gradient. Grazed *Juncus* meadow was the most important discriminating variable (highest standardized discriminant coefficient) and there was, therefore, a higher

Table 58.

Summary of discriminant function analysis for fields in the Harwood Beck Valley in which both Lapwing and Snipe were recorded breeding and Redshank were absent in 1979-80.

		Discriminant fuction coefficients:	
Step No.	Variable entered*	Standardized	Unstandardized
1	Distribution of *Juncus*	0.70	0.19
2	Distance from houses	0.58	0.0030
		constant	-1.21

Prediction results

Actual group	No. of cases	Predicted group membership: Absent	Present
Lapwing and/or Snipe absent	186	142	44
% classified		76	24
Lapwing and Snipe present, Redshank absent	14	4	10
% classified		29	71

Percentage of grouped cases correctly classified: 76%

Group centroids

Lapwing and/or Snipe absent	-0.10
Lapwing and Snipe present, Redshank absent	1.37

* Distribution of *Juncus* - scored according to the number of sections of the field in which *Juncus effusus* occurred; 1-10.

Distance from houses - distance to nearest house in metres.

Table 59

Summary of discriminant function analysis for fields in which Lapwing, Redshank and Snipe were all recorded breeding in 1979-80.

		Discriminant function coefficients:	
Step No.	Variable entered*	Standardized	Unstandardized
2	Field area	0.52	0.084
3	Grazed *Juncus* meadow	0.69	2.49
4	Irregular gradient	0.36	0.76
5	Rough *Juncus* pasture	0.46	1.41
		constant:	-1.17

* Distribution of *Juncus* was the first variable to enter the analysis but was dropped at a later stage as it became insignificant once other variables entered.

Prediction results

		Predicted group membership:	
Actual group	No. of cases	Absent	Present
Lapwing or Redshank or Snipe absent	168	145	23
% classified		86	14
Lapwing, Redshank and Snipe all present	32	10	22
% classified		31	69

Percentage of grouped cases correctly classified: 84%

Group centroids

Lapwing or Redshank or Snipe absent	-0.29
Lapwing, Redshank and Snipe all present	1.52

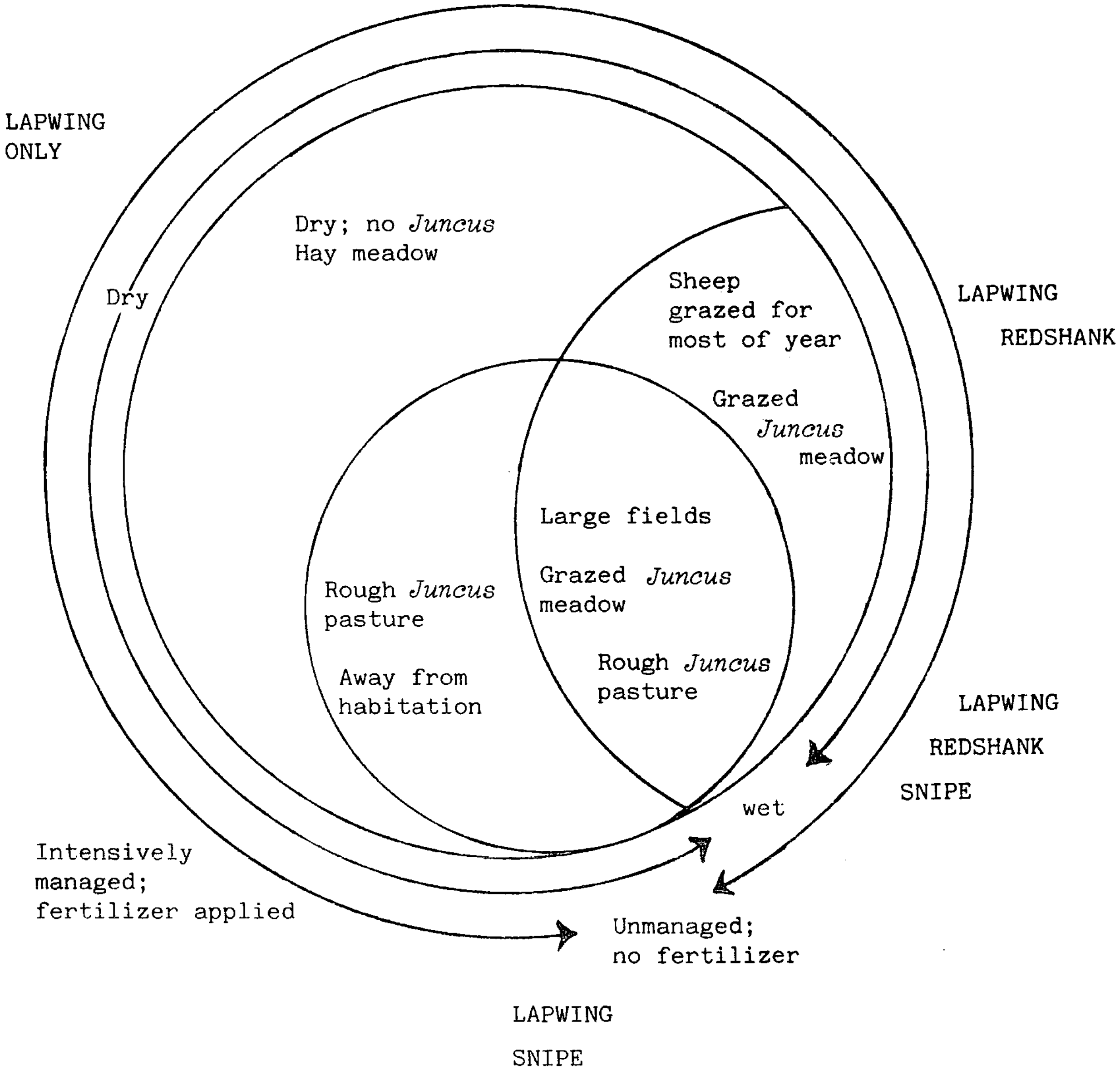
* Field area - in hectares.

Grazed *Juncus* meadow & Rough *Juncus* pasture - vegetation type; scored absent as 0, present as 1.

Irregular gradient - break in slope; scored even as 0; irregular as 1.

Figure 26 .

Diagram to illustrate the principal features of fields occupied by different associations of wader species in the Harwood Beck Valley in 1979 and 1980.


LAPWING
ONLY
Dry; no *Juncus*
Hay meadow
Dry
Sheep
grazed for
most of year
LAPWING
REDSHANK
Grazed
Juncus
meadow
Large fields
Grazed *Juncus*
meadow
Rough *Juncus*
pasture
Away from
habitation
Rough *Juncus*
pasture
LAPWING
REDSHANK
SNIPE
wet
Intensively
managed;
fertilizer applied
Unmanaged;
no fertilizer
LAPWING
SNIPE

probability that fields of this type would have all three wader species present than rough *Juncus* pasture. The selection of sites with *Juncus* indicates that a high water table is an esential feature in the attraction of all three wader species.

A summary of the characteristics of the different types of field used by various associations of waders is presented diagrammatically in Fig. 26. Lapwing tended to occur alone on the drier, more intensively managed fields whilst mixed species assemblages were more common on wetter areas.

Satisfactory separation of the habitats used by the different associations of waders was achieved almost entirely by a consideration of general characteristics of the fields. Variations in land management practices were relatively unimportant and for the most part made no significant contribution in delineating the type of field used. The only exception to this was the influence of grazing regime on Lapwing and Redshank.

Discussion

Each of the multivariate analyses selected a number of salient features characterizing the habitats used by the different wader species. The innate releasing mechanism initiating the settling reaction in a certain habitat is usually responsive to a combination of only a few environmental stimuli (Tinbergen 1948). Therefore, few proximate factors should be involved in habitat selection. The maximum number of significant variables selected in any of the multivariate analyses was seven. However, in the delineation of different types of field occupied by Lapwing, Redshank, Snipe and Curlew not all the significant variables in each analysis can be regarded as the most important proximate factors involved in habitat selection. It is unlikely that the waders could have responded directly to some of the variables, rather they may have been influenced by some associated factor. Birds could not, for example, respond directly to the number of years a field had been drained but may be influenced by the vegetation type and drier habitat produced as a result.

In the discriminant analyses 74-89% of fields were correctly classified. The high degree of discrimination between fields with a particular wader species and those without indicates that selection of certain field types was occurring.

Some of the habitat variables measured were also found to significantly influence the breeding densities of waders to varying degrees. It was for Lapwing, the most cosmopolitan species, that the habitat variables had the poorest capabilities, only being able to account for 23% of the variation in density. For Redshank, Snipe and Curlew, which showed more restricted distributions, the variables were better predictors, accounting for 61, 89 and 60% of the variation in density respectively.

Aspects of land management for the most part seemed to have little direct influence on wader distribution. However, their ultimate effects may be of more consequence because of the structure and type of vegetation they create (grazing, for example, tending to promote tussock formation), or the impact they have on the height of the water-table thereby affecting substrate consistency and the feeding areas of, in particular, the long-billed waders.

The ultimate reasons for the selection of each proximate factor, or correlated variable, by each wader species have been discussed previously in this section. A summary of the factors influencing the distribution of each species is given in Table 60. Although some of the factors affecting habitat selection were common to more than one species (e.g. grazed *Juncus* meadow was attractive to Lapwing, Redshank and Snipe), each species responded to some factors which were different to those influencing the other waders. Features of the habitat that affected whether a bird selects a field or not were not always the same as those determining the density of birds which a chosen field could support.

Although the wader species exhibited some niche differences as exemplified by the proximate factors, areas with a high water-table were preferred by all species. Moreover, it was these grazed *Juncus* meadow and rough *Juncus* pasture areas which had more than one wader species present (Table 47). Therefore, any interaction between species is more likely on these habitats. There may have been competition for territories on grazed *Juncus* meadow since the majority of these fields were used by breeding waders (Table 43) and their availability was low relative to other field types in the valley. Rough *Juncus* pasture fields were larger than the other field types, with the exception of rough pasture, and since they carried low densities of waders by comparison with grazed *Juncus* meadow sites (Fig. 24) it is less likely that there was competition on these areas. However, in each of the discriminant function analyses a proportion of fields without the wader species under consideration were classified as fields with birds present. Although this may be due to a lack of good discriminating variables in the predictive equations, it also suggests that for each species, over the range of habitats used, there may have been some suitable breeding sites which were not occupied.

The reproductive output of a wading bird nesting within the field system of the Harwood Beck Valley may be affected in a number of ways as

Table 60

Comparison of factors affecting the habitat selection and density of Lapwing, Redshank, Snipe and Curlew on marginal hill farmland in the Harwood Beck Valley.

Numbers denote order of significance of variables; symbols denote positive or negative effect.

	Lapwing		Redshank		Snipe		Curlew	
Variable	Presence/ absence	Density	Presence/ absence	Density	Presence/ absence	Density	Presence/ absence	Density
Field area			2+	3–	4+	4–	1+	
Grazed *Juncus* meadow		3+	4+	1+	2+	2+		
Rough *Juncus* pasture					3+			
Distribution of *Juncus*					1+		2+	
Greeny brown field colour			5+	2+		1+		
Tussocks		1–						
Marshy patches	1+		1+					
% bare ground		5–						
Gradient		2–						
Irregularity of gradient	2+		3+					
Trees in field			6–			7–		
Trees adjacent to field						6–		
Telegraph poles		4–		5–				
Distance from houses							3+	1+
Lime								2–
No. of months sheep grazed						5–		
No. of months pony grazed						3–		
No. of months grazed during breeding season				4–				

a direct result of its choice of field type for a breeding territory. The hay meadows are, for the most part, suitable only for Lapwing. Being dry and well drained, apart from the occasional marshy patch, they are suited to species which forage visually and take prey from the ground surface rather than those which probe for food. Early in the season they provide a short, even sward conducive to easy prey location and well suited to the Lapwing's method of locomotion (Klomp 1953). However, any ground nestin bird breeding on hay meadow must breed early in the season and have raised its chicks to fledging, or moved them off the field, before hay cutting. Also, for the Lapwing, the desirability of early breeding will become especially important on such sites as when the vegetation becomes more than about 10 cm tall walking will be impeded.

Of further disadvantage to birds breeding on hay meadows is the danger of nests being destroyed early in the season by farm machinery used to spread manure and inorganic fertilizers and harrow the fields. However, since these fields are grazed for shorter periods during the breeding season than all other field types there is less likelihood of nests being trampled by livestock than on the more intensively grazed sites. Fertilizers are also spread on both grazed meadow and some grazed *Juncus* meadow fields early in the breeding season, therefore nests in these areas may also be vulnerable to farm implements. By contrast, rough pasture fields receive no treatment and therefore nests on these sites are not exposed to such risks.

Hay meadows usually have an even topography and are more featureless than the other field types. Their uniformity and the absence of tall vegetation may make nests more visible to predators. This may also be a problem on grazed meadow fields although usually these are more uneven and not so featureless as the hay meadows. The tendency for

Lapwing to nest on straw-strewn patches of ground where farmyard manure has been spread gives some camouflage on these fields. However, nests are better camouflaged on very tussocky fields or areas with clumps of *Juncus effusus*, the less uniform nature of the habitat making nests and incubating birds less obvious.

Grazed *Juncus* meadow fields offer the near ideal wader habitat. Clumps of *Juncus effusus* provide screened nest sites particularly favoured by Redshank and Snipe, and also provide good hiding places and shelter for chicks. Since both pre- and post-breeding flocks of waders in Upper Teesdale usually chose areas with a good cover of *J. effusus* as roost sites, it may be that such areas have a more favourable microclimate. In particular, the wind chill factor is likely to be less on fields where shelter is provided by clumps of *Juncus*, a feature of importance to wader chicks which are especially susceptible to chilling in early life until they acquire the ability to thermoregulate. In addition to providing suitable nest sites, shelter, and offering some camouflage against predators, grazed *Juncus* meadow also has good feeding sites. Flat, grassy areas are interspersed with the *Juncus* providing feeding localities particularly suited to visual feeders such as the Lapwing, whilst the provision of many marshy patches gives soft, wet feeding sites especially suitable for the probing foraging methods of the long-billed waders.

5. Development of Lapwing chicks during the fledging period.

Within populations of birds differences in brood size, hatching order, time of hatching, habitat and geographical locality have been implicated as factors affecting the growth rates of young (Perrins 1965, Lack 1966, Rickleffs 1968, Rickleffs & Peters 1979, Klomp 1970) whilst Gibb (195 and van Balen (1973) have related growth to ecological conditions, especially th availability of food. Most of this work has been concerned with passerines and little is known about factors affecting the growth rates of wader chicks.

In 1979 and 1980 growth rates of Lapwing chicks in Upper Teesdale were investigated in relation to the habitat on which they were raised, young being ringed as soon as possible after broods were known to have hatched.

Variation in the growth rates of Lapwing chicks raised on different habitats

Growth rates of chicks were studied on the field types where most Lapwing bred, that is grazed meadow, hay meadow and a poorer quality grazed meadow with a high cover of *Juncus effusus*. Few chicks were caught on rough pasture since the larger size of these fields and the low breeding densities of Lapwing meant that broods were more difficult to catch, usually being situated some distance from the nearest stone wall, this providing cover for the observer until the chicks could be located.

From a generalized growth curve based on chick weights it was apparent that growth was geometric up to about 10 days of age after which weight increase was more or less linear until fledging. There was no indication that an asymptote was reached immediately prior to fledging (35-40 days) although the number of chicks caught during this period was relatively small. Growth rates were therefore calculated by a linear regression of chick age with body weight for two age groups, 0-10 days and +10 days, log body weight being used for the younger group.

Due to the small numbers of chicks caught on some field types in 1979 the data has been grouped into chicks raised on wet or dry areas. Fig. 27 shows the growth rates of chicks on these sites. There was no difference in growth rates up to 10 days of age and although thereafter the growth rate of chicks on wet sites was 8.6% faster than those on the

Figure 27.

Weight increases of Lapwing chicks aged 0-10 days and +10 days on wet and dry habitats in the Harwood Beck Valley in 1979.

Regression equations:

Dry	Wet
a) 0-10 days	
$\log y = 0.039x + 1.18$	$\log y = 0.035x + 1.28$
$r = 0.92$	$r = 0.97$
N = 26 individuals	N = 9 individuals
S.E. of slope = 0.0033	S.E. of slope = 0.0027
b) +10 days	
$y = 5.37x - 17.25$	$y = 5.87x - 21.80$
$r = 0.99$	$r = 0.99$
N = 15 individuals	N = 12 individuals
S.E. of slope = 0.23	S.E. of slope = 0.29

The S.E.s have been calculated using the number of individuals on which the data is based and not the number of captures.

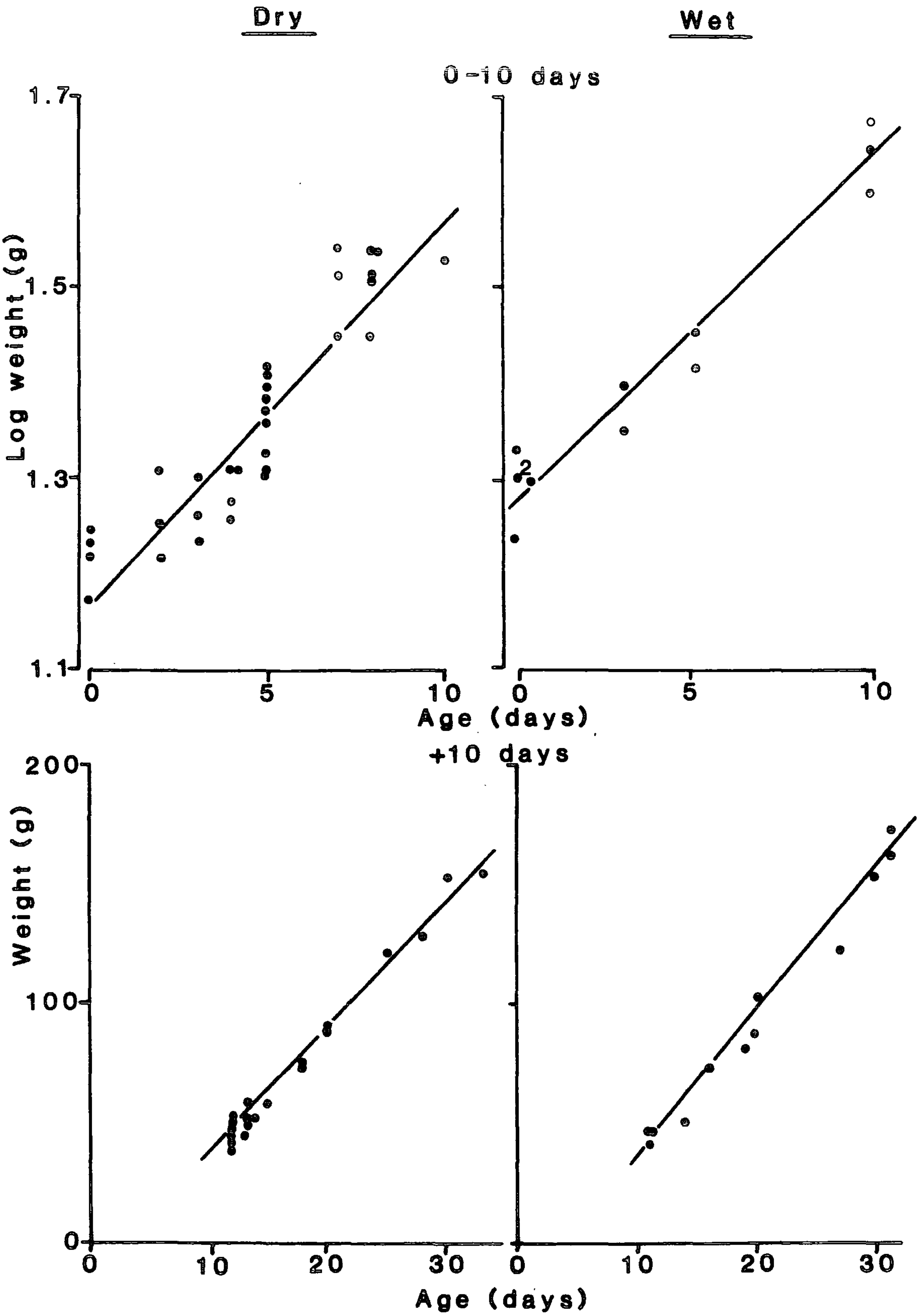

Dry
Wet
0-10 days
1.7
1.5
1.3
1.1
Log weight (g)
0
5
10
2
Age (days)
+10 days
200
100
0
Weight (g)
0
10
20
30
Age (days)

Figure 28.

Weight increases of Lapwing chicks aged 0-10 days and +10 days on dry grazed meadow and hay meadow in the Harwood Beck Valley in 1980.

Regression equations:

	Dry grazed meadow	Hay
a)	0-10 days	
	$\log y = 0.024x + 1.20$	$\log y = 0.033x + 1.19$
	$r = 0.71$	$r = 0.91$
	N = 26 individuals	N = 14 individuals
	S.E. of slope = 0.0049	S.E. of slope = 0.0043
b)	+10 days	
	$y = 4.65x - 14.05$	$y = 5.94x - 26.64$
	$r = 0.97$	$r = 0.97$
	N = 14 individuals	N = 13 individuals
	S.E. of slope = 0.36	S.E. of slope = 0.48

The S.E.s have been calculated using the number of individuals on which the data is based and not the number of captures.

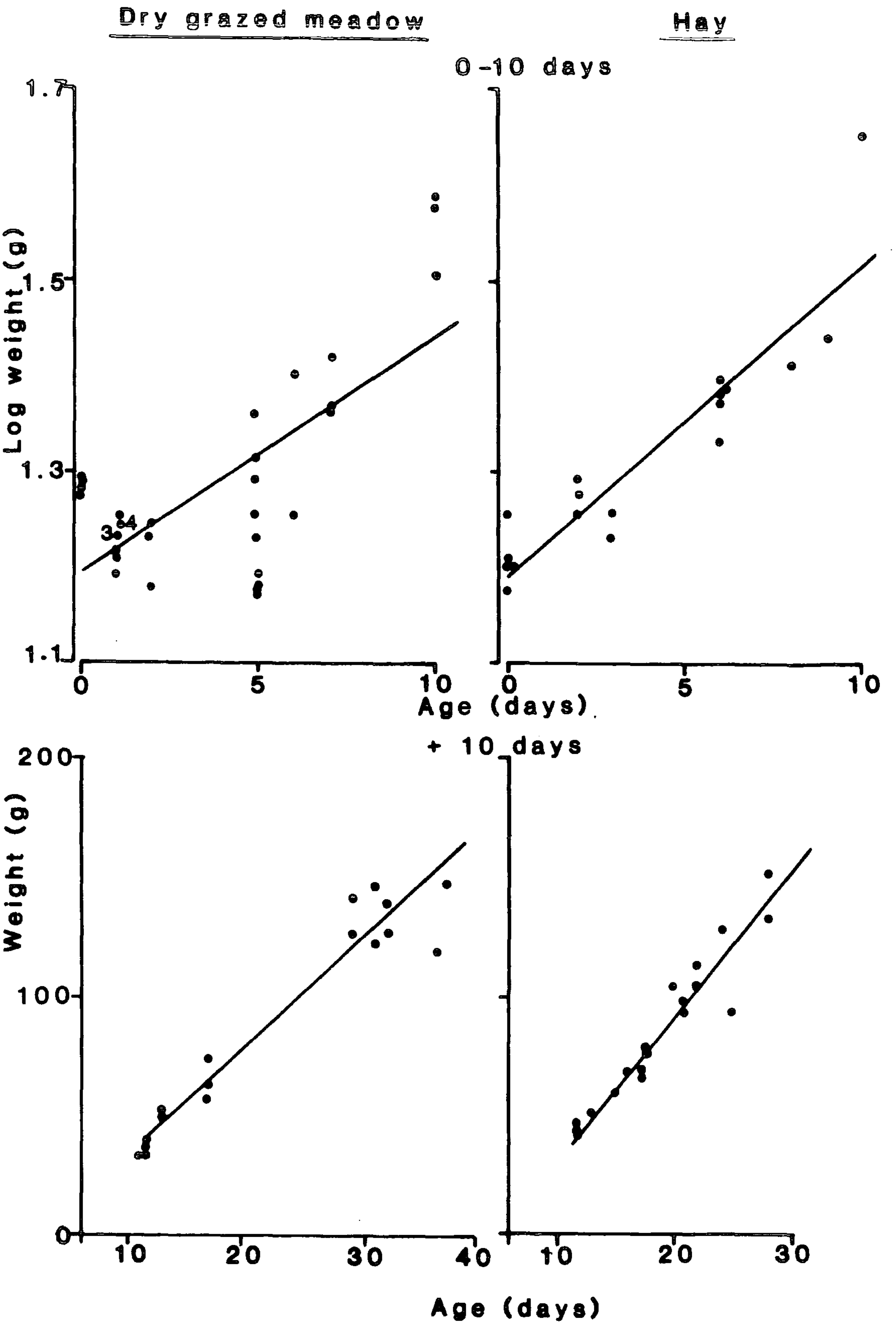

Dry grazed meadow
Hay
0 -10 days
1.7
1.5
1.3
1.1
Log weight (g)
3
4
0
5
10
0
5
10
Age (days)
+ 10 days
200
100
0
Weight (g)
10
20
30
40
10
20
30
Age (days)

Figure 29.

Weight increases of Lapwing chicks aged 0-10 days and +10 days on wet grazed meadow and grazed meadow with a cover of *Juncus effusus* greater than 50% in the Harwood Beck Valley in 1980.

Regression equations:

	Wet grazed meadow	Grazed *Juncus* meadow
a)	0-10 days	
	$\log y = 0.037x + 1.24$	$\log y = 0.038x + 1.24$
	$r = 0.92$	$r = 0.75$
	N = 11 individuals	N = 14 individuals
	S.E. of slope = 0.0051	S.E. of slope = 0.0089
b)	+10 days	
	$y = 5.70x - 17.34$	$y = 5.66x - 16.23$
	$r = 0.96$	$r = 0.98$
	N = 14 individuals	N = 17 individuals
	S.E. of slope = 0.47	S.E. of slope = 0.28

The S.E.s are calculated using the number of individuals on which the data is based and not the number of captures.

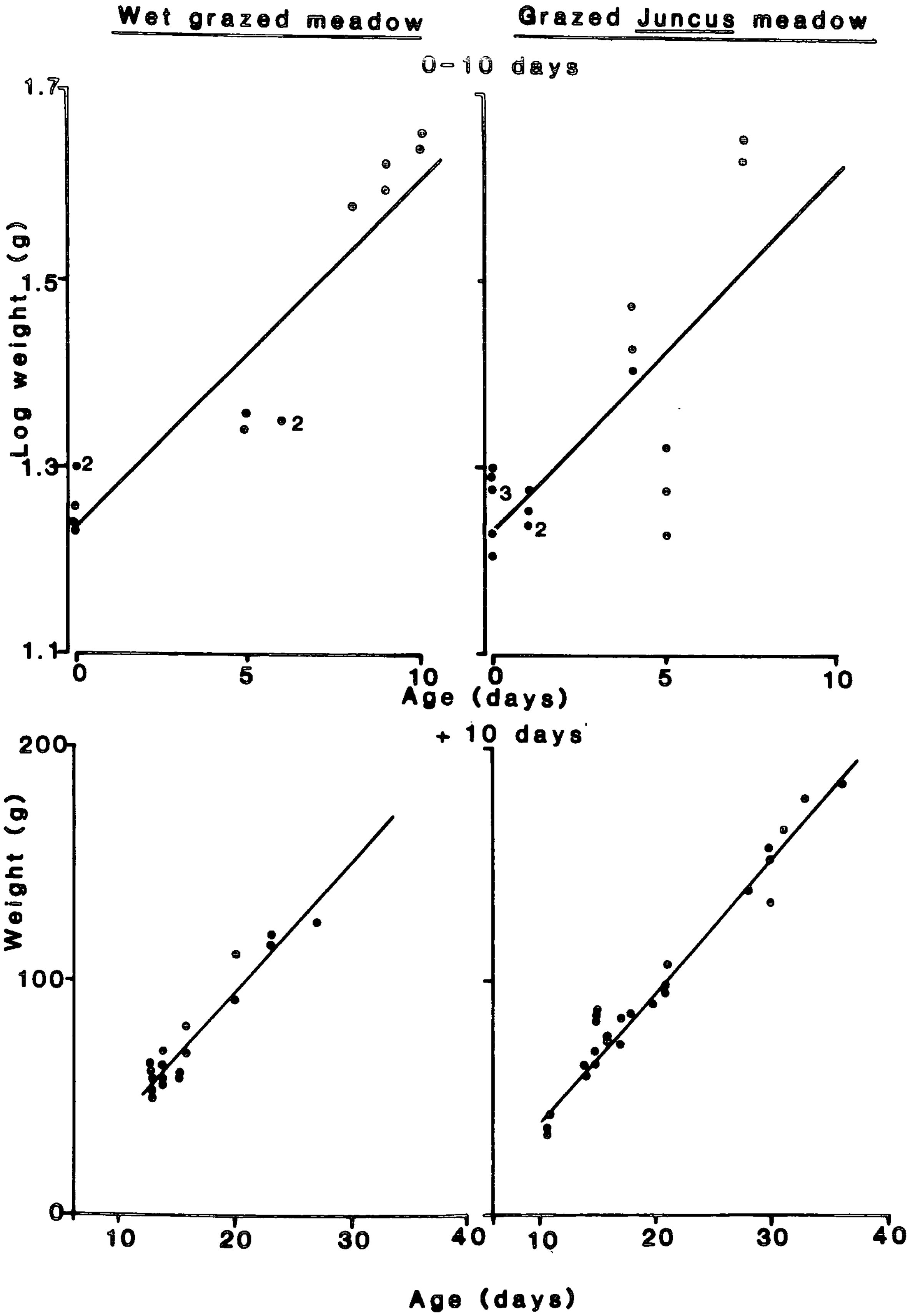

Wet grazed meadow
Grazed Juncus meadow
0-10 days
Log weight (g)
1.7
1.5
1.3
1.1
2
2
3
2
0
5
10
0
5
10
Age (days)
+ 10 days
Weight (g)
200
100
0
10
20
30
40
10
20
30
40
Age (days)

Table 61.

Growth rates of Lapwing chicks raised on different field types in the Harwood Beck Valley in 1980.

Data are from the regression equations in Figs. 27-29.

Sample sizes (N) refer to the number of individuals on which the data was based and not the number of captures.

	Growth rate of chicks	
	0-10 days (log g./day ± S.E.)	+ 10 days (g./day ± S.E.)
Dry grazed meadow	0.024 ± 0.0049 (N = 26)	4.65 ± 0.36 (N = 14)
Hay	0.033 ± 0.0043 (N = 14)	5.94 ± 0.48 (N = 13)
Wet grazed meadow	0.037 ± 0.0051 (N = 11)	5.70 ± 0.47 (N = 14)
Grazed *Juncus* meadow	0.038 ± 0.0089 (N = 14)	5.66 ± 0.28 (N = 17)

dry areas the difference was not significant.

The greater numbers of chicks caught in 1980 made it possible to analyse growth rates with respect to field type. The weight increases of Lapwing chicks raised on different habitats are shown in Figs. 28 and 29. Table 61 summarizes the growth rates to facilitate comparison between the sites. Chicks showed similar growth rates on hay meadow, grazed meadow with *Juncus* and wet areas of grazed meadow throughout the fledging period (Figs. 28 and 29, and Table 61). There were no significant differences in chick growth between habitats up to 10 days of age but the growth rate attained on dry grazed meadow was 27-37% less than that on the wetter sites or hay meadow. After 10 days of age chicks on dry grazed meadow still showed the lowest growth rate (Table 61) growing 18-22% more slowly than chicks on other field types. Their growth rate was now significantly lower than that of chicks raised on hay meadow ($t = 2.16$, d.f. = 25, $P < 0.05$) or grazed meadow with *Juncus* ($t = 2.22$, d.f. = 29, $P < 0.05$). No pronounced differences were found between the other field types.

Discussion

The results suggest that Lapwing chicks attain poorer growth rates on dry sites except for hay meadow. Certain features of the food supply on hay meadow may make it more favourable than other dry sites. Not only was it found to have the highest numbers of surface active invertebrates (Fig. 16) but the practice of spreading large quantities of farmyard manure on hayfields and the subsequent attraction of dung associated invertebrates may produce an evenly distributed food supply which is easy to exploit. Another factor which indicates that the variation in growth rates may be attributable to dry conditions rather than habitat type *per se* was that differences were apparent in 1980 but not in 1979. Between years there was a sharp contrast in the amount of spring rainfall which may have affected feeding conditions later in the season. In 1979 rainfall for March and April totalled 677 mm whereas spring 1980 was much drier, March-April rainfall being only 176 mm, the dry conditions even persisting into May (23.6 mm rainfall compared with 172.2 mm in 1979) (Metereological Office data from Moor House N.N.R., Station No. 7188). Thus there may be a critical wetness for the habitat below which growth rates will be impeded; presumably this level was not reached during the wet breeding season of 1979. Jackson & Jackson (1975) found a difference in growth rates of Lapwing chicks in wet and dry years. In dry years chicks grew more slowly and took 5-10 days longer to fledge than chicks produced in wet years.

The greater favourability of wet sites is also indicated by movements of broods. Movements of broods which also involved a change of habitat were noted on 12 occasions. In all but one of these cases the transition was from a dry habitat to a wet area, usually to grazed meadow with *Juncus*.

There have been few studies examining the growth rates of wader chicks raised in different habitats. Wilson (1978) found that Ringed Plover chicks raised on plough grew faster than those on grassland areas. In Redfern's (1983) study Lapwing showed a delay in weight increase for the first few days after hatching. However, no such delay was apparent in the growth of Lapwing chicks in the New Forest (Jackson & Jackson 1980). It is therefore possible that as well as variations in growth rates between different types of habitat, there may also be variations in growth characteristics both between regions and between years.

In a number of bird species early hatched young grow faster than those hatched later in the season (Gibb 1950, Perrins 1965, Rickleffs & Peters 197 and Hedgren & Linnmann 1979). Due to small sample sizes it was not possible to compare growth rates of early and late hatched Lapwings. Chicks were caught throughout the season on all field types except hay meadow, birds not being able to use this habitat type when the vegetation became long. Therefore the sample of chicks on hay meadow contained a greater proportion of early hatched young than the samples from other habitat types. Thus, if there is a seasonal difference in growth rates this may be a source of bias in the rates calculated for chicks raised on hay meadow. However, Jackson & Jackson (1975) found a difference in the growth rates of chicks from first and repeat clutches, and therefore early and late chicks, in only one year of their four year study; chicks from first clutches in 1973 grew more slowly than those from repeat clutches. The difference may have been due to weather conditions rather than being a characteristic of early and late chicks *per se* as conditions in April and May were very dry compared to June and would therefore have had a much greater effect on the early chicks.

Lower growth rates may imply a longer fledging period since the rate of development may also be lower. Jackson & Jackson (1975) reported that the fledging period of Lapwing was extended in dry years when the young showed lower daily weight increases up to fledging. In the present study there was no indication that the development of the various feather tracts was retarded in chicks with lower growth rates and there were no significant differences in the wing lengths of chicks raised on different field types. Other studies have also indicated that the rate of feather development and the increase in linear dimensions such as wing length and tarsus length are not affected by nutritional deficiencies. In the Robin splitting of feather sheaths occurred independently of body weight (Lack & Silva 1949) whilst

Guillemots leaving the nest at low weight did not appear to have reduced feather development (Hedgren 1981). Conversely, Lack & Lack (1951) showed that a reduction in the food supply of the Common Swift retarded the growth of the young not only in weight but also in linear dimensions such as wing length.

The consequences of reduced growth rates and low fledging weight are likely to be more severe in species where young have been fed by their parents as nestlings but have to fend for themselves once fledged. Post-fledging survival has been demonstrated to be positively correlated with fledging weight in the Great Tit (Perrins 1963 and 1965, Dhondt 1970) and the South African Gannet (Jarvis 1974). However, in the Razorbill and Guillemot there were no significant differences in survival between chicks fledging at different weights (Lloyd 1979 and Hedgren 1981). In addition, Andersson (1978) has suggested that a reduced offspring quality might lead to an increased age at first breeding. Thus low fledging weight may have other negative consequences, even for precocial species which feed themselves from hatching.

SECTION 4

WADERS ASSOCIATED WITH AQUATIC HABITATS

In Upper Teesdale three species of wading birds, Oystercatcher, Ringed Plover and Common Sandpiper, are notably restricted to bodies of permanent water. Typically Oystercatchers (Haematopodidae) are coastal breeders but some nest inland in central Russia, the south island of New Zealand, Holland, northern Germany, Denmark, southern Sweden and northern Britain (Voous 1960, Dare 1966, Heppleston 1972). The British breeding Oystercatcher (*Haematopus ostralegus occidentalis)* has nested inland in the eastern Highlands of Scotland since at least the eighteenth century (Baxter and Rintoul 1953). By contrast, the Scottish lowlands and northern England were apparently not used for inland breeding until the 1880s (Buxton 1961). The first sites occupied on spreading inland were areas of extensive shingle banks on the broader reaches of rivers (Buxton 1961), the habitat used by the pairs of Oystercatchers found nesting in Upper Teesdale. Reasons for the change from coastal to inland breeding have been discussed by Heppleston (1972).

Although breeding inland in the Arctic , in other regions the Ringed Plover favours coastal regions as breeding sites. However, like the Oystercatcher, it has in certain areas extended its breeding habitat to inland sites. In Great Britain it still breeds mainly on the coast but since the 1950s it has shown an increasing tendency to nest inland. The incidence of inland breeding is greatest in Scotland and northern England, where the shingle banks of rivers and lakes are the typical habitats, whilst further south in England, reservoirs, gravel pits and other places modified by man's activities are used (Prater 1976, Sharrock 1976).

Common Sandpiper were well distributed throughout the study area, being present on all the major streams and rivers and around the shores of Cow Green reservoir. This species occurs across the whole of the Palearctic region except for the extreme north and south (Voous 1960, Dement'ev *et al.* 1969). It is widely distributed throughout Great Britain and Ireland although it breeds only occasionally in southern and eastern England (Kennedy, Ruttledge and Scroope 1954, Watson 1972, Parslow 1973). The British and Irish population has recently been estimated as 50,000 pairs (Sharrock 1976) which is within the range of 10,000 to 100,000 pairs given by Parslow (1973). For such a widely distributed and common bird it has received little attention and there is a paucity of published information, much of that which does exist being largely anecdotal. Although its breeding habitat has been described in broad terms there is little quantitative information on breeding densities in different localities.

In Great Britain the Common Sandpiper breeds on waterways from the hills to the coast but its typical haunts are upland streams, rivers and clear lakes with exposed alluvial deposits and shingly rather than muddy or marshy shores (Evans 1911, Coward 1920, Sharrock 1976). It generally prefers running to still waters but nests impartially on stretches where the stream banks are flat or steep, open or wooded (Witherby *et al.* 1940, Dement'ev *et al.* 1969). Saltwater areas (saltmarsh, estuaries and the coast) are used on passage but these are, for the most part, avoided as breeding grounds although nests have occasionally been observed on the coast in England (Robertson 1905-6, Turney 1913) and in parts of Scotland coastal nesting occurs regularly (Raven 1927, Crosby 1951, Baxter and Rintoul 1953, Morton Boyd 1958).

Of the three riparian species, only the Common Sandpiper was present in sufficient numbers in the study area to enable statistical analysis of the distribution of breeding pairs in relation to certain habitat variables.

(i) Oystercatcher

The spread of Oystercatchers in northern England has been traced by Buxton (1961). However, in spite of such studies it seems that the colonization of Upper Teesdale has been largely unrecorded. There were no records of breeding on any of the Durham rivers before the 1950s (Temperley 1951). Dare (1966) gave the Tees/Wear/Derwent river systems as having a maximum of only five pairs whilst Greenhalgh (1972) records seven pairs for the Tees (one pair at a gravel pit near Darlington and six pairs above Barnard Castle). No mention has been made of Oystercatchers nesting in the upper valley of the Tees where up to ten pairs were found during the present study.

Oystercatchers have bred in the vicinity of the study area in Upper Teesdale since the 1930s. Buxton mentions that Oystercatchers had occupied most of the Eden valley by 1950 and that breeding had occurred on the South Tyne since c. 1935, these river systems lying immediately to the west and north of the study area.

Within the study area itself, Oystercatchers were first noted breeding on Harwood Beck in 1957 (R. Allinson pers. comm.), these probably being the first pair to breed in Upper Teesdale. Birds were recorded in the Cow Green area before the impoundment of the reservoir (a pair by the Weel of the Tees in 1967, a pair at East Cow Green Mine in 1968 and a pair on the Isle of Man, Cow Green in 1969). Since the reservoir was formed, none have bred on its shores but a pair has bred below the dam each year since 1974 (I. Findlay pers. comm.).

Table 62 shows the number of pairs of Oystercatchers breeding on the main stretches of the river in Upper Teesdale from 1977-80, the total population being up to ten pairs.

On the River Tees Oystercatchers were observed as far upstream as 580m although the highest nesting area was at 530m. In Scotland, Witherby *et al.* (1940) recorded pairs breeding up to 554m and Dare (1966) mentioned a brood at 646m and a pair at 985m.

Inland breeders usually avoid areas where the upland river valleys are mainly narrow, steep-sided and well-wooded. According to Buxton (1961) the first sites occupied in northern England, after crossing the watershed from the west side of the Pennines, were not the narrowest upper reaches of the rivers but areas where large shingle beds first appear. This is also the case in Teesdale; all sites so far occupied have extensive shingle banks compared to other local stretches of river.

At later stages of inland colonization Oystercatchers began to disperse away from the river shingle beds to nest on surrounding farmland. Most usually nest within 100m of the river although a few pairs have attempted to nest as much as 6km from the nearest water (Greenhalgh 1969 b). In Teesdale there has as yet been no such dispersion from the riversides. Nest sites were restricted to large shingle beds and areas with low vegetation cover on river islands.

Although they are used as nest sites, inland breeding Oystercatchers do not feed to any great extent on the riverain shingle beds (Dare 1966, pers. obs., Teesdale). All pairs of Oystercatchers in Upper Teesdale fed on the alluvial grassland at the sides of the river; those breeding at lower altitudes (e.g. in the Harwood Beck valley) also fed extensively in fields. A land improvement scheme, with a view to increasing grass production and therefore sheep density, carried out in 1977-78 by a local farmer on 16 ha of rough, acid grassland by the

Table 62. Number of pairs of Oystercatcher located on various stretches of river in Upper Teesdale 1977-1980.

	Harwood Beck	Cow Green - below dam	River Tees - Moor House N.N.R.	River Tees - High Force to Middleton	River Tees - Cow Green to Harwood Beck confluence	Maize Beck
1977	5	1 (1 pair early in year but no breeding)	2	2	0	0
1978	4	1	2	N.d.	0	1
1979	4	1	2	N.d.	0	0
1980	4	1	2	3	0	0

N.d. = no data

River Tees, just outside the boundary of the Moor House N.N.R., created a new feeding site for the Oystercatchers at Moor House, the area being used extensively within a year of the improvements. For both adults and chicks, earthworms and tipulid larvae are major components of the diet (Dare 1966 and Heppleston 1972). Soil cores taken on the improved grassland at the end of April 1980 revealed a high density of tipulid larvae (mainly *Tipula paludosa*) (177 larvae m^{-2}) compared to the surrounding rough pasture (56 larvae m^{-2}) and mineral soils (64 larvae m^{-2}). Few other Diptera, earthworms or beetle larvae were found on these areas, except for the mineral grassland close to the riverside which had a significant population of earthworms (179m^{-2}).

(ii) Ringed Plover

The only breeding site of Ringed Plover within the study area was on the eastern shore of Cow Green in an area of extensive shingle banks and bare rock where small streams entered the reservoir. One pair bred during 1977-80 (at the entry of Slapstone Sike in 1977 and 1978 and at the entry of Red Sike in 1979 and 1980). Two pairs (one in each of the above sites) were present in 1981 (I. Findlay pers. comm.). Ringed Plover were first recorded in the Cow Green area, before the impoundment of the reservoir, in April and August 1968 (one bird). Although there were further sightings of a single bird in April and June 1970 and April 1974, there was no evidence of breeding until 1975 when a pair nested by Tinkler's Sike, Widdybank Fell, not far from the shores of the reservoir (I. Findlay pers. comm.).

(iii) Common Sandpiper

Methods

The Common Sandpiper stays close to streams, rivers and lake shores, making it an easy species to observe and allowing accurate counts of breeding pairs to be made. All major streams and rivers within the study area, their main tributaries and the shores of Cow Green Reservoir were censused for breeding sandpipers in 1978, 1979 and 1980. In addition, data from a preliminary survey made in 1977 are also available. A minimum of three visits a year was made to all stretches of stream, the only exceptions being Maize Beck in 1977 (one visit) and 1980 (two visits) and Harwood Beck in 1977 (two visits).

Sandpipers usually start to return to the study area towards the end of April (mean first arrival date 1977-80 was 24 April). Most birds stay in the study area until the second half of July although failed or early breeders may leave as early as the end of June. Only a few pairs and small numbers of fledged chicks remain into August. Birds were therefore censused in May and June to ensure that the entire breeding population was present. Although this spanned the incubation period (the earliest nests being started during the first week of May) when the birds tended to be quieter and more skulking, the fact that they stayed close to the streamsides made counting feasible.

On being flushed, birds moved along the stream away from the observer. Thus they could be pushed gradually up or downstream until they reached a point beyond which they were unwilling to be driven any further and either flew back in the opposite direction or came into conflict with the next pair of Sandpipers. These points were taken as the territorial boundaries.Whenever possible,to back up these observations, pairs were also observed from vantage points without disturbing the birds.

Between 1977 and 1979, 45 adult Common Sandpipers were mist-netted and marked individually with a combination of three 'Darvic' (rigid PVC) colour rings in order to assess site fidelity, mortality and mate faithfullness between years, and to observe any change of territorial boundaries and upstream or downstream movement during the breeding season. Young chicks were marked with British Trust for Ornithology metal rings only, while those close to fledging or already fledged were individually colour ringed as for adults.

For comparison with the upland streams of the study area a lower reach of the River Tees between High Force and Middleton-in-Teesdale was also censused for breeding sandpipers in 1977 and 1980. Here the river was much wider, the banks had, for the most part, lush vegetation and long stretches were tree-lined. Also, each year between 1977 and 1980, at the beginning of the season when sandpipers were moving into the study area, and then again at the end when birds were departing, this stretch was visited to search for up or downstream movement of birds which had been colour-ringed within the main study area.

In order to explain the distribution of Common Sandpiper within the river systems, a series of habitat factors was chosen which measured certain characteristics of the streams. These measurements (see Appendix 7) related only to attributes of the streams themselves and the properties of the banks. Since Common Sandpipers breed in such a wide variety of vegetation types from upland areas to the coast, the presence of some kind of permanent water being the one constant feature, no emphasis was placed on the vegetation type of the stream banks or on the general features of the surrounding area.

Most of the factors measured were not subject to seasonal or annual fluctuations and it is therefore not critical when measurements are made. Factors such as stream width and flat or steep banks are constant features, at least over the time span necessary for these studies. However, characteristics such as the number and area of shingle and muddy banks may fluctuate with the rise and fall in water levels.

It was, therefore, necessary to ensure that measurements were taken at normal summer river levels. No measurements were made within three days of heavy rain in order to give the water levels time to stabilize once more.

The most likely variations in stream characteristics between years are in the locations of exposed shingle beds which may be expected to shift. However, over the period of the study no such changes were apparent.

The set of stream variables (Appendix 7) was measured at 100m intervals along the stream. The data were then averaged or totalled, according to the particular variable, to give measurements specific to each 0.5km length of stream. Using 0.5km stretches gave a range of densities for the number of breeding pairs of Common Sandpiper enabling a stepwise multiple regression analysis to be applied to the data. The number of pairs per 0.5km length was taken from a map of territorial boundaries. Thus if a pair of Common Sandpipers had a territory which extended across two 0.5km lengths of stream such that 25% of their territory lay in one section and 75% lay in the adjacent length, then the scoring for the dependent variable in those two lengths would be 0.25 pairs and 0.75 pairs respectively.

Preliminary measurements were made along 10.5km of stream in 1979. Analysis of these data by multiple regression analysis showed that it was possible to reduce the set of habitat variables by avoiding the use of highly intercorrelated ($r > 0.80$) factors without losing variables important in explaining Common Sandpiper distribution. The number and area of exposed shingle beds was highly intercorrelated ($r = 0.86$, d.f. = 19, $P < 0.001$) as was the number and area of exposed muddy banks ($r = 0.84$, d.f. = 19, $P < 0.001$). The number of these banks had higher correlations with the density of sandpipers than did their areas and a multiple regression analysis (Table 63) indicated that measurements of area made no significant contribution towards explaining Common Sandpiper distribution. Therefore, measurements of the area of exposed shingle and mud were not made in 1980. This enabled data to be collected more rapidly. Using this modified set of variables it was possible to survey a total of 37.5km of stream in 1980, ranging from the narrower upper reaches of streams to wider stretches of the River Tees.

Maps of the territorial boundaries of pairs of Common Sandpipers were superimposed on the series of measurements made at 100m intervals of bank to bank stream width. This allowed territory size to be calculated and an assessment of the influence of stream width on territory size on different stretches of stream and river.

Results

(a) General distribution and territory size.

Figure 30 shows the mean number of breeding pairs and the density of Common Sandpipers found on the river systems within the study area between 1977 and 1980. The birds were present on all the major streams and rivers and although found on the upper reaches of the streams, no pairs extended right up to the headwaters. Stretches of streams less than 2m wide were not used unless a major part of the territory also extended over reaches of greater width. Breeding pairs were also attracted to some of the still water habitats. The largest of these water bodies, Cow Green Reservoir, had sandpipers all round its shores. The upland tarns were not used, except for the largest, Great Rundale Tarn, which had shingle banks along part of its shore and one pair of sandpipers present in three out of the four breeding seasons.

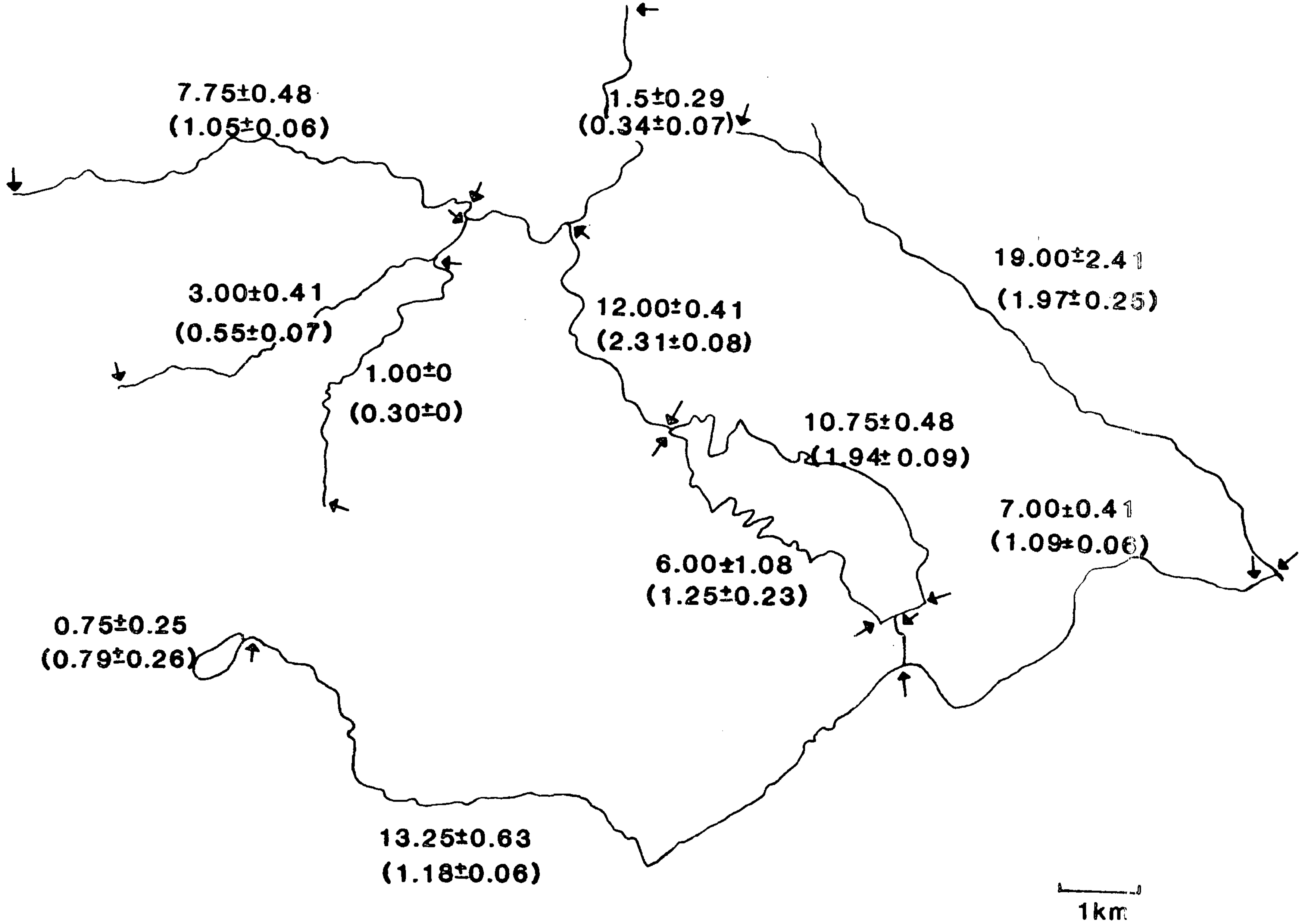
Breeding densities were apparently unaffected by the vegetation type at the stream sides. The stretch of the River Tees between Tees Bridge and Cow Green, although having narrow strips of alluvial grassland along part of its banks, was predominantly surrounded by a mixture of *Calluna vulgaris* and *Eriophorum vaginatum*. Here densities were not significantly different from those on Harwood Beck (Fig. 30) which was surrounded by pasture and hay meadow. The River Tees between High Force and Middleton-in-Teesdale had lush, herb-rich vegetation along its stream banks, was surrounded by pasture and hay meadow and long stretches were tree-lined. Common Sandpipers were censused on this section of the river in 1977 and 1980 when an average of 16.5 ± 1.77 breeding pairs were present. This gave a density equivalent to 1.90 ± 0.20 pairs km^{-1} which was not significantly different from either the densities of Common Sandpipers observed on Harwood Beck or those on the River Tees between Tees Bridge and Cow Green (Fig. 30).

Common Sandpipers defend a strip-like territory along a stretch of stream, river or lake shore. The birds remain in close proximity to the water's edge although pursued birds will often fly overland as a short cut between bends in the river's course. Territorial conflicts were never observed away from the stream and any chasing of intruders was confined to up or downstream movement. The closeness of nests to the water's edge further emphasized the strip-like nature of the territory (see section iii d). Thus territory length is an important factor in determining territory size. This was measured (see Methods) for 87 pairs of Common Sandpipers from the narrow upper reaches of streams within the study area to the broader stretches of the River Tees as far downstream as Middleton-in-Teesdale. Territorial boundaries were clearly defined and there was generally little overlap between pairs. However,

Figure 30. Distribution of breeding pairs of Common Sandpipers within the river systems of the study area in 1977-80.

Figures refer to the average number of breeding pairs ± 1 S.E. present on each stretch of stream over the four breeding seasons 1977-80.

Figures in parentheses are the equivalent densities (no. of pairs km^{-1}) ± 1 SE. Arrows delineate the lengths of stream over which breeding densities are calculated.


7.75±0.48
(1.05±0.06)
1.5±0.29
(0.34±0.07)
19.00±2.41
(1.97±0.25)
3.00±0.41
(0.55±0.07)
12.00±0.41
(2.31±0.08)
1.00±0
(0.30±0)
10.75±0.48
(1.94±0.09)
7.00±0.41
(1.09±0.06)
6.00±1.08
(1.25±0.23)
0.75±0.25
(0.79±0.26)
13.25±0.63
(1.18±0.06)
1km

on some of the broader stretches of the rivers (e.g. around Tees Bridge and upstream of Middleton), although birds still showed aggression to other sandpipers, boundaries were less sharply defined and there was some intermingling of pairs. Cuthbertson, Foggitt and Bell (1952) also noted an overlap of pairs in the Sedbergh area where some birds bred so closely that four pairs freely intermingled.

Territory length was influenced by mean stream width such that territories showed a logarithmic decrease in length as streams became wider (Fig. 31). Territories varied in length from 0.25km to 1.8km but of the eight territories which were more than 1km long, six were held by pairs of sandpipers furthest upstream. In theory, the uppermost pair of sandpipers on any stream is free to move upstream to the headwaters, but in practice they were not found to do so. The upstream "boundary" of such territories was taken as the point beyond which neither member of the pair could be driven upstream. However, the lack of interference of a neighbouring pair of sandpipers may make the apparent length of such territories artificially long. Therefore, these territories are indicated with a separate symbol in Figs. 31 and 32 and have been excluded from the calculation of the regression equations.

The area of a Common Sandpiper's territory can be considered as the length of stream defended multiplied by the average width of the stream along that length. Territory area was correlated with stream width ($r = 0.58$, d.f. = 79, $P < 0.001$; Figure 32) such that the area defended increased as streams became wider. The regression equation must, however, be regarded with caution as the x and y variates are interrelated. Nevertheless, it does indicate that the observed increases in territory length with decreasing stream width were not sufficient to maintain a constant territory area over the range of stream widths examined. Thus territory area was reduced as streams became narrower in spite of the corresponding increase in the length of stream defended.

Figure 31. Relationship between territory length and stream width for pairs of Common Sandpipers breeding in Upper Teesdale in 1977, 1978, 1979 and 1980.

Regression equation:

$\log y = -0.011x - 0.117$

where y = territory length (km)

x = stream width (m)

$r = -0.48$

d.f. = 79

$P < 0.001$

The uppermost territories before the headwaters of the streams have been excluded from the calculation of the regression equation.

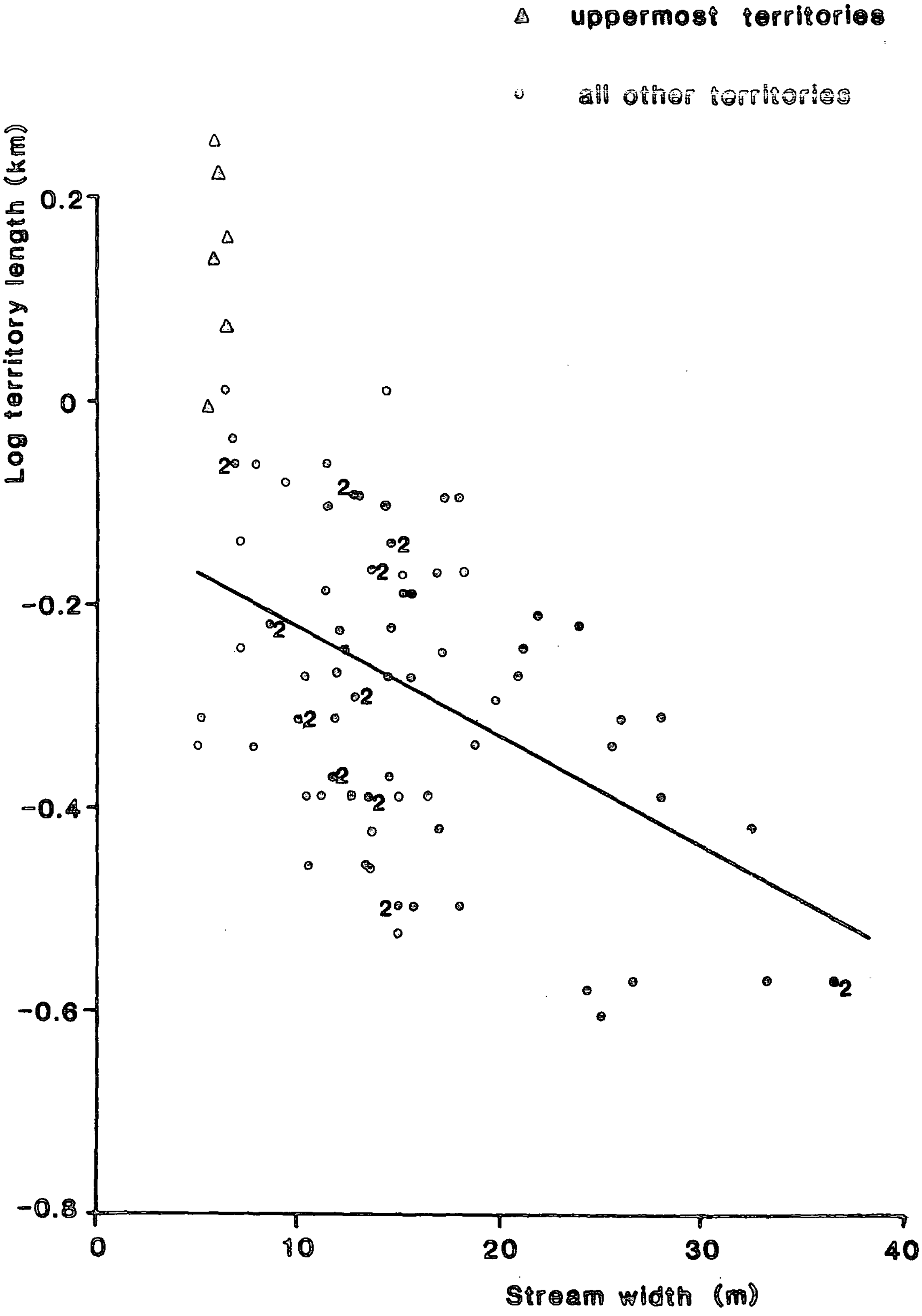

△ uppermost territories
○ all other territories
Log territory length (km)
0.2
0
-0.2
-0.4
-0.6
-0.8
0
10
20
30
40
Stream width (m)
2

Figure 32. Relationship between territory area and stream width for pairs of Common Sandpipers breeding in Upper Teesdale in 1977, 1978, 1979 and 1980.

Regression equation:

$$y = 262.4\,x + 3915.4$$

where y = territory area (m^2)

x = stream width (m)

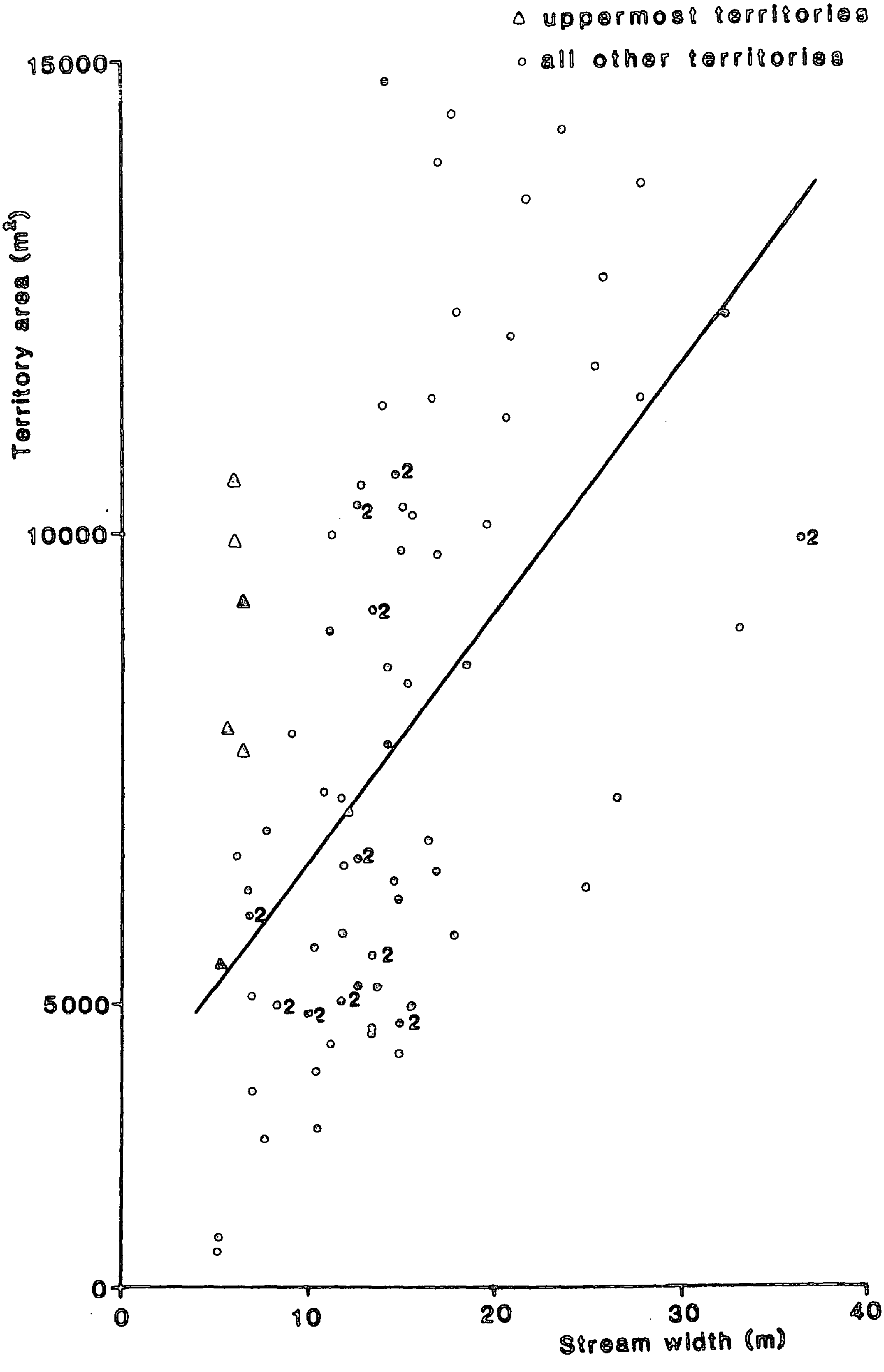
$r = 0.58$

d.f. = 79

$P < 0.001$

The uppermost territories before the headwaters of the streams have been excluded from the calculation of the regression equation.

The regression equation must be regarded with caution as the x and y variates are interrelated.


△ uppermost territories
○ all other territories
Territory area (m²)
15000
10000
5000
0
0
10
20
30
40
Stream width (m)
2

(b) The selection of breeding sites within a river system.

The densities of breeding pairs of Common Sandpipers were apparently unaffected by the vegetation type of the streamsides and surrounding areas (Section 4, iii a)) and birds nested on both flat and steep banks (Section 4, iii c)). Thus it would seem that birds must be responding to the characteristics of the water body and not the general surroundings. Measurements of habitat variables (Appendix 7) made in 1979 and 1980 were aimed at trying to elucidate what these factors may be within a system of streams and rivers.

The results of a stepwise multiple regression analysis applied to the preliminary data collected from 10.5km of stream in 1979 are summarized in Table 63. The results indicate that the number of exposed shingle beds was important in determining the breeding density of Common Sandpiper, this variable alone accounting for 58% of the variation in sandpiper distribution. No additional factors considered had a significant effect.

As stream characteristics did not change from year to year (Methods), the larger sample of data collected in 1980 has been applied to the distributions of sandpipers in 1977, 1978, 1979 and 1980 and the average number of pairs present between 1977 and 1980. The results of the stepwise multiple regression analyses to investigate the effect of the stream characteristics on the density of the birds are summarized in Table 64. The number of exposed shingle beds was once again a significant factor in all years except 1977, explaining between 5 and 21% of the variation in Common Sandpiper density. Average stream width was however the most important variable having the highest F value in all the analyses. The analyses for 1977 and the average density of sandpipers 1977-80 suggest that the size of river islands

Table 63 . Summary of stepwise multiple regression analysis of Common Sandpiper density and the stream variables in 1979.

Dependent variable : No. of pairs of Common Sandpiper per 0.5km length of stream

Independent variables	Slope	S.E. of Slope	F Value	Multiple R	% R^2 change
No. of shingle banks	0.13	0.026	26.33	0.76	58

Constant = 0.50 N = 21

Table 64. Summary of stepwise multiple regression analyses of Common Sandpiper density and the stream variables in 1977, 1978, 1979, 1980 and 1977-80.

Sample sizes were 75 in 1977, 1980 and 1977-80, and 62 in 1978 and 1979.

Dependent variable: No. of pairs of Common Sandpiper per 0.5km length of stream

Year	Independent variables	Slope	S.E. of Slope	Intercept	F Value	Multiple R	% R^2 change
1977	Average stream width	0.027	0.0056	0.197	23.67	0.49	24
	No. of large islands	0.144	0.046		9.78	0.58	10
1978	Average stream width	0.049	0.013	-0.036	14.88	0.46	21
	No. of shingle banks	0.025	0.0067		13.94	0.60	15
1979	No. of shingle banks	0.017	0.0064	-0.317	6.79	0.46	21
	Average stream width	0.051	0.012		17.51	0.58	13
	% boulder cover	0.0062	0.0025		5.96	0.64	7
1980	Average stream width	0.045	0.0067	0.115	43.92	0.60	36
	No. of shingle banks	0.016	0.0064		6.46	0.64	5
1977-80	Average stream width	0.042	0.0063	-0.10	43.76	0.54	29
	No. of shingle banks	0.016	0.0056		8.30	0.65	13
	% boulder cover	0.0062	0.0022		7.80	0.69	6
	No. of small islands	-0.15	0.062		5.66	0.71	2

may influence the distribution of breeding pairs, birds tending to avoid the smaller islands but being attracted to stretches with large islands. This may in part be due to the sandpipers' preference for wider streams, large islands only being found on these stretches.

Two former studies have shown that stream gradient influences Common Sandpiper distribution although neither explained why the relationship occurred. Cuthbertson, Foggitt and Bell (1952) reported that streams with a fall of more than 38m km^{-1} did not hold breeding sandpipers. However, in Teesdale four pairs of Common Sandpipers were present on stretches of stream with gradients in excess of this. More recently Marchant and Hyde (1980) demonstrated an inverse relationship between the density of Sandpipers on 10km stretches of river and gradient, greater densities occurring on streams or rivers with a fall of less than 5m km^{-1}. In the present study, none of the regression analyses indicated that Common Sandpiper density was affected by the gradient of the stream over 0.5km stretches when other habitat variables were taken into account. However, when stream gradient over longer stretches is considered there is a curvilinear relationship with Common Sandpiper breeding density. Thus, sandpiper density is significantly correlated with log gradient ($r = -0.87$, d.f. = 7, $P < 0.01$; Fig.33), density decreasing on areas with a faster fall to the stream. On these stretches of stream, log gradient and stream width were highly correlated ($r = -0.90$, d.f. = 7, $P < 0.01$). Thus, in a multiple regression analysis on these longer stretches of stream, width did not explain a significant proportion of the variation in sandpiper numbers once log gradient was included and log gradient became unimportant if stream width was made to enter first.

Figure 33. The relationship between stream gradient and Common Sandpiper density in part of Upper Teesdale in 1977-80.

Points correspond to the densities shown on stretches of stream in Figure 30 with the inclusion of the stretch of the River Tees between High Force and Middleton. Densities calculated from the mean number of pairs present between 1977 and 1980. Error bars indicate 95% confidence limits.

Regression equation:

$y = 4.19 - 2.25 \log x$ where x = fall of stream (m km^{-1})

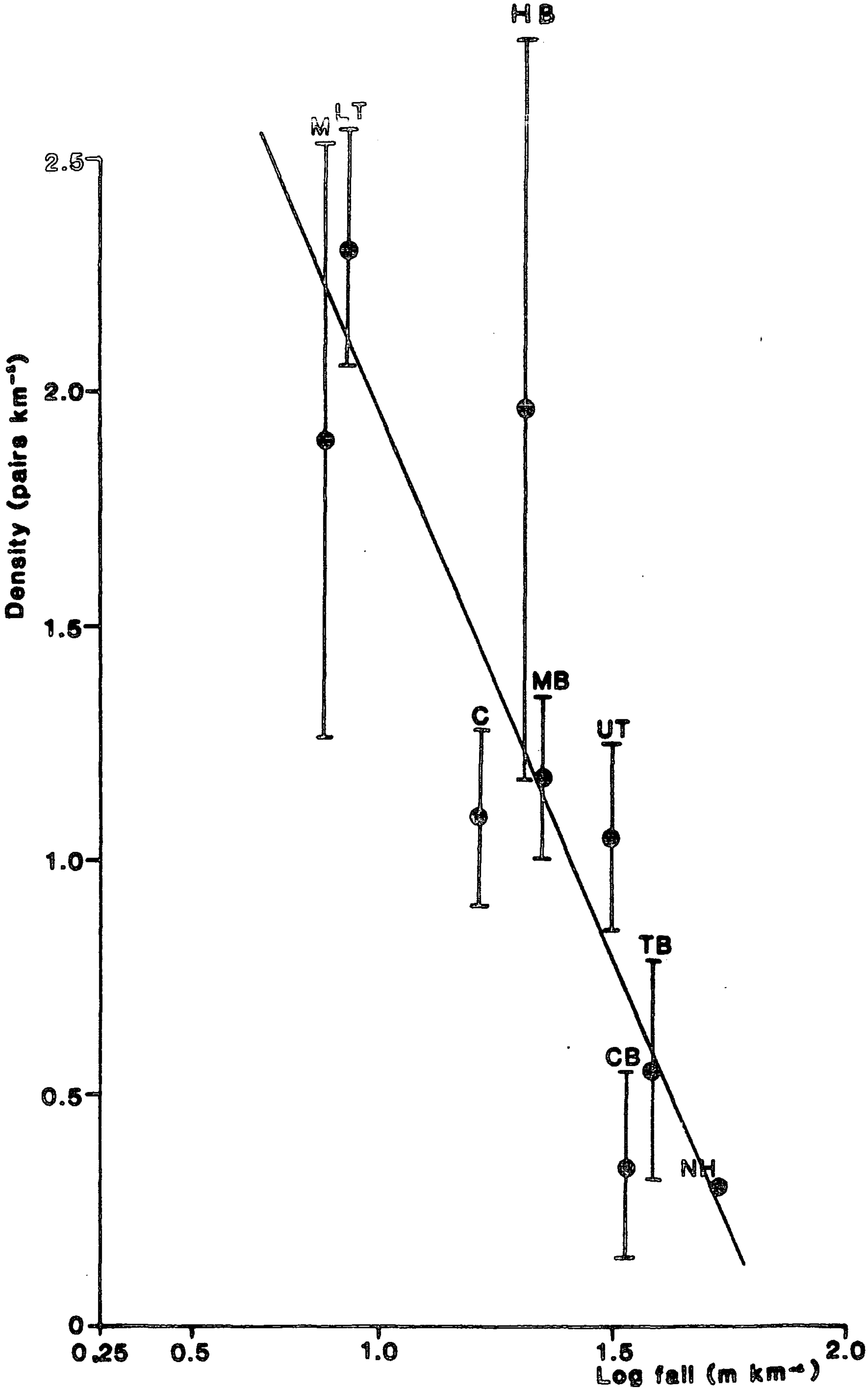
y = no. of pairs km^{-1}

$r = -0.87$

d.f. = 7

$P < 0.01$

UT = Upper Tees - Tees Head to Tees Bridge
LT = Lower Tees - Tees Bridge to Cow Green
TB = Trout Beck
NH = Nether Hearth Sike
CB = Crook Burn
MB = Maize Beck
C = Cronkley
HB = Harwood Beck
M = River Tees, High Force to Middleton-in-Teesdale


HB
M
LT
2.5
2.0
1.5
1.0
0.5
0
Density (pairs km⁻¹)
MB
C
UT
TB
CB
NH
0.25
0.5
1.0
1.5
2.0
Log fall (m km⁻¹)

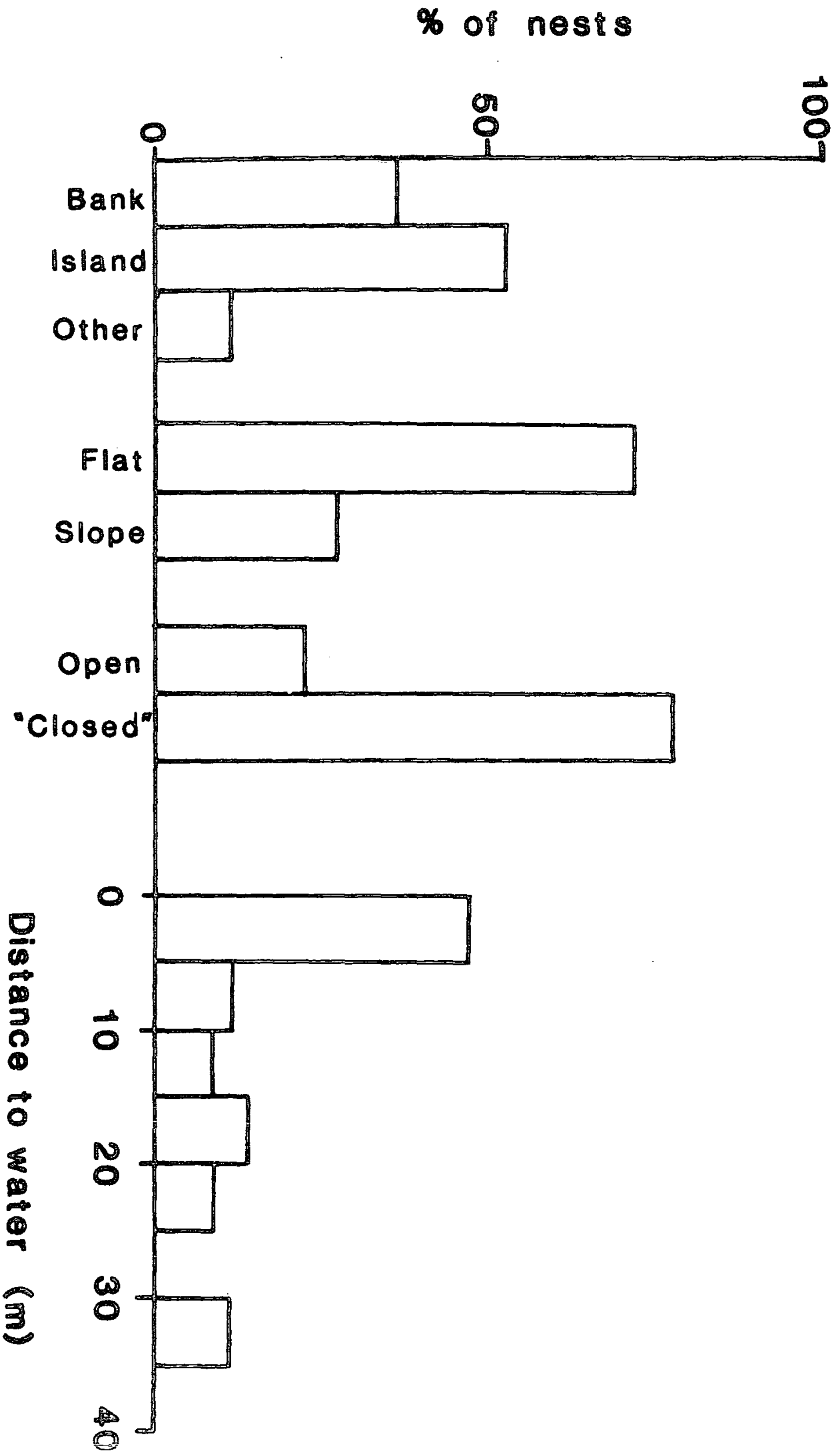
It was considered that stream width was a more meaningful correlate than gradient with sandpiper distribution in Teesdale where most streams were fast flowing. Here, stream width was linked to the availability of feeding sites. Wider streams tended to have larger areas of alluvial grassland along their banks and, in addition, were likely to have more extensive areas of exposed shingle (from measurements made in 1979 on 21 0.5km stretches of stream, the area of exposed shingle and stream width were significantly correlated, $r = 0.69$, $P < 0.001$) which were also used as feeding sites.

(c) Nest site selection.

Common Sandpipers will nest in a wide variety of vegetation types in both open and wooded localities (Macpherson 1892, Coward 1920, Witherby *et al.* 1940, Bannerman 1961, Dement'ev *et al.* 1969, Watson 1972). Nests are found not only in grass and amongst herbaceous plants but also in sand or amongst needles shed by conifers (Dement'ev *et al.* 1969) and have been recorded in gardens and orchards by riversides, turnip fields (Seebohm 1885, Baxter and Rintoul 1953), amongst heather (Baxter and Rintoul 1953), in cornfields (Witherby *et al.* 1940), on cliff ledges (Bannerman 1961) and even on top of a pollarded willow (Walpole Bond 1938).

Figure 34 shows the characteristics of 36 Common Sandpiper nests found within the study area between 1977 and 1980. Here, in Upper Teesdale, nests were found amongst grassland and herbaceous plants, *Juncus effusus*, and low willow *(Salix* sp.). Only eight nests were completely open like those of Lapwing, all others being partly shielded by grass or rushes. Over 50% of the nests were found on the larger river islands, the smallest island used being about $120m^2$.

<u>Figure 34</u>. Characteristics of Common Sandpiper nests found in Upper Teesdale between 1977 and 1980


% of nests
0
50
100
Bank
Island
Other
Flat
Slope
Open
"Closed"
0
10
20
30
40
Distance to water (m)

Cuthbertson, Foggitt and Bell (1952) also found river islands to be favoured nest sites, suitable islands always being used whenever present. Nests designated 'Other' in Figure 34 refer to the four nests made by the sandpipers at Nether Hearth, Moor House N.N.R., in a small, sparsely-planted plantation with extensive areas of gravel.

The majority of nests (72%) were sited on flat ground. However, sloping banks were also used and one nest was found 17m up a vertical rock face.

The distance of nests from water (Fig. 34) reflects the strip-like nature of the sandpipers' territory. The mean distance of nests from the water's edge was 11.7 ± 1.8m, although almost 50% were within 5m of the stream side. The furthest nests (four nests, all made by the pair at Nether Hearth) were 34m away.

No nests were found amongst heather or in fields, and despite intensive searching no nests were found on river shingle banks, one of the commonest nest sites quoted in Witherby *et al.* (1940).

(d) Site fidelity and survival of colour-ringed birds.

Of the 45 adult Common Sandpipers individually colour-ringed between 1977 and 1979, 23 returned to the study area in a subsequent year. Table 65 gives details of the number of marked birds returning and those known to be alive in successive years. The results indicate an average yearly return rate of 47.6 ± 6.3%. Annual survival was estimated to be 54.5 ± 6.1% from a consideration of the number of birds known to be alive each year, based on the return of marked individuals to the study area. However, in considering the survival rate of these colour-ringed individuals, the site fidelity of the birds must also be taken into account. Survival or mortality rates estimated

Table 65. Return rates and survival of adult Common Sandpipers colour-ringed in the study area between 1977 and 1979.

(a) yearly returns of marked adults

(b) the number of individuals known to be alive in successive years.

(a)

	1977	1978	1979	Total
No. of marked birds present	23	18	22	63
No. seen next year	9	8	13	30

$$\text{Return rate} = 100\left[\frac{9}{23} + \frac{8}{18} + \frac{13}{22}\right] = 47.6\%$$

$$\text{S.E.} = 100\sqrt{\frac{0.476 \times 0.524}{63}} = 6.3\%$$

(b)

	No. of birds known to be alive			
	1977	1978	1979	1980
1977	23	11	6	6
1978	-	9	4	1
1979	-	-	13	8

$$\text{Survival rate} = 100\left[\frac{11}{23} + \frac{6}{11} + \frac{6}{6} + \frac{4}{9} + \frac{1}{4} + \frac{8}{13}\right] = 54.5\%$$

$$\text{S.E.} = 100\sqrt{\frac{0.545 \times 0.455}{66}} = 6.1\%$$

from the return of marked individuals are reliable only if all individuals initially marked show good site fidelity. Stretches of stream having a pair of Common Sandpipers one year invariably held a pair in other years. Seebohm (1885), Swaysland (1901) and Gordon (1915) remark that the same pair of sandpipers may breed at the same place for many years, suggesting high site fidelity. However, these birds were not individually identifiable and such observations may solely be due to certain stretches having better quality habitat and therefore being more likely to consistently attract a breeding pair, the birds not necessarily being the same individuals from year to year. From observations in Teesdale, although the same localities held sandpipers each year, in many cases it was known that the individuals had changed because of loss or change of colour-ringed birds.

Common Sandpipers returning to the study area were usually faithful to the territories they had defended previously. Of the 23 colour-ringed birds which returned, 74% reoccupied their old territories. Only six individuals changed site, the maximum distance involved in these moves being 2.1km (one bird) measured between the centres of the territories along the stream's course. However, five of the sandpipers changing site moved only into the adjacent territory (four birds) or next but one territory (one bird), with a maximum movement of only 0.75km.

At Nether Hearth on the Moor House N.N.R. a pair of sandpipers nested in the same grass tussock for four consecutive years (pers. obs. and J. Parkin pers. comm.). One member of the pair was colour-ringed in 1977 and this bird returned to the same territory in each subsequent year, changing mates at least twice between 1977 and 1980 (mates colour-ringed in 1977 and 1979). This suggests that site fidelity is good at least for one member of the pair, or possibly one sex.

Since Common Sandpipers are not obviously sexually dimorphic it was not possible to determine whether the majority of marked birds which returned were male or female. However, there was no indication that return rates in the year after ringing were lower than the numbers returning in subsequent years which would be expected if only one sex was site faithful, assuming equal proportions of males and females are initially marked.

Of 15 pairs in which both birds were colour-ringed, in eight cases only one member returned and in four cases neither individual returned to the study area. There were only three instances where both birds returned; in two of these they did not form a pair bond with the original mate. However, as return rates are only 47.6% each year there is little opportunity for mate-faithfulness.

There was no indication that failure to return to the study area was related to unsuccessful breeding the previous season. Neither was failure to return solely due to birds dying. Some individuals were not present during one breeding season but returned to the area in a subsequent year. Two birds were not present on the study area for one of the breeding seasons and one bird was absent for two years. There is, therefore, a possibility that birds may use alternative breeding sites or that they do not breed every year. In addition, some individuals were obviously not site faithful; one bird colour-ringed as a breeding adult on Harwood Beck in 1978, when it fledged two chicks, did not return in 1979 or 1980, neither was it present in late May 1981, but it was seen in West Yorkshire in April 1981. Thus the annual survival rate inferred from these studies can only be regarded as the minimum yearly survival.

47.6

The annual mortality rate of 45.5 ± 6.3%, calculated from the survival of colour-ringed birds, does not significantly differ from that of 48.4 ± 8.34% estimated by Boyd (1962) from ringing recoveries. Given the mortality rate of 45.5%, for every 100 adults in the population 55 will survive to the following year. However, for the Upper Teesdale population the number of birds returning to breed each year (47.6%) was lower than the number surviving. Thus, for every 100 birds, only 48 will return to breed. Therefore for the population to be stable, every 50 pairs need to rear 52 young each year. The fledging success of Common Sandpipers in the study area was, on average, one chick per pair. This approximates to the production of young required to balance the loss of breeding adults and so the population can be considered to be self-maintaining. However, Boyd (1962) estimated that post-fledging mortality in the first year was as high as 79%. Taking this into account, neither the return rates of breeding adults nor the estimated survival rate can maintain a stable population. Of 56 chicks ringed, only one returned to breed in the study area a year later. However, there was no evidence between 1977 and 1980 that the number of breeding pairs of Common Sandpipers was decreasing. It therefore seems likely that the Upper Teesdale population must be balanced in part by the immigration of new breeding birds.

(e) Arrival on the breeding grounds and post-breeding dispersal.

Many authors seem to have tacitly assumed that during spring passage birds move inland to their breeding sites along river valleys, the autumn migration following similar courses in the reverse direction until the coast is reached (Gordon 1915, Walpole Bond 1938, Chislett 1954, Dement'ev *et al.* 1969). However, there have been no studies on the movements of marked individuals. Within the study area in Upper Teesdale and along the River Tees (this being the main valley into the area) up to 10km to the south east, there was little evidence of up or downstream movement of colour-ringed adult sandpipers. No gradual upstream movements were detected at the beginning of the season. As regards post-breeding dispersal, the only times adults began to move downstream was when the downstream territory had already been deserted; in four cases they were then observed to move downstream into the vacated site with their chicks.

The breeding places are deserted as soon as the young fledge (Macpherson 1892, Bolam 1912, Baxter and Rintoul 1953). Several authors have maintained that the birds move in family parties to the coast (Macpherson 1892, Landsborough Thompson 1910, Bolam 1912, Walpole Bond 1938, Bannerman 1961), although the southward passage may take place by inland as well as coastal routes (Witherby *et al.* 1940). By contrast Chapman (1924) states that Common Sandpipers do not always accompany their progeny, parental bonds dissolving and the adults departing as soon as the chicks fledge.

On the Moor House N.N.R. Parkin (1977) recorded the downstream movement of a family party over a distance of about 850m during a two-day period when the chicks were ten days old, after which they were not seen again. However, observations made between 1977 and 1980 suggested that these downstream wanderings were not typical. Apart from the four cases where both adults and chicks moved into vacated territories, there was no evidence of gradual downstream movements of family parties. On the contrary, it seems that the family group breaks up on the breeding grounds. One parent often leaves before the young fledge, departure occurring at any time between the brood hatching and fledging, but usually taking place when the chicks are about 10 days old. The parent remaining with the young may be male or female (P. Holland pers. comm.) and usually leaves soon after the chicks fledge. Fledged chicks often remained on the study area after their parents had departed and many wandered freely up and downstream. Two chicks ringed on hatching at the top of Harwood Beck were retrapped one month later, after their parents had left, 4.25km downstream.

It seems likely that adults either make long distance movements along the river valleys, or arrive directly on, and leave from, their territories. A bird was seen to fly in from a great height early in the season and towards the end of the breeding season a bird flew up from its territory, towered high into the air calling, and circled several times before flying off south-east. Further evidence for a rapid and direct dispersal comes from a colour-ringed adult which was sighted on Draycote Reservoir, Warwickshire, about 288 km directly south of the study area, only six days after it was last seen at Moor House. Although downstream wanderings were recorded, post-fledging movements of young may also be rapid and direct in some cases; an unfledged chick ringed on Harwood Beck at about ten days old was sighted at Draycote Reservoir 33 days later.

Discussion

The range of the Common Sandpiper extends over almost the whole of the Palearctic region (Dement'ev *et al.* 1969). However, in spite of its wide distribution and the fact that it is the most numerous of the sandpipers, it is not the least specialized in its choice of breeding habitat (Voous 1960). Although nesting in both lowland and upland areas, in Great Britain the typical breeding areas are upland streams with stony margins (Witherby *et al.*1940, Sharrock 1976). The river systems of Upper Teesdale therefore constitute good breeding habitats for Common Sandpiper.

Breeding pairs of Common Sandpiper in Teesdale were restricted by the size of the stream or water body, not using stretches of stream less than two metres wide or the smaller moorland tarns. It is unlikely that this effect is mediated by an altitude restriction on birds using the narrower stretches towards the headwaters of the streams since in Asia pairs have been found nesting at 3385m (Osmaston 1926) where the habitat was suitable. In Upper Teesdale, the highest breeding pair was at 670m on Great Rundale Tarn, slightly higher than the maximum of 650m given as the altitude limit by Sharrock (1976) although Witherby *et al.* (1940) gives the breeding range as extending to 769m in the Central Highlands of Scotland.

Breeding densities were unaffected by the vegetation type of the stream bank and surrounding area. Both open and wooded localities were used impartially, as were areas with flat and steep banks. However, several characteristics of the streams were found to significantly affect the distribution of sandpipers. These factors may be important for a variety of reasons. The selection of areas with large vegetated river islands (Table 64) is of value since these provide nest sites and may confer some protection at least from mammalian predators. River islands were found to be favoured nest sites both in this study and that conducted by Cuthbertson, Foggitt and Bell (1952).

The other habitat variables found to be of importance, namely the number of exposed shingle beds, boulder cover and average stream width (Tables 63 and 64) may all have some consequence as regards food supply. Areas with exposed shingle are favoured since these constitute important feeding areas. As well as being refuges for some aquatic invertebrates, oligochaete worms such as *Allolobophora chlorotica* and *Eiseniella tetraedra* are present at densities of around 200 individuals m^{-2} (Kirkland 1978). Shingle banks also provide suitable habitat for the larvae of some Tipulidae which live in damp mud and under stones in shallow water (Mellanby 1951). A preference for streams with high boulder cover (Table 64) may be of food value since in addition to providing midstream perches the rocks also act as feeding sites where emerging stoneflies (*Plecoptera*) and mayflies (*Ephemeroptera*) may be caught. Larvae of some of the larger stonefly species also crawl out onto rocks to moult (Mellanby 1951), making them easy prey for sandpipers.

Common Sandpiper breeding density was reduced on streams with steep gradients (Fig 33) as in the studies of Cuthbertson, Foggitt and Bell (1952) and Marchant and Hyde (1980). However, in Teesdale this relationship was thought to arise because of a response to a highly intercorrelated variable, stream width, as wide streams had larger areas of alluvial grassland along their banks and more extensive areas of exposed shingle which were used as feeding areas.

The speed of the water current and the corresponding nature of the river bed are the factors which affect the flora and fauna of the river most (Macan and Worthington 1951). The streams and rivers of the study area were all fast flowing with little rooted vegetation and bottoms of bare rock or stones. The steep gradient and increased flow prevents the accumulation of silt and macrophytic plants and excludes many stream invertebrates. The flash floods characteristic of the upper reaches also help wash away fine sediment and plant material as well as many invertebrates, the effects of such flooding sometimes being evident a year later (Davies & Dick 1978). The fauna present in the turbulent upper reaches of rivers can therefore consist only of those species adapted to the rapid flow, such as the larvae of stoneflies and mayflies. No pairs of Common Sandpiper extended as far upstream as the narrowest upper reaches below the headwaters. Sampling of a small stream near Moor House showed that no visible macroscopic animals were present in the first 100m stretch (Davies 1977), probably because of the combined effects of flash floods and the tendency to dry out in the summer. However, from 100-500m limnephilid caddis larvae, water beetles (*Agabus* sp.) and some chironomid larvae were present.

For the Common Sandpiper territory length is probably a more meaningful measurement than territory area since, as well as the stream banks, the birds only feed in shallow water and are, therefore, more reliant on the stream margins than, for example, the Dipper. Several factors may explain the observed increase in territory length as stream width decreases (Fig. 31). In respect of feeding areas adjacent to the stream sides, the acid grasslands and blanket bog by the narrower streams at higher altitudes have a poorer food supply than the surrounding pastureland and hay meadow at lower altitudes (Section 1, Invertebrates). Also, alongside the wider streams there are more extensive areas of alluvial grassland which are often used as feeding areas. Thus, an increase in territory length on the narrower streams may be important to offset the poorer food supply on the stream banks. Stream width was positively correlated with the area of exposed shingle (Section 4, (iii) (b)). Therefore, to maintain sufficient feeding area, the defence of a longer territory may be necessary on the narrowest reaches where shingle banks are smaller. Partly compensating for this reduction in the amount of exposed shingle on the narrower streams is that extra feeding sites become available on these upper reaches compared to those on the broader rivers. Here, as well as the margins, shallow water areas and exposed rocks or sections of the stream bed may become available in the centre of the stream as water levels fall during the summer. However, on the uppermost reaches of the narrower territories, invertebrate abundance will be reduced, and feeding areas will be lost, if the streams dry out completely. Also, these central feeding areas only become available when water levels are low, the margins of stream banks being the only secure feeding sites. Thus, the increase in territory length on the narrower streams may also act as an insurance to offset possible losses in central feeding areas either due to high water levels or parts of the stream drying out completely.

The annual mortality rate of 45.5 ± 6.3% calculated for the colour-ringed population of Common Sandpipers in Upper Teesdale is in agreement with that of 48.4 ± 8.34% estimated by Boyd (1962) from ringing recoveries. However, in a recent study of Common Sandpipers breeding in the Peak District of Derbyshire, Holland *et al.* (1982) reported annual mortality rates as low as 19%. In this area 76-81% of the breeding population returned each year compared to an average annual return of only 47.6 ± 6.3% in Upper Teesdale. In both areas birds which returned in subsequent years generally went back to the same or adjacent territory but although site fidelity was good mate-faithfulness was slight. The low return rate of the Upper Teesdale birds suggests that the area is inferior to the Peak District. The average altitude of a Common Sandpiper territory in the Peak District was 230m. This is considerably lower than the altitudes of territories on the main study area in Upper Teesdale, where birds ranged from 360m to 670m, although pairs on the stretch of the River Tees just upstream of Middleton-in-Teesdale, which was used as a comparison with the main study area, were as low as 230m. It is possible that sandpipers prefer the Peak District as its lower altitudes may be expected to have a more amenable climate and a better food supply. However, although birds may preferentially select the lower altitudes, there is no indication that one area is more favourable than the other in terms of breeding output, fledging success being about one chick per pair for both sites. Also, there was no indication that birds which did not return to Upper

Teesdale had been failed breeders. Differential mortality on the wintering grounds or during migration could cause the discrepancy in return rates between Upper Teesdale and the Peak District. At present there is, however, no evidence to suggest that different wintering grounds are used or that such factors are operating.

SECTION 5

THE CONSERVATION AND MANAGEMENT OF UPLAND AREAS AS BREEDING HABITATS FOR WADERS

The uplands of Britain are of prime importance for the conservation of our native flora and fauna. They represent most of the remaining wilderness areas in Britain and are amongst the few places where natural and semi-natural habitats can still be found. The environment they offer to birds is generally bleak and the upland avifauna is characterized by both low diversity and low density (Ratcliffe 1977b). However, some groups, such as the waders, are well represented and for many rare and uncommon avian species, such as the Red Kite and Dotterel, the uplands comprise the only significant breeding area.

The conservation of birds has received much attention in Britain. Birds are the only faunal group covered by comprehensive protective legislation (e.g. the Wildlife and Countryside Act 1981). A national policy for nature conservation was formally drawn up in 1947 with the publication of the Government White Papers 'Conservation of nature in England and Wales' (Cmd. 7122) and 'National Parks and the Conservation of Nature in Scotland' (Cmd. 7235) (Ratcliffe 1977a). These stated that nature conservation in Britain should centre round the safeguarding of a number of key areas which adequately represent all major types of natural and semi-natural vegetations with their characteristic assemblages of plants, animals and habitat conditions. The implication was that areas chosen on vegetational grounds were likely to contain reasonable populations of the common and widespread breeding birds appropriate to the habitat. Although this is largely true, it is sometimes necessary to know in more detail the exact habitat requirements of a particular species to ensure that a suitable area is provided. This is especially necessary in the case of rare species or those with a restricted distribution. Even for more common species, a detailed knowledge of habitat requirements may be needed to ensure that they continue to breed in the area. For example, heather moorland may not continue to provide a suitable breeding habitat for Golden Plover unless the vegetation height is kept below 15 cm (Ratcliffe 1976) either by grazing or periodic burning. Similarly, Lapwing will avoid grassland areas if the vegetation height exceeds 10 cm (Klomp 1953). Studies of habitat and nest site selection are therefore essential to the effective management of habitats for waders.

The settling reaction of meadow birds is primarily dependent on the topographical features of the terrain and habitat structure (Larsson 1976). The response may ultimately be dependent on the structural and functional adaptations of the species (Bergman 1946, Klomp 1953, Klopfer & Hailman 1965). Most waders appear to prefer large areas of exposed, closely cropped vegetation. It is, therefore, necessary to conserve large, open areas. Small areas may not be acceptable as a breeding habitat for many wader species even if conditions, other than area, appear to be suitable. In Upper Teesdale low vegetation height is maintained by grazing on the grassland areas and a combination of grazing and moor-burning on the heather dominated areas. The extensive treeless moorland and marginal hill farmland provide suitable breeding habitat for waders, which occurred in 76% of the km^2 in the study area (Table 9).

Major changes of land use in upland areas have affected both marginal hill farmland and moorland areas placing the avifauna under threat in various ways. The most serious change has been the extensive conversion of lower moorlands to coniferous forest since the formation of the

Forestry Commission in 1919. It has been proposed that the rate of afforestation in upland Britain should be increased (Forestry Commission 1979, Centre for Agricultural Strategy 1980). If this occurs, unplanted sites will be of increasing importance as a breeding habitat for moorland birds. As well as destroying suitable breeding habitat, the planting of trees may also influence wader distribution on adjacent unplanted areas. Klomp (1953) observed that Lapwing preferred open areas and avoided nesting in areas near trees as they were less able to deter predacious crows which used the trees as vantage points. In Upper Teesdale the presence of trees was a proximate factor which decreased the favourability of fields as breeding sites for Redshank and Snipe (Table 50 and 53).

Reclamation for farmland has so far been on a much more local scale than afforestation. However, it could become an increasing threat as pressure on the land increases. The practice of digging small drainage ditches, or "gripping", on some moorland areas to create drier pastures for sheep is liable to lead to the loss of suitable breeding sites for Dunlin and Curlew. It may also effect Snipe which sometimes nest at the higher altitudes although at reduced densities compared to the lower pastures (Fig. 4).

On marginal hill farmland land improvement schemes are generally less expensive and easier to effect than on moorland areas. The drainage, ploughing, reseeding and use of fertilizers and herbicides associated with these schemes all have consequences for breeding waders. Of these factors drainage is likely to have the most profound effect. Many waders are associated with damp habitats (Witherby *et al.* 1940, Sharrock 1976) and the provision of such areas is, therefore, desirable in maintaining breeding populations. "The Atlas of breeding birds in Britain and Ireland" reports that Lapwing have generally increased in northern England but in the south have shown a gradual decline which has been largely attributed to changes in land use and farming practice, including the drainage of damp meadows (Sharrock 1976). Snipe have also shown a marked decline in some areas (e.g. Sussex) since 1930-40, due to the increased drainage of rough, wet fields on lowland farms (Shrubb 1968, Sharrock 1976). The wet pastures in Upper Teesdale are in short supply compared to the drier grazed meadows and hay meadows. All the field-breeding waders exhibited a preference for the wetter habitats, breeding there at higher densities than on dry sites (Section 3). Drainage of wet, rough pasture areas occurs at the expense of waders such as Snipe, Curlew and Redshank which feed largely by tactile means, probing for invertebrates in soft substrates. However, it may not always be unfavourable to Lapwing. Lapwing were common on some of the relatively dry fields in Upper Teesdale frequenting both the better quality grazed meadows and hay meadows.

Birds with precocial young should select a breeding habitat in which food is available at sufficiently high densities to minimise the movement of chicks between feeding sites and hence reduce exposure to predation (Safriel 1975). Observations in Upper Teesdale suggested that wet habitats may provide wader chicks with more suitable feeding areas than dry sites. Waders breeding in the fields of the Harwood Beck Valley generally raised their young in the vicinity of their nest sites. Movement of young between fields was not usual but where such changes did occur the transition was from a dry habitat to wet areas (Section 3).

Modern farming techniques have deemed mixed herbaceous communities as inefficient converters of energy and nutrients into fodder (Ratcliffe 1978). To boost productivity, large amounts of artificial nitrogenous and phosphate fertilizers have been added. To further increase nutrient levels the vegetation has, in some cases, been completely replaced by herbicide treatment, ploughing and reseeding with commercial seed nutrients containing rye grass (*Loluim perenne*) and timothy (*Phleum pratense*). Within the Harwood Beck Valley fertilizer applications at the levels currently used appear to have little direct effect on the distribution of waders (Section 3). However, reseeding could potentially be of some consequence as the reduction in the diversity of plant species may in turn reduce the diversity of the accompanying invertebrate fauna and hence the range of prey available to birds. Within the Upper Teesdale N.N.R. all such farming practices are being strictly controlled and the Nature Conservancy Council is paying compensation to farmers to reduce the amount of fertilizer, and therefore crop yield, on some meadows and pastures in order to preserve the floristic diversity.

Drainage, the use of herbicides and ploughing and reseeding all prevent the growth of *Juncus effusus*. In recent years selective herbicides have been used on some of the poor quality pastures in the Harwood Beck Valley. As yet applications have been limited and mainly directed at infestations of the rush *J. effusus*. The destruction of this plant, whether by drainage, ploughing and reseeding or the use of herbicides, has important consequences for breeding waders. *J. effusus* provides nest sites for Snipe and Redshank and occasionally for other wader species. Fields with *Juncus* offer better camouflage to wader nests than more uniform habitats such as hay meadows and provide good cover in which wader chicks can hide from predators. The large tussocks which the rush forms gives shelter from wind and driving rain which is especially important for young chicks in the open habitats preferred by waders. Lapwing, Redshank, Snipe and Curlew were all demonstrated to prefer fields with a good cover of *Juncus* (Table 44) and these fields had the highest densities (Fig. 24) and diversity (Table 47) of waders. Also, the presence of *Juncus* was a proximate factor in the waders' habitat selection (Tables 49, 50, 52 and 54). Thus, destruction of the rush may decrease the attractiveness of the habitat and lead to reduced densities of breeding waders.

As a whole, the Upper Teesdale farmers are slow to implement changes or accept new farming methods. Although about half the fields in the Harwood Beck Valley have been drained and improved as hay meadows the use of herbicides has been limited and as yet reseeding is not extensive. The late (July and August) cutting of hay compared to lowland regions is favourable to the waders since most chicks will have fledged before hay cutting and so escape the threat of farm machinery. However, one farmer has in recent years cut several of his fields early for silage. If this trend continues and spreads it could reduce the breeding success of some wader species. Lapwing in particular would be affected as 40% of the field breeding pairs nested in hay meadows (Fig. 23).

Human recreational pressure, use for water catchment and military training are all likely to affect our uplands. The creation of Cow Green Reservoir in Upper Teesdale seems to have benefitted certain wader species, notably Common Sandpiper and Dunlin, which nest and feed along its shores. It also seems to have been responsible for the introduction of a new wader species to Teesdale as one to two pairs of Ringed Plover now nest annually on its shores (Section 4). The reservoir may, however, have attracted even more people to the region. At Cow Green visitors number around 50,000 a year and an estimated 150,000 people visit High Force (Valentine 1978). Although people are largely directed to nature trails and footpaths there is inevitably some disturbance to wildlife. Disturbance of breeding sites by people, dogs and grazing animals may all cause waders to desert their nests (Olney 1965, Heppleston 1971). Disturbance by people and dogs was occasionally a cause of nest failure in Upper Teesdale and cattle caused desertion if part of a clutch was destroyed by trampling. Fortunately, the overall effect of these factors was minimal. Most visitors to the region keep to the prescribed areas but further wardening may be necessary if visitor pressure increases.

Most of the British uplands are now managed for sheep, Red Grouse or Red Deer. The fells in Upper Teesdale are at present managed partly as grouse moor and partly as sheep walk. Although grouse are the primary concern certain areas, such as Herdship Fell (Fig. 1) are managed specifically for sheep. Moor-burning over some areas is an integral part of the management regime, maintaining a good growth of young heather which the grouse can exploit. Where the grazing intensity of sheep is heavy burning may cause the conversion of *Calluna* heath to *Festuca-Agrostis* grassland (Ratcliffe 1977a and 1978). On wetter ground heather reverts to *Nardus stricta*, *Juncus squarrosus*, *Molinia caerulea*, *Trichophorum caespitosum* or *Eriophorum vaginatum*. Sheep walks therefore tend to be largely grassland dominated. Carefully controlled grazing of blanket bog prevents the change from a heather dominated community to grassland and may improve *Calluna* shoot production and thereby benefit grouse populations. This type of management may be more important than burning on high, wet moorlands (Heal *et al.* 1975) such as those in Upper Teesdale. Controlled grazing or moor burning benefits Golden Plover as it keeps the heather short, vegetation more than 15 cm tall usually being avoided for nesting (Ratcliffe 1976). Conversely, heavy grazing reduces heather moorland at the expense of Golden Plover, the typical wader of this habitat. It does, however, provide closely grazed grass swards at the higher altitudes suitable as breeding sites for Lapwing which would otherwise be unlikely to penetrate blanket bog areas. Of the Dunlin in the study area, 70% nested on cotton grass areas (Fig. 8). Therefore Dunlin are favoured if heavy grazing causes the vegetation to change to *Eriophorum vaginatum*, their presence becoming more likely as the proportion of cotton grass increases, particularly if there is a high water table providing many small pools and marshy feeding areas (Yalden 1974).

Sheep grazing, on a free-range system, has been practised on the Moor House N.N.R. for more than 500 years (Heal *et al.* 1975). As sheep have been present in Upper Teesdale for a considerable period,and are likely to remain unless there is a radical change in agricultural economics, they must be accepted as an integral part of the biological system. At Moor House the effect of grazing has been to maintain or slightly extend the areas of grassland. However, in other parts of Upper Teesdale, especially on high ground, long continued heavy grazing by sheep combined with repeated moor-burning has caused the conversion of heather communities to grassland (Ratcliffe 1978). Although such changes may be detrimental to Golden Plover (almost half the Golden Plover in the study area nested on heather dominated communities; Fig. 8), in general sheep walk areas are desirable in the management of upland areas as habitats for breeding waders. Controlled grazing helps maintain a mosaic of heather dominated and grassland communities and thereby favours a greater number of wader species over the area as a whole. The distribution of breeding pairs within the study area in Upper Teesdale indicated that the presence of these upland grasslands is of particular importance in ensuring a high species diversity. Grassland areas supported both a greater number of wader species and a greater abundance of breeding pairs than blanket bog areas (Section 2). Patches of upland grassland are valuable feeding sites for waders, their presence in conjunction with blanket bog communities ensuring a high food availability throughout the breeding season. Waders such as Golden Plover and Curlew nesting on blanket bog can exploit the huge spring peak in invertebrate biomass available on the peat and then move their broods to feed on the adjacent grassland areas where there is a later peak in invertebrate numbers and a more prolonged period of abundance (Section 1). Redfern (1982) noted similar movements in Lapwing, adults moving their broods from blanket bog areas to adjacent pasture soon after hatching. *Festuca-Agrostis* grasslands on limestone soils are of particular value as feeding sites since they support high densities of invertebrates relative to other upland grasslands (Section 1).

The importance of grazing in the management of wader habitats has been recognised previously (Fog 1976). In Upper Teesdale waders favoured the grazed habitats and only Lapwing bred extensively in hay meadows (Fig. 23) where grazing pressure was light, stock being on the fields for only a small part of each year. Grazing and trampling affects the growth of plant species and may cause dwarfing (Gillham 1955) thus resulting in low vegetation height regardless of any direct reduction in height due to the consumption of plant material by the herbivores. Grazing can also promote tussock formation in some species (e.g. *Festuca rubra*, *Eriophorum vaginatum*) thereby giving protection to the vulnerable growing points (Wein 1973). Tussocks are commonly used as nest sites by Redshank, Snipe, Dunlin and Common Sandpiper, therefore these species may be favoured under a grazing regime.

Grazing and trampling also prevents the formation of a deep litter layer (Welch and Rawes 1964). The lowering of the vegetation height exposes this litter to the drying action of the sun and wind and trampling fragments it until it is finally dispersed by the wind. Plants with a dwarfed growth form are in turn favoured by the loss of the litter layer.

The short vegetation produced by grazing is particularly suitable for Lapwing being appropriate to their breeding displays and allowing easy locomotion on the ground (Klomp 1953). It is also conducive to prey location for any species feeding mainly by visual cues such as the plovers. Hogstedt and Larsson (1971) found that the frequency of foraging waders was inversely related to vegetation height at feeding sites in coastal meadows. The hay meadows in Upper Teesdale were favoured feeding sites for pre-and post-breeding flocks of waders. Feeding activities declined as the vegetation increased in height and once the grass was more than 10–12 cm tall the fields were rarely visited by waders until after hay cutting. The decline in the breeding populations of many wader species in Fenno-Scandia is thought to have been due to changes in vegetation height resulting from the abandonment of coastal grazing (Larsson 1969, von Haartman 1975, Hildén 1978). It is therefore necessary that upland pastures are grazed if they are to provide suitable breeding habitat for waders.

Grazing provides suitable invertebrate prey for waders in the form of dung-associated invertebrates (Section 1). Harrison (1973) recognised the importance of this easily located and readily obtainable food supply for breeding waders and recommended the application of cattle slurry to habitats which were not grazed. Curry (1976) found that applications of cattle slurry resulted in a 41% increase in earthworm numbers and a 56% increase in biomass compared to control plots. However, further work indicated that the level of application was crucial. Cotton and Curry (1980a) reported an increase in earthworm populations following applications of cattle and pig slurry at the rate of 80–100 t ha^{-1} yr^{-1} but found that high applications of pig slurry (345 m^3 ha^{-1} yr^{-1}) significantly reduced earthworm populations (1980b). In Upper Teesdale fields which are largely ungrazed (i.e. the hay meadows) receive annual applications of farmyard manure and there is therefore likely to be a dung-associated fauna on all field types. Differences may arise according to the grazing intensity and whether an area is cattle or sheep grazed, cattle dung generally raising a larger biomass of invertebrates than sheep dung (cf. Laurence 1954, Papp 1971 and Olechowicz 1974). It was not possible to quantify the impact different levels of farmyard manure may have had on lumbricid populations in Upper Teesdale as farmers did not use specific amounts per unit area each year, merely spreading whatever manure they had available. Earthworm abundance on hay meadows was, however, similar to that found on the other field types (Section 3). Thus, if low grazing intensity on the hay meadows reduced earthworm populations the practice of spreading farmyard manure compensated for this.

Trampling of eggs and chicks by herbivores is an important consideration in the management of wader habitats. Klomp (1953) implicated the destruction of eggs and chicks by cattle in the decline of Lapwing in the Netherlands and Heppleston (1971) found that Oystercatcher nests had a hatching success of only 5% in grazed fields in Scotland. The timing of the introduction of grazing animals onto the wader breeding habitat may be critical. Moller (1975) recommended that it should not be performed until the end of the breeding season. However, such a delay is not always advisable if dung-associated invertebrates form an important part of the waders' diet (Rankin 1979). The trampling of eggs or chicks by sheep in Upper Teesdale is unlikely to pose a serious threat to the waders at the low grazing intensities of 0·02–0·6 sheep per hectare (Rawes and Welch 1964 and 1966, Eddy, Welch and Rawes 1968) on the blanket bog areas. Even at the higher grazing intensities on fields in the Harwood Beck Valley, where cattle, sheep and ponies were present, few nests were found trampled.

The diversity and abundance of breeding waders in Upper Teesdale is due to the mosaic of habitats and land management practices as they exist today. Eight species commonly nest there and another three breed in small numbers. Species richness is therefore even better than that recorded on the machair grasslands in the Outer Hebrides (Fuller 1978, Fuller *et al.* 1979) which are noted for their wader populations. Breeding densities are, however, generally lower than on the machair. All species which commonly occur in lowland regions and on the coast also breed in Upper Teesdale. It is therefore desirable that this diversity is maintained. The most serious threat to wader diversity would be the loss of suitable habitat at the lower altitudes. Although it has been noted that the upland avifauna shows some degree of altitudinal zonation, and that species diversity increases with increasing elevation (Ratcliffe 1977b), changes in the wader populations have not previously been quantified. In Upper Teesdale both the abundance and diversity of waders was found to decrease with increasing altitude (Section 2). The effect was not just a function of the variety of habitat types available since the same relationship was apparent within vegetation types (Fig. 14). The lower altitude sites with high wader diversity have a less extreme climate than higher regions and are hence likely to be those most under threat from afforestation or reclamation for farmland. The upper altitude limit of trees is where mean temperatures fail to exceed 10°C for at least two months in the summer (Manley 1952). The present limit of woodland in Teesdale, in the absence of grazing animals, is therefore at about 600m (Pigott 1978a). Within the study area the greatest range of wader species was found below 600m (Fig. 12) and the number of species fell below two species km^{-2} above this limit (Fig. 12). Therefore, the loss of lower altitude moorland areas should give particular cause for concern as they may constitute some of the most important upland breeding areas for many wader species. The results from Upper Teesdale suggest that it is conservation of moorland areas at relatively low altitudes which is necessary to ensure a diverse and abundant assemblage of breeding waders.

At present there are no major changes of land use in Upper Teesdale which are likely to seriously affect the wader species which nest there annually. Apart from one small plantation and some small experimental tree-growing sites at Moor House, there is little afforestation. Land management practices, as they exist today, were found to have no detrimental effect on the wader populations. Should they occur, changes which would have the most serious consequences for waders breeding in this area would be afforestation and drainage of the wet pastures or some of the wetter moorland areas. Afforestation would affect all wader species, apart from Woodcock, by the direct loss of breeding sites, and, as already mentioned, may render adjacent open sites unattractive. Due to the correlations found between wader diversity and altitude in this study, planting of the lower altitudes would cause the greatest reductions in wader species richness and abundance. As many wader species are associated with damp habitats (Sharrock 1976) the provision of such areas is desirable in the management of wader breeding habitats. Drainage is of most consequence to the long-billed wader species which require soft, wet substrates in which to probe for invertebrates. In Upper Teesdale drainage of the wet pastures would probably cause reductions in the Redshank, Snipe and Curlew populations. All these species would also be affected by the drainage of wet blanket bog sites, although to a lesser extent, as they breed there at reduced densities compared to the wet fields of the marginal hill farmland. On the moorland areas Dunlin are likely to suffer most from drainage as they select wet areas, often with pools of standing water, as breeding sites. Drainage may not have the same impact on Lapwing and Golden Plover as they frequented both wet and dry areas (Sections 2 and 3). Plovers largely feed from the ground surface and are therefore not reliant on wet feeding areas.

A management plan should only be implemented when the exact habitat requirements of the species involved have been elucidated. An assessment of the proximate and ultimate factors responsible for the range of habitats utilized is essential. Within the upland environment, major changes of land use in many areas are making the aquisition of such knowledge vital to ensure the survival of Britain's wader populations. As pressure on land use for both agriculture and industry increases even more relentlessly in the lowlands, upland areas are likely to become increasingly important wader breeding habitats.

SUMMARY

1. Factors affecting the diversity and abundance of wading birds during the breeding season were investigated on an area of moorland and marginal hill farmland in part of Upper Teesdale.

2. The study area provided an altitudinal range of over 500m, rising from 358m in the south of the Harwood Beck Valley to 893m on Cross Fell. The altitudinal gradient and range of soil types, including both peat and mineral soils, gives rise to a mosaic of vegetation types. There was, therefore, a variety of habitats available to the waders. Management of most of the area either as grouse moor or sheep walk maintains a treeless environment with low vegetation height suitable as wader breeding habitat.

3. Differences between the invertebrate fauna on peat and mineral soils were discussed with reference to the implications for wading birds.

4. A survey of 105 km squares in 1978, and repeat visits to 57 of these squares in 1979 and 1980, allowed wader distributions to be related to certain habitat variables. The distributions of Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin were all significantly aggregated suggesting that selection of specific breeding areas was occurring. Measures of the relative abundance of each species in different habitats gave a preliminary index of habitat preferences. Multivariate analyses (discriminant function analysis and stepwise multiple regression) provided information concerning the general habitat characteristics associated with each wader species. These suggested

that vegetation type and altitude were amongst the most important determinants of species distribution.

5. Selection ratios indicated that only Curlew and Dunlin selected blanket bog areas preferring km squares where *Eriophorum* predominated. Curlew, however, also selected meadow. Most wader species were attracted to grassland sites, their preferences being apparent in that:
a) a higher percentage of km squares with grassland had waders present than the km squares where blanket bog predominated;
b) species richness and species diversity was higher than on blanket bog sites;
c) densities of Lapwing, Redshank and Snipe were all significantly higher on grassland as opposed to blanket bog. The same trend was apparent for Curlew and Golden Plover although the differences in denisty were not significant.

6. Joint occurrences of species within the same km squares indicated a high degree of overlap between Lapwing, Redshank and Snipe, Lapwing and Curlew, and Dunlin and Golden Plover. The degree of overlap was highest for Lapwing and lowest for Golden Plover. The latter occurred monospecifically more frequently than all other waders, 30% of the squares in which they were found in 1978 having no other species present.

7. Overlap between species was higher on grassland sites than blanket bog areas. However, Lapwing and Redshank also had a high degree of concurrence on blanket bog sites as did Dunlin and Golden Plover on *Eriophorum*.

8. Lapwing, Redshank and Snipe all tended to nest at the lower altitudes; over 50% of their populations occurred below 500m. Curlew were characteristic of the lower fell slopes, over 50% breeding between 450 and 550m. Only Golden Plover and Dunlin were found above 750m.

9. Most overlap between species occurred from 500-550m, decreasing towards 600m. These altitudes coincide with Cow Green Reservoir which was the only part of the study area where Lapwing, Redshank, Snipe, Curlew, Golden Plover and Dunlin were all found breeding within the same km square. There was little overlap between species at higher altitudes.

10. In 1978, 1979 and 1980 there was a significant negative correlation between wader species richness and altitude, approximately one species being lost for every 100m increase in altitude. Paralleling the altitudinal decline in the number of species was a decrease in breeding densities. Both relationships were independent of changes in vegetation type with increasing elevation and were thought to be food-related.

11. The highest breeding densities of Lapwing, Redshank, Snipe and Curlew occurred within the marginal hill pasture of the Harwood Beck Valley. Here, wet fields where the cover of *Juncus effusus* exceeded 5% were the most important breeding sites for the following reasons:-

a) A greater proportion of grazed *Juncus* meadow fields were used than any other field type, only 10 and 15% of these fields being without waders in 1979 and 1980 respectively.

b) Selection ratios indicated that Lapwing, Redshank and Snipe all selected grazed *Juncus* meadows, Snipe in addition showing significant evidence of selection for rough *Juncus* pasture sites. Curlew also selected fields with *Juncus* but preferred the less well managed rough pasture areas bordering the lower fell slopes. Thus all species preferentially selected the wet fields with *Juncus*. There was no evidence of selection for the drier grazed meadows or hay meadows.

c) Grazed *Juncus* meadow supported the highest overall breeding density of waders.

d) Wader species richness was highest on the *Juncus* sites and lowest on the relatively dry hay meadows where less than 16% of fields had more than one wader species present in either 1979 or 1980.

12. Other wader species often bred in the same fields as Lapwing because of similar habitat preferences and as an anti-predator strategy. Almost all fields with breeding pairs of Redshank, Snipe or Curlew also had Lapwing present. In contrast, joint occupancy by all other pairs of species was much less common.

13. Data from pitfall traps indicated that grazing influenced the invertebrate fauna such that a heavily grazed meadow had a significantly higher peak in invertebrate numbers and a period of abundance twice as long as a lightly grazed meadow. Wet rough pasture sites had the lowest number of invertebrates throughout the waders' breeding season whilst hay meadow provided good feeding areas, particularly early in the season when invertebrate numbers were as much as 40% higher than those on other field types.

14. Soil sampling revealed no significant differences in either the number of earthworms or tipulid larvae between field types. There was no

correlation between Lapwing density and the abundance of soil invertebrates. Neither was there any significant difference in the abundance of soil invertebrates on fields with and without breeding Lapwing.

15. Soil water content had no relationship with the abundance of soil invertebrates but was related to the distribution of Lapwing. The proportion of fields with Lapwing was higher where soil water content exceeded 50% in both 1979 and 1980 and breeding densities were significantly higher on the wetter sites. Not only are wet substrates easier to probe for prey, but sampling during prolonged periods of dry and wet weather suggested that wet areas had a more constant food supply.

16. The proximate factors involved in the selection of fields as breeding sites by Lapwing, Redshank, Snipe and Curlew were determined by multivariate analyses (discriminant function analysis and stepwise multiple regression). All species were influenced by vegetation type or associated features such as the distribution of *Juncus effusus*. Factors associated with wet habitats were also significant variables in the selection process for all species. Thus fields with *J. effusus* and marshy patches were favoured as were flat areas since these were likely to be more poorly drained than sites with steep gradients. Lapwing, Redshank and Snipe all avoided fields with trees or telegraph poles which provided perches for predacious crows. The behavioural requisites of some species also influenced the selection process, e.g. Redshank and Snipe commonly used clumps of *J. effusus* as nest sites and therefore tended to select fields where the plant was well distributed or had relatively high cover.

17. Lapwing, Redshank and Snipe bred together in 16% of the fields surveyed. At least two of these species were present in almost 40% of the fields. Discriminant function analysis indicated that there was more overlap between species on large, wet, unmanaged fields where the cover of *J. effusus* exceeded 5%. Only Lapwing were characteristic of the intensively managed, relatively dry hay meadows.

18. Growth rates of Lapwing chicks were investigated in relation to the habitat on which they were raised. In 1980, chicks raised on dry grazed meadow had significantly lower growth rates, between 10 days of age and fledging, than chicks raised on hay meadow or grazed *Juncus* meadow. They grew 18-22% more slowly than chicks raised on other field types. No other significant differences were found in either 1979 or 1980.

19. Three species of wading birds, Common Sandpiper, Oystercatcher and Ringed Plover, were restricted to bodies of permanent water. Of these only Common Sandpiper were sufficiently abundant to allow statistical analysis of their distribution. The formation of Cow Green Reservoir in 1970 appears to have been responsible for the introduction of Ringed Plover as a new breeding species to Upper Teesdale.

20. Common Sandpiper territories were mapped in 1978, 1979 and 1980. Pairs were present on all the major streams and rivers but stretches less than 2m wide were not used unless a major part of the territory also extended over reaches of greater width. The size of still water bodies was also important. Pairs bred along the shores of Cow Green Reservoir and the largest of the upland tarns but smaller tarns were avoided.

21. Breeding densities of Common Sandpiper were unaffected by the

vegetation type at the streamsides. Sites adjacent to blanket bog or pasture, open or wooded areas were all acceptable.

22. Common Sandpiper territory length was influenced by mean stream width such that territories showed a logarithmic decrease in length as streams became wider. The observed increases in length were not sufficient to maintain a constant territory area thus territory area was reduced as streams became narrower. Correlations between stream width and certain habitat variables suggested that the length of territory defended was related to the availability of feeding sites.

23. Stepwise multiple regression analyses were used to investigate the effect of stream characteristics on Common Sandpiper breeding density. Wide streams and stretches with a large number of shingle banks, which were used as feeding areas, were associated with high densities. A high percentage of exposed boulders was also favoured since these provided mid-stream perches. The number of large islands was the only other significant factor, these often being used for nesting.

24. The distance of nests from water reflected the strip-like nature of the Common Sandpiper's territory. The mean distance of nests from water was 11.7 ± 1.8m although almost 50% were within 5m of the streamside.

25. Based on observations of colour-ringed individuals, the average yearly return rate of Common Sandpipers to the study area was 47.6 ± 6.3%. Those birds which returned showed good site fidelity, 74% reoccupying their old territories. Fledging success appeared to be sufficient to compensate for the loss of breeding adults. However, after considering post-fledging mortality it seems likely that the Upper

Teesdale population must be balanced in part by the immigration of new breeding birds.

26. Changes of land use which may have important consequences for some wader species are occurring in many upland areas. The implications of these changes and factors affecting the variety and abundance of wading birds in Upper Teesdale were discussed with reference to the management and conservation of upland areas as habitats for breeding waders.

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APPENDIX 1

The scientific names of birds and mammals mentioned in the text, based on the check lists of K.H. Voous (1977) "List of Recent Holarctic Bird Species" and G.B. Corbet & and N.H. Southern (1977) "The Handbook of British Mammals".

Birds

Common Name	Scientific Name
South African Gannet	*Sula capensis*
Red Kite	*Milvus milvus*
Red Grouse	*Lagopus lagopus*
European Oystercatcher	*Haematopus ostralegus*
Lapwing	*Vanellus vanellus*
Ringed Plover	*Charadrius hiaticula*
Golden Plover	*Pluvialis apricaria*
Dotterel	*Eudromias morinellus*
Snipe	*Gallinago gallinago*
Woodcock	*Scolopas rusticola*
Curlew	*Numenius arquata*
Common Sandpiper	*Actitis hypoleucos*
Redshank	*Tringa totanus*
Dunlin	*Calidris alpina*
Kittiwake	*Rissa tridactyla*
Black-headed Gull	*Larus ridibundus*
Razorbill	*Alca torda*
Guillemot	*Uria aalge*
Common Swift	*Apus apus*
Tree Pipit	*Anthus trivialis*
Rook	*Corvus frugilegus*
Carrion Crow	*C. corone corone*

APPENDIX 1 (Continued)

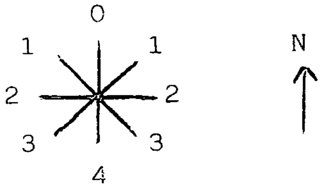
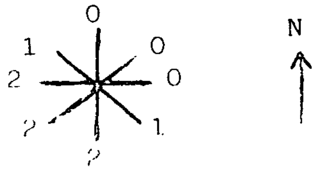
Common Name	Scientific Name
Dipper	*Cinclus cinclus*
Robin	*Erithacus rubecula*
Great Tit	*Parus major*
Lapland Longspur	*Calcarius lapponicus*

Mammals

Common Name	Scientific Name
Dog (domestic)	*Canis*
Horse (domestic)	*Equus*
Cow (domestic)	*Bos*
Sheep (domestic)	*Ovis*
Red Deer	*Cervus elaphus*

APPENDIX 2

Measurement and scoring of habitat variables for each km square within the study area.

Factor	Measurement/Scoring
Altitude	Measured as the median altitude, in metres
Aspect with respect to:	
Insolation	Scored according to the aspect of the main slope; if no main slope scored as 0. 
Wind	Scored according to the aspect of the main slope; if no main slope scored as 0. Prevailing wind is S.W. 
Gradient	The gradient of the main slope measured from 1:10,000 + 1:25,000 Ordnance Survey maps.
Ground roughness (topography)	An increasing subjective scale of 0 to 2, from a flat, even topographic profile to many undulations, excluding vegetation profile.
Soil type	Scored as the approximate percentage of the km square covered by mineral soils, the inverse of this variable being an estimate of peat coverage.
Cattle grazed	Scored; cattle absent as 0, cattle present as 1.
Sheep grazed	Scored; sheep absent as 0, sheep present as 1.
Grazed	Scored; cattle and sheep absent as 0, cattle or sheep present as 1.
Houses/farms	The number of dwellings within each km square.

APPENDIX 2 (Continued)

Factor	Measurement/Scoring
An index of the level of human disturbance	An increasing subjective scale of 0 - 6. 0 = no obvious disturbance 1 = infrequently used track 2 = road 3 = frequently used footpath e.g. Pennine Way 4-6 = a combination of factors 1 - 3.
Trees	Scored; trees absent as 0, few trees as 1, many trees or plantations as 2.
Stream size	Measured as the predominant stream width and then scored 1-3. If no streams present, scored as 0. Small streams <2m wide = 1 Streams > 2m <10m wide = 2 Large streams > 10m wide = 3
Standing surface water	Scored on an increasing scale of 0-3 according to the size of the water body. 0 = no surface water present 1 = pools 2 = tarns 3 = reservoir
Average vegetation height	The typical height of the predominant vegetation type (excluding tussocks). Vegetation heights grouped as <10cm, 10-20cm and >20cm to give vegetation height a score on an increasing scale of 1-3.
Tussock abundance	An increasing subjective scale of 0-2, from no tussocks to tussocks present over most of the km square.

APPENDIX 2 (Continued)

Factor	Measurement/Scoring
Tussock height	Typical height of tussocks in the predominant vegetation type measured to the top of the dense tussock mat. 0 = no tussocks 1 = tussock height 10-15cm 2 = " " 16-20cm 3 = " " 21-25cm 4 = " " >25cm
Outcropping rock	Area of outcrop (m^2) measured from 1:10,000 and 1:25,000 Ordnance Survey maps.
Crags	The length of the crag (m) measured from 1:10,000 and 1:25,000 Ordnance Survey maps.
Index of past mining activity	The number of disused mines, old shafts, old levels or hushes
Enclosed land: % fields	The percentage of the km square with land enclosed as fields.
Peat hags	Scored; no peat hags as 0, peat hags present as 1.
Diversity of vegetation types	A measure of habitat patchiness; the number of the eight vegetation types given below which had an extent of at least 1ha. Score 1-8.

APPENDIX 2 (continued)

Factor	Measurement/Scoring
Vegetation type: Grazed meadow Hay *Festuca* grassland *Nardus* grassland *Eriophorum* *Calluna/Eriophorum* *Calluna* *Juncus squarrosus* dominated grassland	Each vegetation type scored as: 0 = absent 1 = present 2 = the predominant vegetation type

APPENDIX 3

Correlation coefficients for counts of each of six wader species between 1978, 1979 and 1980 and the average count 1978-80, for the 57 km squares of the study area which were surveyed in all three years.

Significant correlations (P > 0.05) are indicated by *; d.f. is 55 for all years.

Lapwing

	Lapwing 1979	Lapwing 1980	Lapwing average
Lapwing 1978	0.90*	0.81*	0.93*
Lapwing 1979		0.96*	0.99*
Lapwing 1980			0.96*

Redshank

	Redshank 1979	Redshank 1980	Redshank average
Redshank 1978	0.79*	0.69*	0.91*
Redshank 1979		0.72*	0.92*
Redshank 1980			0.88*

Snipe

	Snipe 1979	Snipe 1980	Snipe average
Snipe 1978	0.88*	0.69*	0.93*
Snipe 1979		0.66*	0.94*
Snipe 1980			0.85*

Curlew

	Curlew 1979	Curlew 1980	Curlew average
Curlew 1978	0.73*	0.67*	0.91*
Curlew 1979		0.79*	0.92*
Curlew 1980			0.86*

APPENDIX 3 (Continued)

Golden Plover

	Golden Plover 1979	Golden Plover 1980	Golden Plover average
Golden Plover 1978	0.37*	0.18	0.60*
Golden Plover 1979		0.51*	0.83*
Golden Plover 1980			0.79*

Dunlin

	Dunlin 1979	Dunlin 1980	Dunlin average
Dunlin 1978	0.40*	0.27*	0.44*
Dunlin 1979		0.70*	0.81*
Dunlin 1980			0.97*

APPENDIX 4

Correlation coefficients between a selection of habitat variables and counts of six wader species in 1978, 1979 and 1980 and the average count 1978-80, for the 57km squares of the study area which were surveyed in all three years.

Significant correlations ($P < 0.05$) are indicated by *; d.f. is 55 for all years. All habitat variables not included in the matrices had no significant correlation with bird counts in any year. The measurement/ scoring of the habitat variables is explained in Appendix 2.

Lapwing	Lapwing 78	Lapwing 79	Lapwing 80	Lapwing average
Altitude	-0.58*	-0.62*	-0.60*	-0.62*
Mineral soils	0.64*	0.76*	0.74*	0.74*
Disturbance	0.55*	0.54*	0.52*	0.55*
Houses	0.33*	0.58*	0.62*	0.53*
Trees	0.31*	0.45*	0.48*	0.43*
Fields	0.75*	0.89*	0.87*	0.87*
Vegetation height	-0.45*	-0.48*	-0.44*	-0.47*
Tussocks	-0.33*	-0.42*	-0.42*	-0.40*
Tussock height	-0.16	-0.26*	-0.26*	-0.24
Hay	0.69*	0.79*	0.76*	0.78*
Meadow	0.69*	0.89*	0.88*	0.85*
Eriophorum	-0.24	-0.28*	-0.28*	-0.28*
Calluna/Eriophorum	-0.41*	-0.46*	-0.46*	-0.46*

APPENDIX 4 (continued)

Redshank	Redshank 78	Redshank 79	Redshank 80	Redshank average
Altitude	-0.62*	-0.58*	-0.52*	-0.63*
Mineral soils	0.63*	0.66*	0.44*	0.64*
Disturbance	0.60*	0.54*	0.44*	0.57*
Houses	0.61*	0.63*	0.55*	0.66*
Trees	0.38*	0.38*	0.35*	0.42*
Ground roughness	-0.29*	-0.19	-0.18	-0.24
Grazing	0.26*	0.23	0.24	0.27*
Fields	0.70*	0.80*	0.56*	0.76*
Vegetation height	-0.41*	-0.52*	-0.35*	-0.47*
Tussocks	-0.45*	-0.33*	-0.28*	-0.40*
Tussock height	-0.26*	-0.18	-0.23	-0.24
Hay	0.65*	0.69*	0.50*	0.69*
Meadow	0.69*	0.81*	0.60*	0.77*
Nardus stricta	-0.34*	-0.28*	-0.15	-0.27*
Calluna/Eriophorum	-0.36*	-0.46*	-0.39*	-0.45*
	0.28*	0.20	0.21	0.24

APPENDIX 4 (Continued)

Snipe	Snipe 78	Snipe 79	Snipe 80	Snipe average
Altitude	-0.42*	-0.44*	-0.46*	-0.48*
Mineral soils	0.62*	0.53*	0.55*	0.60*
Disturbance	0.40*	0.35*	0.43*	0.43*
Houses	0.39*	0.40*	0.22	0.33*
Trees	0.30*	0.19	0.26*	0.28*
Fields	0.71*	0.75*	0.63*	0.75*
Vegetation height	-0.50*	-0.55*	-0.37*	-0.52*
Tussocks	-0.33*	-0.32*	-0.38*	-0.37*
Hay	0.61*	0.59*	0.48*	0.60*
Meadow	0.64*	0.55*	0.43*	0.57*
Eriophorum	-0.25	-0.12	-0.27*	-0.22
Calluna/Eriophorum	-0.35*	-0.45*	-0.30*	-0.40*

APPENDIX 4 (Continued)

Curlew	Curlew 78	Curlew 79	Curlew 80	Curlew average
Altitude	-0.46*	-0.31*	-0.23	-0.40*
Mineral soils	0.36*	0.20	0.16	0.28*
Gradient	0.17	0.32*	0.19	0.25
% Fields	0.51*	0.51*	0.33*	0.53*
Vegetation height	-0.32*	-0.41*	-0.25	-0.35*
Hay	0.34*	0.27*	0.21	0.33*
Meadow	0.30*	0.18	0.08	0.24
Calluna/Eriophorum	-0.32*	-0.39*	-0.28*	-0.37*
Diversity	-0.10	-0.28*	-0.16	-0.20

Golden Plover	Golden Plover 78	Golden Plover 79	Golden Plover 80	Golden Plover average
Tussock height	0.28*	-0.04	0.18	-0.03
Mines	0.29*	0.25	0.12	0.28*
Festuca	0.55*	0.37*	0.12	0.43*
Nardus	0.01	-0.25	-0.20	-0.22
Juncus squarrosus	0.19	0.24	0.29*	0.32*
Diversity	0.19	-0.06	-0.03	0.04

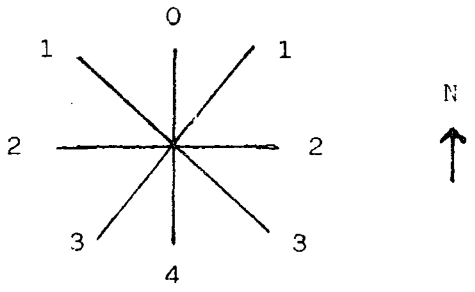
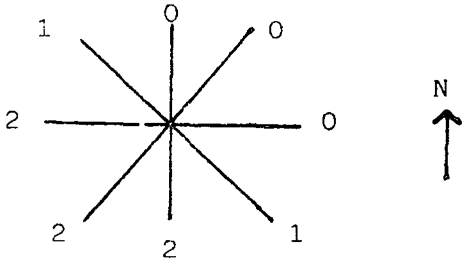
APPENDIX 4 (Continued)

<u>Dunlin</u>	Dunlin 78	Dunlin 79	Dunlin 80	Dunlin average
Ground roughness	-0.32*	-0.13	-0.04	-0.10
Water	0.51*	0.72*	0.52*	0.62*
Streams	-0.39*	-0.46*	-0.45*	-0.49*
Eriophorum	0.40*	0.31*	0.35*	0.39*

APPENDIX 5

The measurement and scoring of habitat variables for fields in the Harwood Beck Valley.

Variable	Measurement/scoring
Field area	Area of field in ha. Measured from 6":1 mile Ordnance Survey maps with a planimeter.
Gradient	Gradient of main slope; measured with a clinometer.
Irregularity of gradient	Break in slope; scored; even as 0, irregular as 1.
Boundaries:	
Stone walls Fences	The number of sides of the field enclosed by walls/fences; 0-4.
Enclosure of land	The number of sides on which the surrounding ground was higher than the field itself; 0-4.
Topography	An increasing subjective scale of 0-3.
Tussocks	Relative abundance of tussocks; no tussocks as 0, tussocks in part of field as 1, tussocks over whole field as 2.
Trees in field	Scored; trees absent as 0, clump of trees as 1, row as 2.
Trees adjacent to field	Scored as above.
Telegraph poles	The number of telegraph poles in the field or round perimeter.
Footpath or track in field	Scored; absent as 0, present as 1.

Variable	Measurement/scoring
Road at field side	Scored; absent as 0, present as 1.
Building in field or at edge	Scored: absent as 0, present as 1.
Distance to nearest house (m.)	Measured from 6":1 mile Ordnance Survey maps.
Altitude (m.)	Taken from 1:25,000 Ordnance Survey maps.
Aspect:	
with respect to sun	Scored; 
with respect to prevailing wind	
Surface water:	
Streams Pools	Scored; absent as 0, present as 1.
Marshy areas	Scored; absent as 0, present as 1.
Bare ground	Estimated as a percentage.
Moles	Presence of molehills scored according to the number of sections of the field in which they were found; 1-10.

Variable	Measurement/scoring
Juncus effusus:	
cover	cover estimated as a percentage.
distribution	scored according to the number of sections of the field in which it was found; 1-10
Gulls or crows	Gulls or crows seen in field during the breeding season. Scored; absent as 0, present as 1.
Ground colour:	
Pale green Green Pale brown Brown Green-brown	Scored as 0/1 according to the ground colour at the start of the breeding season (i.e. March/April).
Field type:	
a) Hay b) Grazed meadow c) Grazed meadow with *Juncus effusus* cover >5% d) Rough pasture e) Rough pasture with *Juncus effusus* cover >5%	Scored as 0/1 according to field type.
Average vegetation height in June	Measured in cm.
Grazing regime:	
Grazed	Scored; not grazed as 0, grazed as 1.
Cows	The number of cows and calves grazing the field.
Sheep	The number of sheep and lambs grazing the field.
Horses	The number of horses grazing the field.
Proportion of year that field is grazed	In months; 1-12.
Proportion of breeding season that the field is grazed	The number of months grazed between March and July; 1-5.
Years grazed	The number of years for which the present grazing regime has been used.

Variable	Measurement/scoring
No. of months grazed by:	
cows sheep horses	Total no. of months grazed by cows/sheep/horses; 1-12.
No. of months during breeding season grazed by:	
cows sheep horses	No. of months grazed by cows/sheep/horses during breeding season (March-July); 1-5.
Haytime	Month when has is usually cut if field is a hay meadow; 1-12.
Drainage	Scored; field not drained as 0, drained as 1.
No. of years field has been drained	Actual dates usually unknown; estimated by tennant farmers.
Machinery	Scored; machinery not used in field as 0, machinery used as 1.
Fertilizer:	
Field fertilized	Scored; not fertilized as 0, fertilized as 1.
Inorganic Organic	Type of fertilizer; scored as 0/1.
Lime Slag	Lime/Slag applied; scored as 0/1.
Amount of inorganic fertilizer used	Kg/ha.
Date of application	Coded as month of year; 1-12.
No. of applications of inorganic and lime and slag per year.	Inorganic and organic usually one application per year. Lime and slag usually once every 10 years.
Years fertilized	The number of years for which the above treatments have been used.

APPENDIX 6

Correlation coefficients for the densities of each wader species in the same sample of fields in the Harwood Beck Valley between the years 1979 and 1980.

N (number of fields = 200)

	Correlation coefficient
Lapwing	0.61, $P < 0.001$
Redshank	0.27, $P < 0.01$
Snipe	0.55, $P < 0.001$
Curlew	0.58, $P < 0.001$

APPENDIX 7 Measurement and scoring of habitat variables for 0.5km stretches of stream within the study area

Factor	Measurement/scoring
Stream width (m) Maximum Minimum Average	Bank to bank stream width measured at 100m intervals along the stream. Width estimated wherever water was too deep to permit direct measurement.
No. of exposed shingle beds	No. of exposed shingle beds along each 0.5km stretch
Area of exposed shingle beds	Total area of exposed shingle in each 0.5km stretch. In m^2
No. of exposed muddy areas	No. of muddy banks along each 0.5km stretch
Area of exposed mud	Total area of exposed mud in each 0.5km stretch. In m^2
No. of vegetated river islands:- Small ($<10m^2$) Medium ($<100m^2$) Large ($>100m^2$)	No. of islands in each size category in each 0.5km stretch
Boulder cover	Percentage boulder cover estimated at 100m intervals; data averaged to give mean percentage cover for each 0.5km stretch
No. of bends	The total no. of bends in the stream's course along each 0.5km stretch
No. of tributaries	The no. of tributaries entering each 0.5km stretc
Average width of tributaries	The mean width of tributaries entering each 0.5km stretch. 0 if no tributaries
Stream banks flat or steep	Banks scored flat or steep for each side of the stream for each 100m stretch. Data then totalled to give score for steep banks for each 0.5km stretch; maximum score 10.
Gradient	The fall of the stream (m) over each 0.5km stretch.