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ABSTRACT

Between 1985 and 1987, ten areas of upland, marginal grassland were surveyed for breeding waders; eight areas West of the Pennines in the Eden Valley, Cumbria, and two East of the Pennines at Alston, Cumbria and Teesdale, Co. Durham. Grassland improvement resulted in the virtual disappearance of snipe and marked decreases in both the density and the proportion of fields used by breeding lapwing, curlew and redshank. The absence of snipe following improvement was due to land drainage, whereas reduced curlew densities resulted from vegetation changes, redshank were relatively unaffected provided wet areas persisted nearby. Data on lapwing breeding success were obtained from a study of 637 clutches. Fewer clutches suffered predation on unimproved than on improved pastures and resulted in higher hatching success. This, combined with more failed clutches being replaced and better survival by young chicks, resulted in higher productivity on unimproved than on improved pastures. The role of predation in reducing hatching success was confirmed experimentally. In addition, more clutches were destroyed by agricultural activities on improved than on unimproved meadows, resulting in lower productivity. Productivity on unimproved areas was enough to sustain the population, but was insufficient on improved areas and it is suggested that this, together with high philopatry, causes the decline in density of lapwings on improved areas. Invertebrates were sampled by chemical expellents, soil cores and pitfall traps. Grassland improvement resulted in increased earthworms and beetles other than carabids, but decreased spiders and carabid beetles. Fewer species of spider after improvement were largely due to a lowered vegetation architecture diversity, whilst fewer species of tipulids resulted from reduced soil moisture and loss of food plants. Changes in species composition were apparent when comparing the seasonal pattern of pitfall catches on unimproved and improved grassland.

THE EFFECTS OF IMPROVEMENT OF UPLAND, MARGINAL GRASSLANDS ON BREEDING WADERS (CHARADRIIFORMES) AND INVERTEBRATES

David Baines, B.Sc. (Durham)

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A thesis presented in candidature for
the degree of Doctor of Philosophy
in the University of Durham, 1988.

18. JUL. 1988

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CHAPTER 1 GENERAL INTRODUCTION

Throughout agricultural history man has had strong influences on the status and distribution of breeding wading birds (Charadriiformes) in Britain. Cultivation replaced the natural vegetation of woodland with grassland some 5-7000 years ago in lowland Britain creating large, open areas suitable for wading birds.

Since the 1940's, agricultural practices in many northern and western European countries have moved towards maximising food production. Government policy, combined with technological innovation, has enabled farmers to intensify production. In Britain, the rate of development of farming dramatically increased in the 1960's (Shrubb 1970, Murton 1974, Murton & Westwood 1974). The most dramatic advances in yields have been made in the lowlands, where traditional managements of summer grazing and hay-making have been superseded by intensive grazing and silage production and, in the extreme, converted to cereal crops. In the decade prior to 1982, an estimated 8000ha of damp grassland were drained each year (Carter 1982). A survey of waders of wet, lowland grasslands demonstrated the very low numbers of waders which breed on lowland grasslands in England and Wales, with five sites holding 23% of all lapwings found, 36% of redshank and 48% of snipe (Smith 1983). Large tracts of land held no waders at all. In Jutland, Denmark, the intensification of agricultural practice led to an increase in the area used for growing barley and the abandonment of many areas of grassland. These changes had a significant effect on the breeding birds, with grassland species such as the lapwing *Vanellus vanellus*, snipe *Gallinago gallinago*, redshank *Tringa totanus*, meadow pipit *Anthus pratensis*, yellow wagtail *Motacilla flava* and reed bunting *Emberiza schoeniclus*

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decreasing by 50-80% or more (Møller 1983). The apparent decline in wader populations of lowland grasslands has enhanced the importance of upland areas as a stronghold for breeding waders.

In the uplands, climatatological and edaphic factors have largely restricted agriculture to sheep, and to a lesser extent, cattle breeding. Three zones of decreasing intensity of agricultural useage in the uplands have been identified by Ball et al. (1982);

i) farmland, which has been continually under intensive cultivation,

ii) moorland fringe, which has interchanged between moorland, farmland and forestry, and

iii) moorland core, which has always been under extensive management.

The intensity of agriculture in the uplands has fluctuated considerably, especially over the last 200 years. The zone of upland which has exhibited the greatest degree of change is the moorland fringe zone or marginal habitat. This study, is concerned with the enclosed grasslands or inby land within the marginal zone that occur immediately below the moor or fell boundary. This land is at the limit of agricultural practice and is usually between 300 and 500 metres a.s.l.

The history of marginal land development is documented for Upper Teesdale in Co. Durham, an area researched during this study (see Chapter 2), by Roberts (1978). By 1000 B.C., the dominance of a woodland vegetation in Teesdale had drawn to a close. Radiocarbon dating from two sites showed a sharp transition from an ash/alder assemblage to a grass/plantain/heather assemblage by 620 B.C. and 1200 B.C. respectively (Turner 1978). From 1100 A.D., the dale sides were used for arable farming, the dale floor as meadowland and the fells as rough grazing areas. This trend continued until the fourteenth century, when less favourable climatic conditions and

Scottish raids resulted in abandonment of the upland margins.

Following climatic improvement, the uplands were recolonized and by 1900 the arable strips had been enclosed and converted to meadowland. This was accompanied by the enclosure of large tracts of newly reclaimed land and an increase in the dale population, with an associated increase in the number of grazing animals. In order to retain pastures and prevent them from reverting to rough grazing areas, land drainage and the use of fertilizers was necessary. Drainage schemes in Teesdale were undertaken in the nineteenth century, when many fields were provided with underdrains, whilst on some of the more marginal pastures, open drains or grips were dug.

Within the last forty years, there has been a tendency to create larger farming units within which the tenant farmers concentrate on the better agricultural land. As a result much of the more impoverished marginal grassland is reverting back to moorland.

Agricultural improvement within the marginal zone defined by Ball _et al_. (1982) has been in two main forms

a) the improvement of existing rough grasslands, chiefly below the moor wall, and

b) the reclamation of previously non-productive areas above the moor wall.

Improvement is accomplished by land drainage, followed by either replacement of the existing semi-natural vegetation with competitive grass mixes by ploughing and subsequent reseeding and fertilizing, or merely by increasing fertilizer applications to existing grasslands to encourage more nutritious grass species. Such unimproved areas often have relatively acidic and nutrient poor soils, consequently lime is added to raise the pH and to release nurients.

In recent years, agricultural improvement of upland grasslands within the marginal zone has progressed rapidly. Since 1946, the area of agricultural rough grazing in England and Wales has decreased by 31% within the E.E.C. defined less-favoured areas (Sydes in press), with a loss of 11% in Scotland (RSPB 1984). Though rates of loss are increasing over the whole of the United Kingdom, the scales and rates of loss are not constant and in some areas loss is to forestry, while in others it is to agricultural improvement, and in some both (Ball et al. 1982). The rate of loss has increased markedly within the last decade, though mainly through afforestation, (ULS 1981) and land reclamation and enclosure is estimated at 5000ha/year (Parry et al. 1981).

The replacement of rough grazing land with improved grasslands containing quicker growing, more nutritious grass strains has allowed increases in stocking density. Variations in grazing pressure can alter the vegetation (Hewson 1977, Anderson & Yalden 1981) and changes in numbers and type of stock can be expected in response to social and economic factors and to variation in other land uses such as recreation and forestry (ITE 1978).

The Upland Landscapes Study (1981) reported that the recent upward trend in stock numbers suggested that for the near future the loss of moorland to agricultural reclamation would continue. This conclusion was also reached by an I.T.E. desk study (1978), which indicated that dramatic changes in land use were unlikely to occur in the foreseeable future, but that recent trends would continue, with agriculture remaining strong in some areas but declining in others.

The broad future pattern of the uplands will depend on the extent to which farming and forestry are encouraged to expand, or contract, in response to national policies. The extent to which these industries respond will vary between areas, depending on environmental, social and economic conditions, and on constraints of competing land uses such as grouse shooting, conservation and amenity interests.

This thesis examines the effects of improvement of existing rough grazing pastures and traditionally managed hay-meadows on breeding wading birds. First the breeding density and distribution of lapwing *Vanellus vanellus*, curlew *Numenius arquata*, redshank *Tringa totanus* and snipe *Gallinago gallinago* are compared on unimproved and adjacent improved grassland. The lapwing, the most numerous of the waders on marginal grassland, is selected for further study. The breeding biology and factors regulating fledgling production are investigated. Finally, the effects of land improvement on the invertebrate community are considered, both in terms of the lapwing diet, and as a part of the grassland fauna.

This thesis is presented as a series of scientific papers.

CHAPTER 2: STUDY AREAS

Two main study areas on marginal farmland were used:

i) Eden Valley: the study area was on the West side of the Pennines at the head of the Eden Valley near Brough and Kirkby Stephen, Cumbria, (within nat. grid squares NY60, 61, 71 and 81). The study fields occurred at altitudes of 150 - 375 metres a.s.l. and

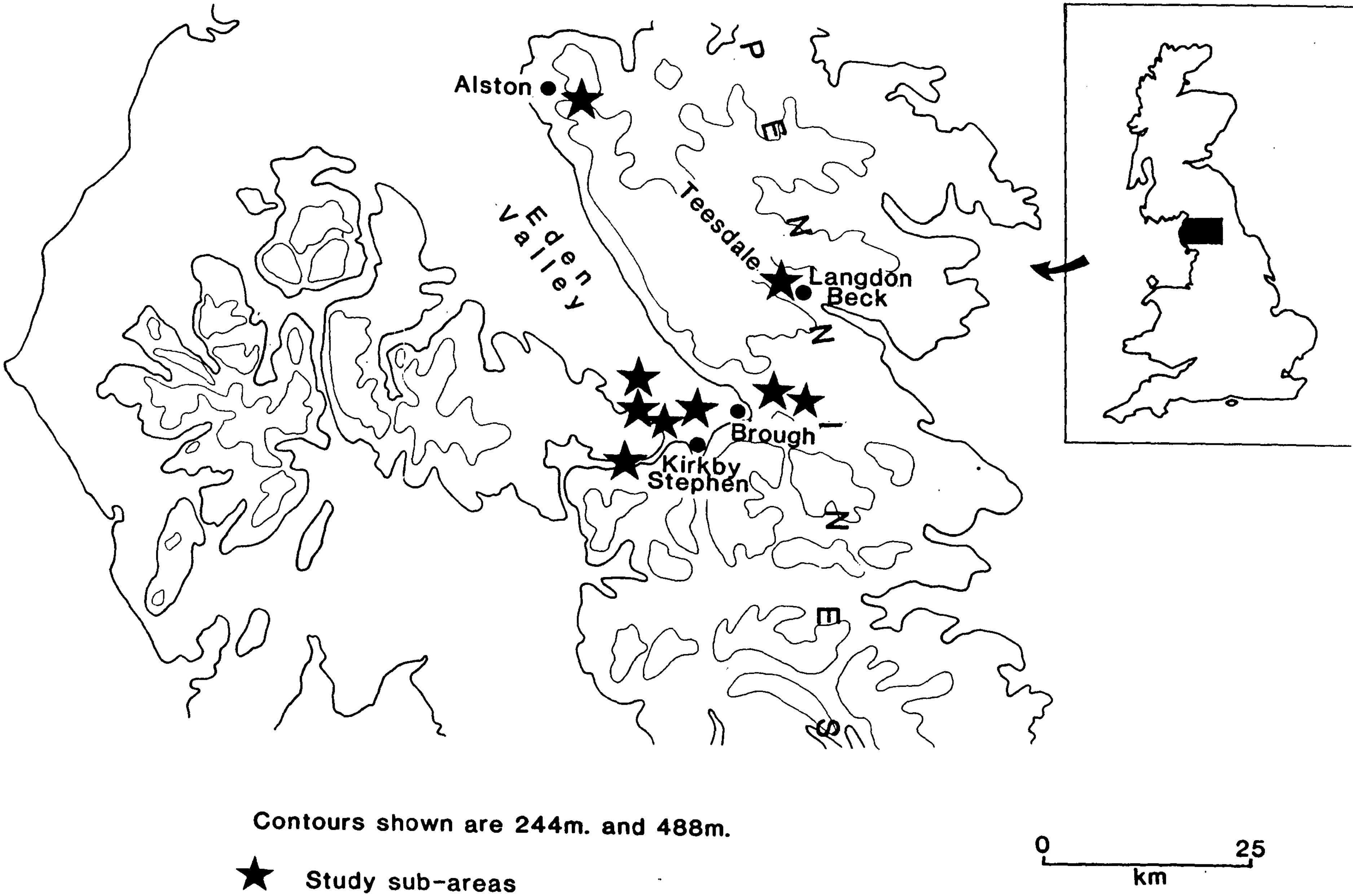
ii) Teesdale: the study area lay on the Eastern flank of the Pennines between Alston, Cumbria and Langdon Beck in Upper Teesdale, Co.Durham, (within grid squares NY74, 82 and 83) at altitudes of 350 - 475 metres a.s.l.

Each main study area was composed of a number of discrete study sub-areas containing 20-85 fields (75 to 325 hectares (ha)). Eight sub-areas comprised the Eden Valley study area and two sub-areas the Teesdale study area, the location of these sub-areas are shown in Fig. 2.1. Four figure grid references to the centre of each study sub-area are given in Appendix 1. Six figure grid references to each field where pitfall traps were placed are given in Appendix 2.

The fields were usually enclosed by dry stone walls and varied in size from 0.8 ha to 35 ha, but 50% were between 3 and 6 ha in area. Overall, 331 fields, comprising a total of 2230 ha were covered by the study.

Fields were classified using the criteria in Table 2.1, into either unimproved (n=163) or improved (n=168). Improved fields were more intensively managed and were characterized by having a lower water-table and a drier soil as a result of land drainage. Unimproved fields were managed in a more traditional manner and had either never been drained, or had inefficient old tile drains which had become blocked and had caused the

FIGURE 2.1 Location of the study areas and sub-areas.



Contours shown are 244m. and 488m.

TABLE 2.1 Characteristics of unimproved and improved fields.

	Unimproved	Improved
Drainage.	Relatively poor. Either no drains or only inefficient, old ones.	Moderate to good. On naturally well draining soils or recent, more efficient drainage systems.
Field Colour.	Greenish-brown	Yellowish-green to bright green.
Vegetation Structure.	Patchy and heterogenous. Rich mosaic of species, often with abundant _Juncus_.	Uniform and relatively homogenous, often reseeded. Limited no. of species. Usually no _Juncus_.
Fertilizer.	Little or no inorganic, some manuring on meadows.	Moderate to high applications of inorganic, additional slurry or manure on meadows.
Crop.	Hay, cut in mid-July.	Silage, cut in late June and again in August. Little as hay.
Grazing.	Meadows: sheep for periods between August and end of April. Pastures: sheep for periods all year round, beef cattle largely Summer and Autumn.	Meadows: sheep, at intervals, Sept. to May. Pastures: heavy sheep grazing for periods all year round with dairy cattle in Summer/Autumn.

deterioration of grassland of former high agricultural quality to rough grazing land. Improved fields were both physically and vegetatively much more homogenous. Levelling and ploughing removed undulations and hummocky terrain. Reseeding removed the previous diverse vegetation (diverse both structurally and in number of species) and replaced it with a more uniform sward. Subsequent applications of inorganic fertilizer enhanced vegetation uniformity by encouraging competitive grasses to the detriment of herbaceous plants (Elliot et al. 1974, Traczyk et al. 1984). Little or no inorganic fertilizer was added to unimproved fields, the only fertilization being dung from grazing animals sometimes supplemented by applications of manure. As a result, improved areas had more fertile soils of a higher pH and were more productive with increased grass yields or a higher livestock holding capacity. Improved pastures have a capacity of 7-10 sheep per hectare compared to 4-7 on unimproved pasture (Ball et al. 1982).

It is assumed that the nature of improved fields prior to improvement was essentially similar to the remaining unimproved fields. This assumption is supported by a knowledge of the history of improvement of many fields and by several fields undergoing improvement during the course of the study. Study areas containing unimproved and improved fields were selected so enabling, wherever possible, unimproved fields to be paired with adjacent improved ones with similar topography and soils so that only the management of the fields differed.

The grasslands were subdivided into meadows and pastures. Meadows were fields where stock were excluded for approximately seven weeks during late spring and early summer to grow a grass crop. On improved meadows, two cuts of silage were usually taken, the first in late June and a second at the end of August, whereas on unimproved meadows a single cut of hay was usual in July. Pastures were fields where no grass crop was grown, instead stock were allowed to graze during the main growing season amd at other times of the year. Improved pastures were typically bright green in spring and characterized by the presence of several dominant, introduced plant species of high agricultural value such as Lolium perenne, Dactylis glomerata and Trifolium repens together with a limited range of herbs and overall, a uniform vegetation architecture. Conversely, unimproved pastures were coloured greenish-brown and were characterized by a wide range of native species. The vegetation structure was more diverse with tussock forming grasses such as Deschampsia cespitosa and Nardus stricta and a mosaic of Juncus, Carex and moss species in areas of poorer drainage.

By area, the study sites were comprised of 39% unimproved pasture, 28% improved pasture, 13% unimproved meadow, 16% improved meadow and 4% arable land.

CHAPTER 3 THE DISTRIBUTION AND DENSITY OF BREEDING WADING BIRDS ON UNIMPROVED AND IMPROVED GRASSLAND

METHODS

Breeding waders were censused by several methods. Different methods were used for different species because it was found that no single approach worked equally well for each species.

The methods used for individual species were as follows;

Lapwing, Vanellus vanellus: Where the entire field was visible, counts of individual birds, pairs of birds and incubating females were made from a vehicle. Alternatively, in fields where topography prevented viewing, walking through fields counting the number of birds flushed was undertaken. A check of the latter was made by making thorough nest searches in several fields. This showed that 7% more pairs of lapwing were counted than nests found (n=108 pairs).

Redshank, Tringa totanus: Incubating birds were relatively inconspicuous, therefore totals were based on counts of birds observed from vehicles, from walking through fields and by mapping song-flights. Breeding redshank were most obvious when with chicks, and for this species observations were continued until mid-June. Behavioural observations were important to distinguish breeding birds from others merely using the field for feeding.

Curlew, Numenius arquata: As for redshank; mapping song-flights was particularly suitable for curlew.

Snipe, Gallinago gallinago: Flushing birds by walking through the fields and mapping of song-flights were initially used to detect the presence of this inconspicuous species. Where snipe were known to be present quantitative estimates were made by walking transect lines 30 metres apart over likely nesting habitat whilst hand clapping to flush individuals, or by dragging a rope between two observers over the vegetation to flush both feeding and incubating birds.

Oystercatcher, Haematopus ostralegus: Because of the low numbers and their conspicuous nature direct counting of oystercatchers was straightforward.

Counts of breeding waders in each field were made every two weeks between the beginning of April and the end of May giving, on average, five counts in each field. A minimum of four counts were made at all sites.

The timing of counts influences the number of birds detected, (Reed, Williams and Webb, 1983). The number of breeding pairs of lapwing in a field was taken either as the peak number of nests present at any one time or the mean of the two highest counts of pairs per field. Redshank and curlew numbers were also taken as the mean of the two highest counts. Snipe totals were based on the number of nests found by rope dragging, augmented if necessary, by counts of displaying birds.

The area of each field was obtained from 1:2500 O.S. maps and the counts of breeding waders were converted to the density of pairs/100ha. In all, 331 fields totalling 2230ha were surveyed for breeding waders between 1985 and 1987. Except where sub-areas were used, the analysis has been carried out using each field as a separate sample. A comparison of the densities of each wader species in the Eden Valley and in Teesdale showed that lapwing, redshank and snipe were at similar densities in both areas. The densities of curlew were significantly higher in the Eden Valley and they were absent from all meadows examined in Teesdale. Accordingly, the data from the two study areas have been combined, except in the case of curlew, where results are given separately (Table 3.1).

Unimproved pastures varied considerably in vegetation structure, especially in their degree of rush (Juncus effusus) cover, often as a result of differences in water-table. Juncus was indicative of a high water-table. Consequently, unimproved pastures were further categorised according to the density of the rush Juncus effusus. The field was divided into ten equal sized plots and the presence or absence of Juncus patches in each was recorded. To be present in a plot the Juncus had to cover a minimum of 5% of the area. The unimproved pastures were sub-divided into;

a) sparse or no Juncus, where Juncus was recorded in less than three plots of the field,

b) medium Juncus, recorded in three to five plots, and

c) dense Juncus, over five of the plots. The density and distribution of breeding waders was investigated in relation to differing Juncus densities.

RESULTS

Density of breeding waders on unimproved and improved grassland.

The densities of each wader species breeding on unimproved and improved grassland are given in Table 3.1. Analyses by t-tests show marked and significant differences. As improved fields were selectively paired with unimproved (see Methods) these differences appear to be attributable to land improvement and are subsequently referred to as such. Improvement of pastures caused snipe densities to decline by 99%, whilst redshank and lapwing decreased by 81% and 74% respectively. In the Eden Valley, curlew appeared to decline by 82% following pasture improvement and were not found

TABLE 3.1 Density of breeding waders on different field types. Data for curlew are split into two areas, Teesdale (T) and the Eden Valley (EV).

	No. of fields	Mean pairs/100ha±1 standard error						
		Lapwing	Redshank	Snipe	Curlew		Oystercatcher	Total
					(T)	(EV)		
Pastures								
Unimproved	115	53.9±4.6	6.2±0.9	15.6±3.2	3.4±1.2	10.9±1.5	0	84.7±6.7
Improved	85	14.1±2.6	1.2±0.5	0.1±0.1	0	2.0±0.5	0.1±0.1	17.3±2.9
% change		-74±10	-81±17	-99±20	(-100)	-82±15	positive	-80±9
		p<0.001	p<0.001	p<0.001	p<0.01	p<0.001	ns	p<0.001
Meadows								
Unimproved	48	59.5±7.9	4.8±1.4	6.1±2.1	0	9.8±3.4	0	73.9±9.6
Improved	83	26.2±4.9	2.6±1.3	0	-	6.3±1.8	1.1±0.6	35.3±5.6
% change		-56±16	-46±40	-100*	-	-36±39	positive	-52±15
		p<0.002	ns	p<0.01	ns	ns	ns	p<0.002

*Teesdale only; no snipe recorded on meadows in Eden Valley study sites. Figures in brackets represent only small samples available.

breeding at all on improved pastures in Teesdale. The apparent declines in densities recorded following improvement of meadows were not as great as those following pasture improvement, but were significant for lapwing (56%) and redshank (46%). In the Eden Valley, curlew decreased by 36% following meadow improvement. The distribution of snipe in meadows was more restricted. In Teesdale, they occurred in unimproved meadows, but were absent from all meadows examined in the Eden Valley. Densities of redshank, curlew and snipe were highest on unimproved pastures with, on average, 6.2, 10.9 and 15.6 pairs/100ha respectively. Lapwing densities were highest on unimproved grassland with a mean of 53.9 pairs/100ha on pastures and 59.5 pairs/100ha on meadows. On improved land, lapwing had mean densities of 14.1 pairs/100ha on pastures and 26.2 pairs/100ha on meadows but no other species, except curlew with 6.3 pairs/100ha on improved meadows, attained densities greater than 5 pairs/100ha.

The relationship between the proportion of improved land in groups of fields forming discrete study sub-areas and the density of breeding waders is summarised in Figures 3.1a to 3.1d. Lapwing decreased by one pair/100ha for every 3% land improved, snipe by one pair/100ha for every 6% land improvement, and curlew by one pair/100ha for every 14% land improvement. Redshank appeared to be able to breed in improved habitats if sufficient damp areas were retained. These damp areas were found to be important as chick foraging sites. Therefore the response to improvement varied widely, probably according to the intensity of improvement and the nature of neighbouring land. The declines associated with improvement are expressed as a percentage of the estimated number of pairs present if 100% of the land is unimproved, data derived from Figure 3.1. Snipe showed the highest rate of decline with a 12.2% decrease in the population per 10% of fields improved. Comparable rates for lapwing, curlew and redshank were 8.2%, 7.2%

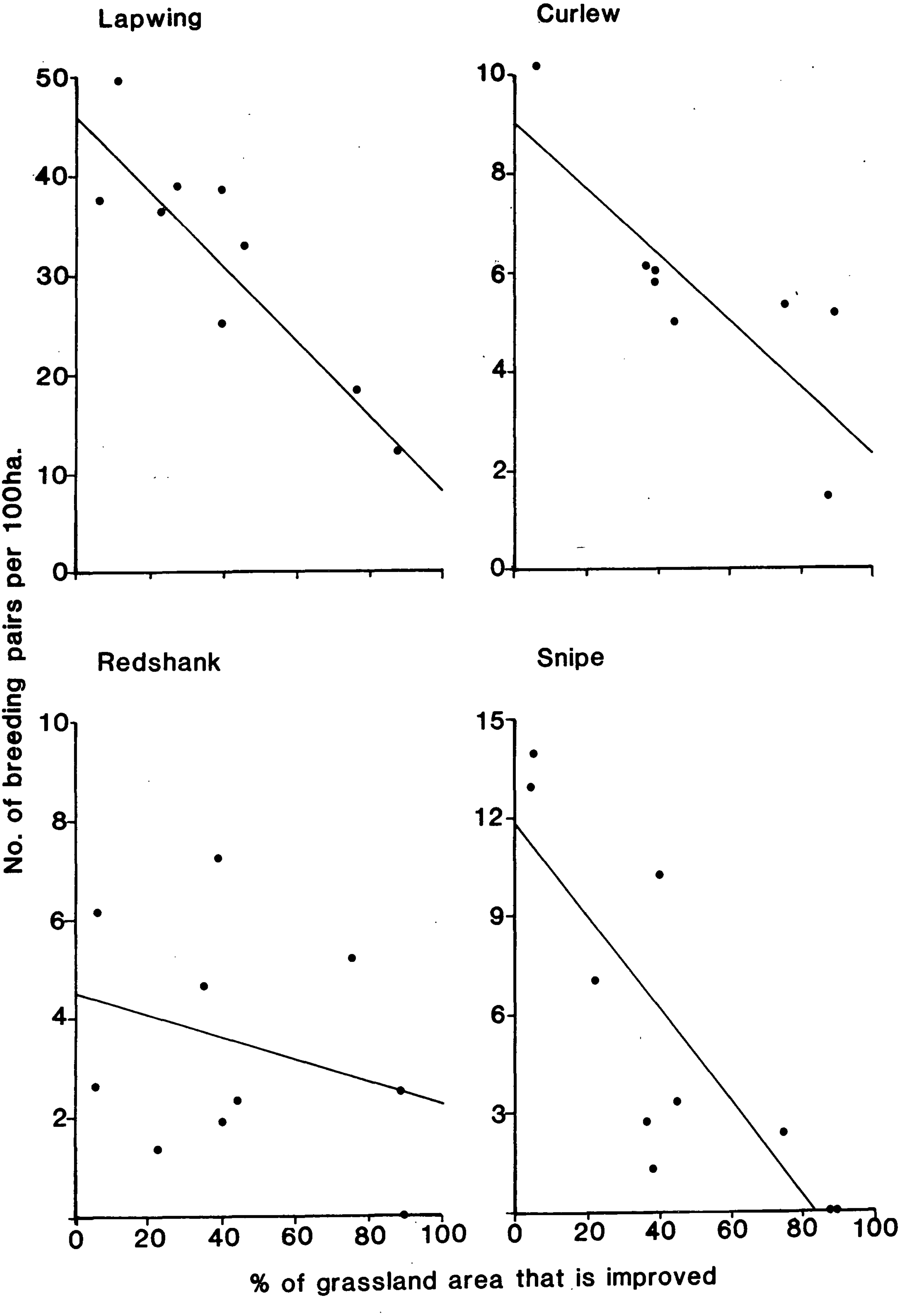
FIGURE 3.1 The relationship between the proportion, by area, of improved land in each of ten study sub-areas and the densities of breeding waders. One area which contained a high proportion of arable land is omitted for lapwing, the two Teesdale sites are omitted for curlew (see Methods). The slopes with standard errors and the significance of the regressions are as follows:

a) lapwing, slope $=-0.37 \pm 0.07$, $P<0.01$,

b) curlew, slope $= -0.07 \pm 0.02$, $P<0.02$,

c) redshank, slope $= -0.02 \pm 0.03$, n.s.,

d) snipe, slope $= -0.14 \pm 0.03$, $P<0.01$.


Lapwing
Curlew
Redshank
Snipe
No. of breeding pairs per 100ha.
% of grassland area that is improved
50
40
30
20
10
0
10
8
6
4
2
0
10
8
6
4
2
15
12
9
6
3
0
20
40
60
80
100
0
20
40
60
80
100

and 4.9% respectively. Snipe decreased faster than the rate at which land was improved, indicating that breeding snipe are likely to disappear from an area before all of the fields are improved, whereas the other species are merely reduced. It is evident from these relationships that grassland improvement did not just cause a redistribution of waders; it resulted in a decline in total numbers within a given area.

Proportions of unimproved and improved grassland with waders present.

Improved land, as well as having lower densities of breeding waders, also had fewer fields occupied (Table 3.2). Overall, 90% of unimproved pastures supported breeding waders compared to only 44% of improved pastures, (X^2 =53.5,df=1,P<0.001). All waders, except oystercatchers, were found in a significantly smaller proportion of the improved pastures than the unimproved. Lapwing and snipe were found in significantly fewer improved meadows. Snipe disappeared as a breeding species from improved meadows, whereas decreases of 42% and 58% were found for lapwing and redshank respectively and a 31% decline for curlew in the Eden Valley. The relationship between the proportion of improved land within discrete study sub-areas and the percentage of fields containing breeding waders is summarised in Figures 3.2a to 3.2d. The proportions of fields with breeding lapwings and snipe were significantly reduced as the proportion of improved grassland increased, 5% fewer fields were occupied per 10% increase in improved fields. The proportion of fields occupied by curlew and redshank did not change significantly with respect to the percentage of improved fields.

TABLE 3.2 The proportion of fields, of different classes, with breeding waders.
Data for lapwing and curlew are split into two areas;
Teesdale (T) and the Eden Valley (EV).

% of fields±1 standard error.

	No. fields	Lapwing	Redshank	Snipe	Curlew		Oystercatcher	Total
Pastures					(T)	(EV)		
Unimproved	115	76±4.0	40±4.6	46±4.6	18±5.8	63±5.7	0	90±2.7
Improved	85	39±5.3	7±2.4	1±1.0	0	16±4.1	1±1.0	44±5.4
% change		-49±10	-82±13	-97±10	(-100)	-75±11	positive	-52±7
		p<0.001	p<0.001	p<0.001	p<0.01	p<0.001	ns	p<0.001
Meadows								
Unimproved	48	77±6.1	23±6.1	21±5.9	0	38±12.1	0	81±5.6
Improved	83	45±5.5	10±3.2	0	-	26±4.8	5±2.3	63±5.3
% change		-42±11	-58±30	(-100)*	-	-31±35	positive	-23±10
		p<0.001	ns	p<0.001	-	ns	p<0.05	p<0.02

*Teesdale only; no snipe recorded in meadows in Eden Valley study sites.
Significance levels are derived from Chi-squared analysis.

FIGURE 3.2 The relationship between the proportion by area, of improved land in each of ten study sub-areas and the percentage of fields containing breeding waders. One area which contained a high proportion of arable land is omitted for lapwing, the two Teesdale sites are omitted for curlew (see Methods).

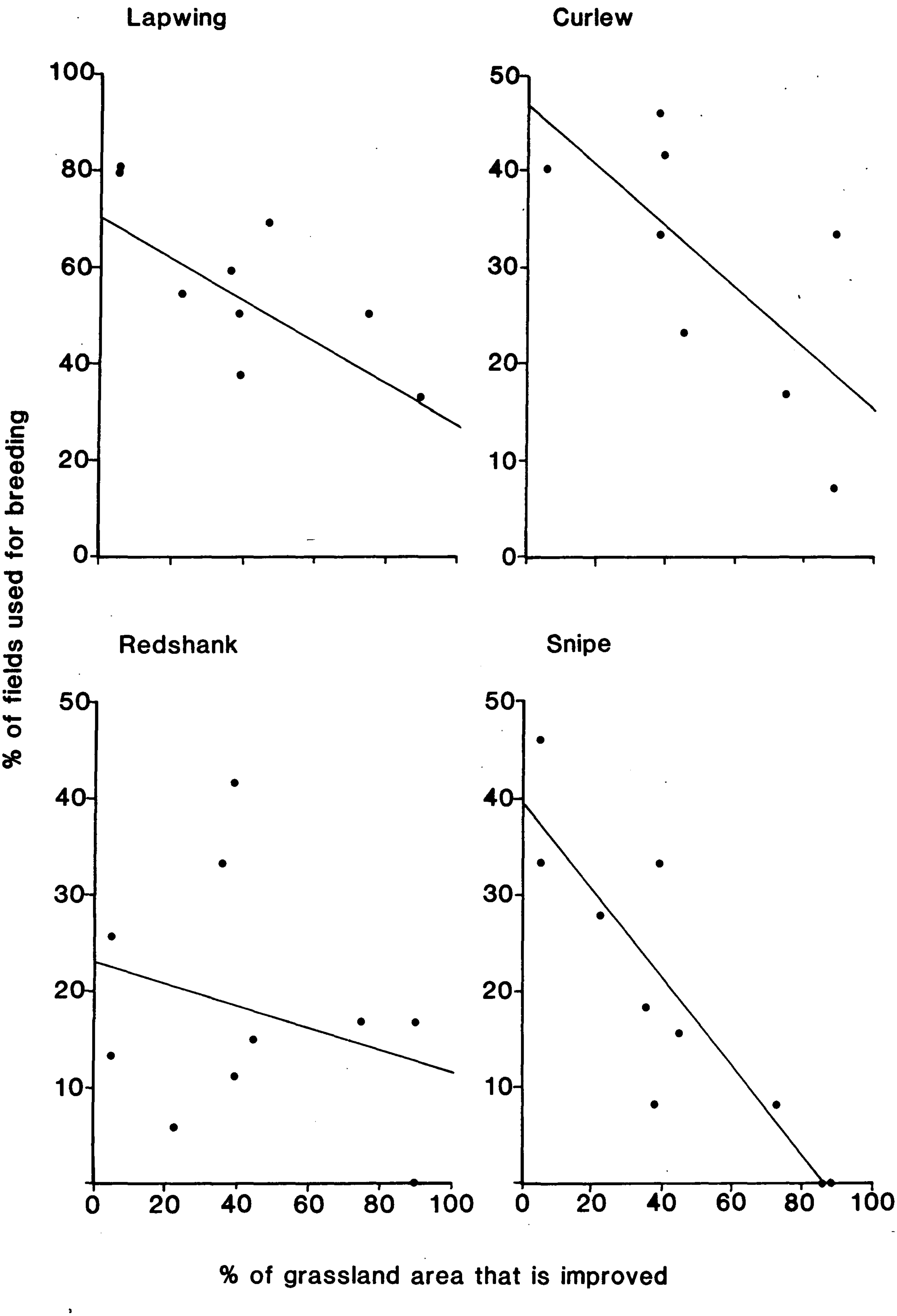
The slopes with standard errors and the significance of the regressions are as follows:

a) lapwing, slope $= -0.45 \pm 0.15$, $P < 0.02$,

b) curlew, slope $= -0.31 \pm 0.14$, $P < 0.02$,

c) redshank, slope $= -0.11 \pm 0.14$, n.s.

d) snipe, slope $= -0.45 \pm 0.08$ $P < 0.001$.


Lapwing
Curlew
Redshank
Snipe
% of fields used for breeding
% of grassland area that is improved
100
80
60
40
20
0
50
40
30
20
10
0
20
40
60
80
100

Density of waders on pastures of differing Juncus effusus content.

The preference of breeding waders for each of three classes of unimproved pasture was examined by comparing breeding densities (Table 3.3). In the Eden Valley, lapwing densities declined with increasing Juncus cover from 63.1 pairs/100ha in fields containing sparse or no Juncus to 12.0 pairs in densely Juncus covered fields, ($t=4.74, df=42, P<0.001$), whereas, in Teesdale no relationship was found between lapwing and Juncus densities. The absence of a relationship in Teesdale is possibly attributable to greater heterogeneity within the dense Juncus fields of Teesdale providing areas of shorter vegetation more suitable to lapwing. Redshank showed no significant difference in density in relation to rush density at either locality, but snipe were significantly more abundant in areas of dense Juncus both in Teesdale ($t=2.30, df=19, P<0.05$) and in the Eden Valley ($t=2.47, df=42, P<0.02$). Although the curlew density in the samples studied was higher in fields with large amounts of rushes this trend was not significant. Curlew densities were significantly higher in the Eden Valley than in Teesdale, and this difference was most marked on fields with medium Juncus cover with 11.9 pairs/100ha in the Eden Valley compared to 2.8 pairs/100ha in Teesdale ($t=3.12, df=46, P<0.01$). The overall density of breeding waders in the Eden Valley was very similar between fields of differing Juncus content, with reduced densities of lapwing being balanced by increased numbers of snipe and curlew. Densities were higher in the dense Juncus pastures in Teesdale, but not significantly so, 140 pairs/100ha compared with 77 and 68 pairs/100ha for the fields of sparse and medium Juncus cover.

TABLE 3.3 Differences in the breeding densities of waders in Teesdale and the Eden Valley on three types of unimproved pasture.

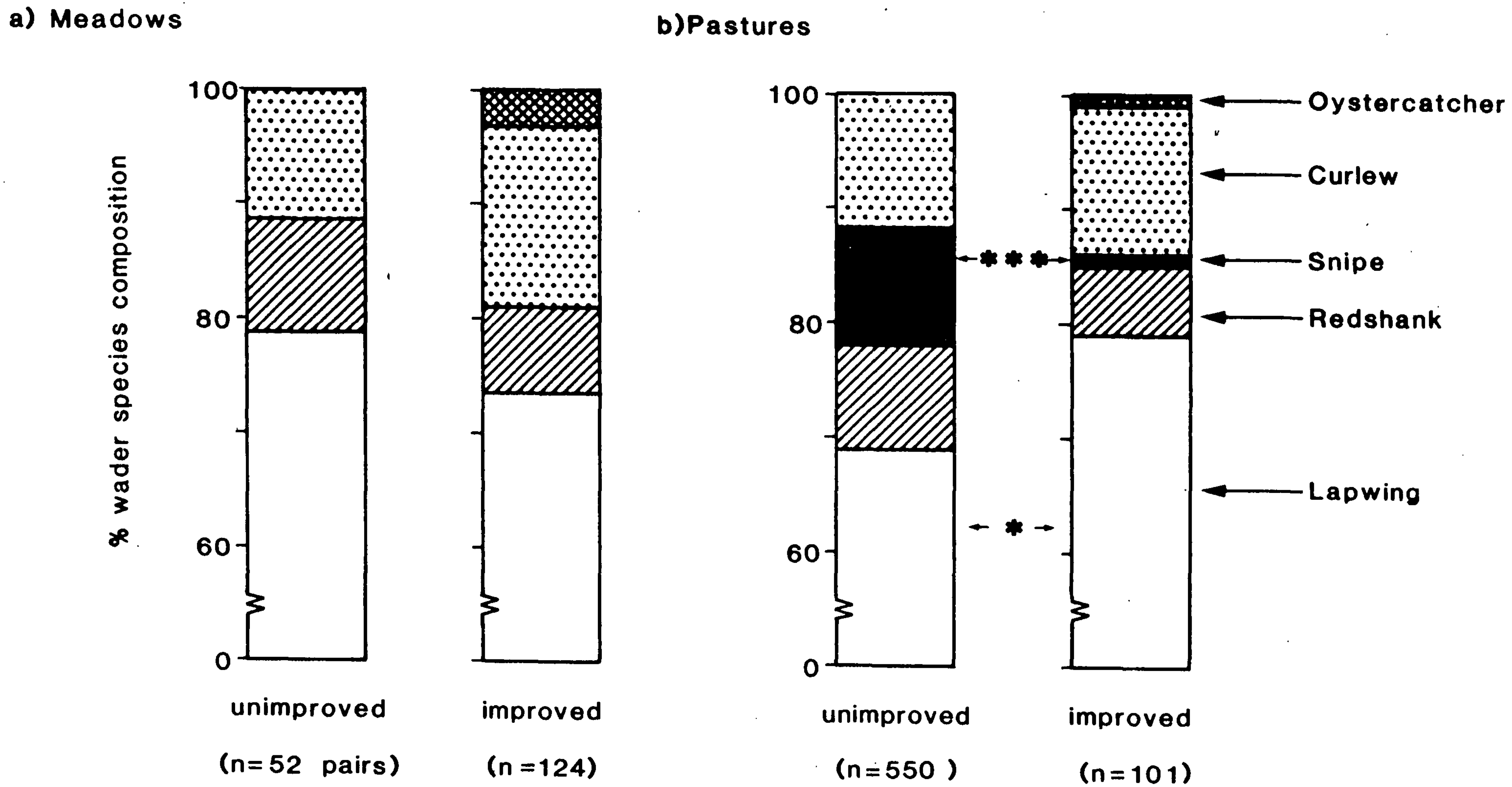
	No. fields	Mean pairs/100ha$\pm$1SE				
Teesdale		**Lapwing**	**Redshank**	**Snipe**	**Curlew**	**Total**
Sparse Juncus	12	65.9±13.6	3.2±1.7	6.1± 2.8	2.0±2.0	77.4±15.5
Medium Juncus	22	42.6± 8.6	5.5±2.3	12.2± 3.3 *	2.8±1.8	68.0±13.0
Dense Juncus	9	57.9±18.7	5.0±2.6	* 68.6±27.1	7.3±4.3	140.3±43.4
Eden Valley						
Sparse Juncus	36	63.1± 7.0	8.0±2.0	3.0± 0.9	9.9±2.1	83.8± 8.0
Medium Juncus	26	59.8±12.8 ***	5.6±1.7	12.7± 3.4 *	11.9±2.3	89.4±16.8
Dense Juncus	8	** 12.0± 8.2	8.4±4.5	44.5±16.8	14.1±4.1	79.1±19.7

* $p<0.05$
** $p<0.01$
***$p<0.001$

Composition of the breeding wader community

Improvement of marginal farmland was found to have a pronounced effect on the composition of the breeding wader communities (Fig. 3.3). The percentage of snipe amongst breeding waders declined significantly from 10% on unimproved pastures in the Eden Valley to virtually nil on their improved counterparts ($X^2=14.3, df=1, P<0.001$). Snipe were not found on meadows in the Eden Valley. Curlew formed 12% of the total breeding waders on unimproved meadows and 16% on improved meadows. Neither curlew or redshank showed a significant change associated with improvement of pastures. Reductions in the proportion of snipe following improvement resulted in significant increases in the proportion of lapwing on pastures from 69% to 79% ($X^2=3.84, df=1, P<0.05$). Oystercatchers were only found on improved fields in the Eden Valley, where they formed a small (2%), but increasing part of the wader community.

FIGURE 3.3 The species composition of breeding waders on unimproved and improved grassland in the Eden Valley (E.V.). There were too few improved areas studied in Teesdale to justify inclusion. Note that the scale is broken between 0 and 60%. Significancelevels from chi-squared are $*P<0.05$, $**P<0.01$ and $***P<0.001$.


a) Meadows
b)Pastures
% wader species composition
100
80
60
0
unimproved
(n=52 pairs)
improved
(n=124)
unimproved
(n=550)
improved
(n=101)
Oystercatcher
Curlew
Snipe
Redshank
Lapwing
***
*

DISCUSSION

The agricultural improvement of upland grassland results in several changes in the nature of the fields. Drainage lowers the water-table appreciably, addition of fertilizers changes the plant communities, including the grass species, an effect which is hastened by reseeding. Such changes typically result in a major reduction of Juncus effusus and related species, a loss or reduction of invertebrates dependent on moist habitats and an increase in earthworms. In general, improved fields are greener and they lose their patchy, tussocky nature.

Table 3.4 compares the breeding densities obtained from this study with those found in other investigations. Wader densities found on marginal grasslands were consistently higher than those found on lowland grasslands by Fuller (1981) and Smith (1983), or on arable land by Ettrup & Bak (1986). In this study, lapwings bred at densities approximately 12 times higher than those found by Smith (1983) in the B.T.O./R.S.P.B. wader survey of wet, lowland grasslands in England and Wales, whilst redshank densities were about 4 times higher, snipe 6 times higher and curlew 25 times higher.

Only in locally distributed habitats, such as the machair of the Outer Hebrides and coastal saltmarshes, were wader densities greater than those found on marginal land. Lapwing densities in this study, 35 pairs/100ha, were very similar to densities on the Outer Hebrides, 31-39 pairs/100ha, (Fuller et al.1986), but were considerably less than the 80-110 pairs/100ha recorded on a Danish saltmarsh (Ettrup & Bak 1986). Redshank were found in much higher densities on the machair, 46 species/100ha, and saltmarsh, up to 100 pairs/100ha on the Ribble (W.G. Hale), than on marginal land.

TABLE 3.4 A comparison of the overall breeding densities found in this study and other recent studies.

Habitat/Region	Pairs/100ha				
	Lapwing	Redshank	Snipe	Curlew	Workers
Marginal grassland, N. England	35.3	4.0	4.7	5.0	This study
Arable, Denmark	5	-	-	-	Ettrup & Bak 1986
Saltmarsh, Denmark	80-110	-	-	-	Ettrup & Bak 1986
Lowland grassland, Bucks.	8.2	0.4	0	3.5	Fuller 1981
Dry Machair, Outer Hebrides	31	-	-	0	Fuller _et_ _al_. 1986
Damp Machair, Outer Hebrides	39	46	-	0	Fuller _et_ _al_. 1986
Blacklands, Outer Hebrides	33	25	-	-	Fuller _et_ _al_. 1986
Washes, Cambs & Norfolk	-	-	up to 110	-	Green 1983
Saltmarsh, Ribble, N. England	-	up to 100	-	-	W. G. Hale
Lowland grass, England & Wales	2.7	0.9	0.8	0.2	Smith 1983
Peatland, Manitoba, Canada	-	-	9-17	-	Tuck 1972

The five species of wader studied show differences in distribution and density in relation to grassland improvements; whilst oystercatcher colonized improved grassland, snipe virtually disappeared and curlew, redshank and lapwing showed appreciable declines. The virtual absence of snipe from improved areas can probably be explained solely by drainage. Green (1983), has shown that snipe cease to nest in areas where the soil becomes too dry for them to probe. Extensive Juncus in a field is a good indicator of a high water-table and densities of snipe closely follow Juncus densities. It is probable that nesting cover is also important to this species.

Drainage does not exclude redshank from improved areas although their densities are appreciably reduced. Redshank frequently lead their chicks to small, wet areas to feed, and providing that such areas persist nearby redshank numbers are only reduced. Curlew breed in similar areas to redshank, but appear to require more cover for nesting, the density of curlew being positively correlated with rush density. Although curlew are progressively expanding into lowlands and areas given over to cereal production (Watson 1954, Parslow 1967, Sharrock 1976), their densities on improved areas in this study were lower than on unimproved areas.

The reason for the decline of lapwings on improved upland grassland is not clear. Such improved areas are still suitable for the species, albeit at a lower density and a higher proportion of these improved fields are unused. Water-tables and food do not appear to be limiting, but their influences need to be investigated in detail. One possibility which requires study is whether the nature of improved areas with their more uniform, non-tussocky surface causes increased nest predation, thus shifting the equilibrium population to about half that in unimproved fields. These aspects are investigated in chapter 5.

CHAPTER 4 THE BREEDING SUCCESS OF THE LAPWING ON UNIMPROVED AND IMPROVED GRASSLAND

METHODS

In all, 760 lapwing clutches were studied between 1985 and 1987, 474 on unimproved grassland, 193 on improved grassland and 93 on arable land. The grassland data were further divided into pastures and meadows. Nests were found either by observing incubating birds from a vehicle or by systematic searches.

Nests were revisited on average every four days and were relocated using compass bearings taken from nearby landmarks, thus overcoming the need for nest markers which tend to lead to increased predation (Picozzi 1975). The majority of nests were found during incubation, and for these nests the clutch size was recorded as the number of eggs present on finding. Variation in mean clutch size resulted from differing proportions of four egg clutches, therefore, differences in mean clutch size, between field types, and first and replacement clutches were tested by comparing the proportion of clutches of four eggs using the chi-squared test.

Unsuccessful clutches were often replaced. Clutches were considered to be replacements by the original pair, if they satisfied at least one of the following criteria;

i) one or both of a pair of birds were individually colour ringed and their first breeding attempt had been recorded,

ii) the eggs were particularly distinctive and matched those of the first clutch,

iii) a clutch was lost and another appeared in close proximity approximately

10-14 days later.
Using the above criteria it was possible to estimate the proportion of unsuccessful clutches that were replaced.

The frequency of observer visits to nests increased towards the end of incubation to determine the number of eggs that hatched and to ring the chicks. A clutch was considered to have hatched if one or more chicks were present either in the nest or nearby, or, if no chicks were obvious, but tiny fragments of egg shell were in the nest lining. Many of the nests were found during incubation, and in order to utilize the data from these nests, hatching success was calculated by the Mayfield method (Mayfield 1961,1975), with standard errors derived from equations in Johnson (1979), and Hensler and Nichols (1981). The Mayfield method assumes that the chance of predation is constant throughout the incubation period. Hatching success has been expressed as the percentage of eggs laid that hatched and includes replacement clutches.

The same methods were used for data collected on other species of waders.

Chicks were marked with brood specific leg flags in 1985, but in 1986 and 1987 they were only marked with metal B.T.O. rings as brood identity was readily obtained by recapture of chicks during growth studies. Broods were examined, on average, every four days and the number of surviving chicks counted. Virtually all broods that were reared in meadows or on arable land moved, at some point before fledging, into adjacent pastures as increasing grass length in the meadows hindered feeding. However, only rarely did chicks move out of pastures. Chicks that hatched in improved meadows tended to be reared in adjacent pastures, which often had also been improved. Similarly, chicks hatched in unimproved meadows were most often reared in adjacent unimproved pastures. As a result, the data for chick survival were grouped into unimproved and improved grassland categories only, whereas data for hatching success and fledgling production were divided into four categories; unimproved pastures and meadows, and improved pastures and meadows. Chicks hatched on barley fields usually moved first into adjacent areas of root crops where bare ground was still available and then later onto nearby pastures.

Broods were followed until the chicks had fledged or all of the members had died. Productivity is defined as the number of chicks per pair which survived to fledge and includes pairs that did not rear any chicks.

The proportion of pairs of lapwing that hatched chicks and fledged young on unimproved and improved grassland was compared with data available on other species of waders occupying the same habitats.

The data from the two study areas have been combined since the pattern of differences in the breeding biology of the lapwing between unimproved and improved grassland were similar.

RESULTS

Clutch size

Over the three years of study, the mean clutch size of lapwings on unimproved land, excluding replacements was 3.73 eggs, significantly more than the mean of 3.61 eggs on improved fields (X^2=5.1,df=1,P<0.05) (Table 4.1). In contrast, replacement clutches were significantly larger on improved land than on unimproved, (3.90 compared to 3.47 eggs, X^2=5.2,df=1,P<0.05).

TABLE 4.1 The clutch size of lapwings breeding on unimproved and improved grassland. Differences were examined by the chi-squared test.

	1985		1986		1987		Total	
Unimproved land	n	mean	n	mean	n	mean	n	mean
First clutches	103	3.88	201	3.65***	28	3.86	332	3.73*
Relayed clutches	34	3.77	48	3.17	7	4.00	89	3.47
Improved land								
First clutches	27	3.78	76	3.50	27	3.67	130	3.61*
Relayed clutches	8	3.88	5	4.00	11	3.91	24	3.90

Significance levels: * P<0.05, **P<0.01, ***P<0.001.

Hatching success

Overall, 40% of eggs laid on unimproved pastures hatched, whereas only 17% hatched from clutches laid in their improved counterparts ($P<0.001$) (Table 4.2). This pattern was evident in each of the three years of study. There was no significant difference between hatching success on unimproved and improved meadows which averaged 28%.

Replacement clutches

Over the three years, 73% of pairs on unimproved pastures which lost the first clutch laid replacement clutches, significantly more than the comparable value of 26% on improved pastures ($X^2=30.8$, df=1, $P<0.001$)(Table 4.3).

No difference was found in the estimated proportion of replacement clutches between unimproved and improved meadows with 35% of failed clutches being replaced in each field type, therefore the data for meadows were pooled. Over the three years, the proportion of replacement clutches on meadows was significantly less than that on unimproved pastures ($X^2=27.2$, df=1, $P<0.001$), but did not differ significantly from the proportion on improved pastures. There was year to year variation in the percentage of replaced clutches on meadows. Significantly fewer failed clutches were replaced in 1986 than in 1985 or 1987, ($X^2=3.9$, df=1, $P<0.05$ and $X^2=8.1$, df=1, $P<0.01$ respectively).

TABLE 4.2 The proportion of lapwing eggs that hatched on different grassland types.
Data includes replacement clutches.
(n) = the no. of eggs whose fate were known.

	1985			1986			1987			Total		
	n	mean	s.e.	n	mean	s.e.	n	mean	s.e.	n	mean	s.e.
Unimproved pasture	474	37.9	3.9	669	37.7	3.4	88	79.4	3.5	1231	39.9	2.5
		***			***			***			***	
Improved pasture	67	12.2	5.6	250	16.3	3.9	17	22.6	16.0	334	16.7	3.4
Unimproved meadow	74	13.1	7.2	240	36.0	5.1	44	46.5	15.0	358	32.3	4.5
Improved meadow	53	28.2	10.4	102	25.3	5.4	125	22.3	6.3	280	22.3	4.0

Significance level: *** $P < 0.001$.

TABLE 4.3 The estimated proportion of unsuccessful lapwing clutches that were replaced on different grassland types.
Differences were examined by the chi-squared test.

	1985		1986		1987		Total	
	n	% relaid	n	% relaid	n	% relaid	n	% relaid
Unimproved pasture	42	73.8	64	71.9	3	66.7	109	72.5
		**		***				***
Improved pasture	20	35.0	29	20.7	4	25.0	53	26.4
Unimproved meadow	10	50.0	26	23.1	4	75.0	40	35.0
Improved meadow	9	44.4	24	16.7	19	52.6	52	34.6

Significance levels: ** P < 0.01, *** P < 0.001.

Chick survival

Chick survival from hatching to fledging increased with age in 1986 and 1987 (Fig. 4.1). In 1986, chick survival from hatching to four days old was significantly higher on unimproved than on improved land with 59% surviving on unimproved, but only 44% on improved (X^2=7.7,df=1,P<0.01). These rates over four days represent daily survival rates of 88% and 81% respectively (Table 4.4). There was no significant difference between the two field types in survival rate of chicks from five to ten days old. Survival in chicks over ten days old was high on all fields and tended to be higher, but not significantly so, on improved areas. As a result, the proportions of chicks surviving from hatching to fledging in 1986 were equal, with 28% on both unimproved and improved fields, despite a difference in the timing of the mortality.

In 1987, differences in chick survival between unimproved and improved grassland continued up to ten days old. On unimproved grassland, 62% of chicks survived to ten days old, a significantly higher proportion than on improved grassland, where only 19% survived (X^2=12.0,df=1,P<0.001). In 1987, 43% of chicks survived to fledge from unimproved grassland. This was significantly higher than from improved grassland where only 15% of chicks survived to fledge (X^2=8.1,df=1,P<0.01).

A significantly higher proportion of chicks survived to fledge on unimproved areas in 1987 than in 1986 (X^2 =7.0,df=1,P<0.01). Proportionally fewer chicks survived on improved grassland in 1987 than in 1986, but here the difference was not significant. The differences in survival between the two years are due to a significantly higher survival rate for chicks aged five to ten days on unimproved pastures in 1987 (X^2=12.0,df=1,P<0.001) and a significantly lower survival rate for the same age class on improved grassland (X^2=4.3,df=1,P<0.05).

FIGURE 4.1 The survival of lapwing chicks on unimproved and improved grassland , a) in 1986, unimproved n=494, improved n=109. b) in 1987, unimproved n=76, improved n=27.

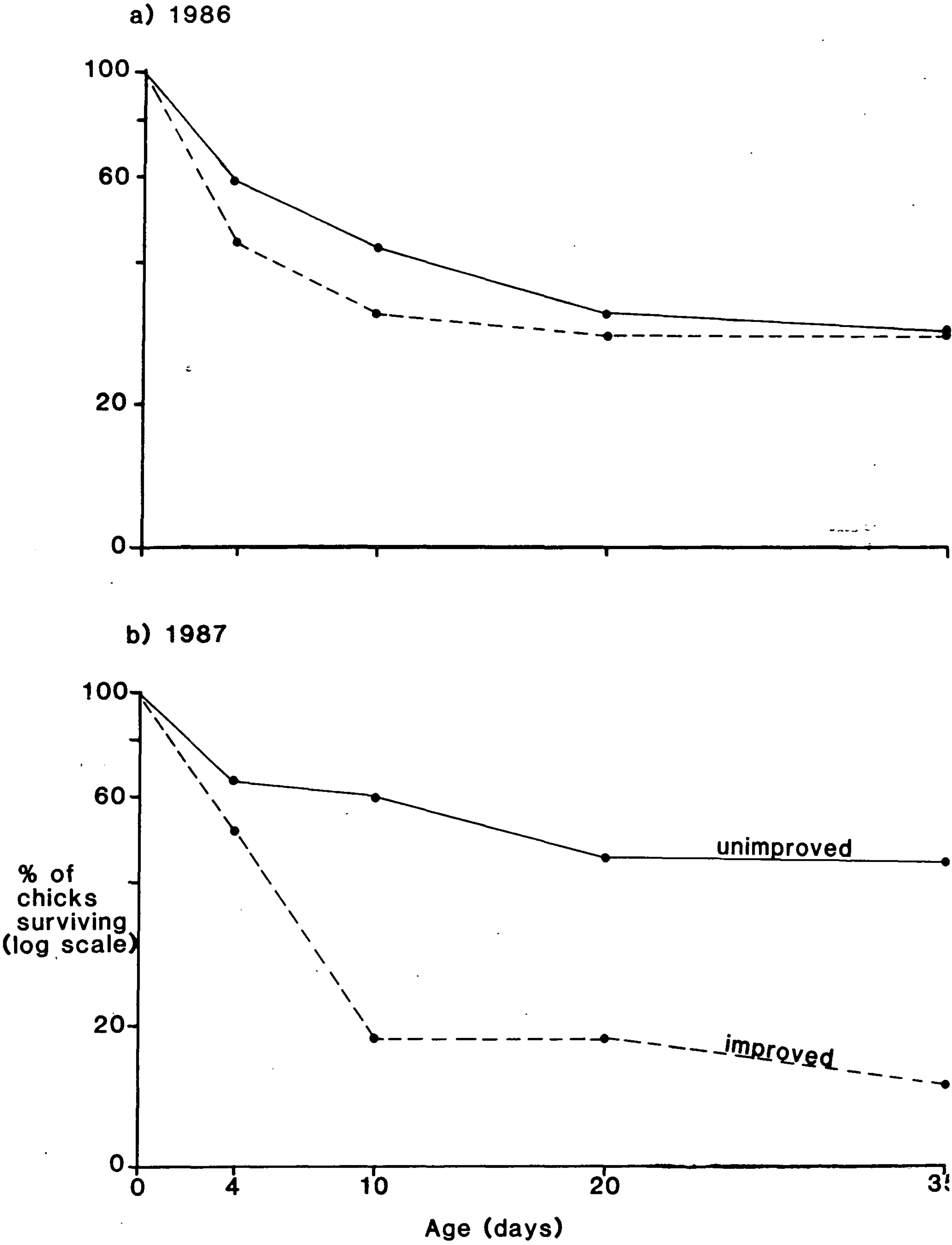

a) 1986
100
60
20
0
b) 1987
100
60
20
0
% of chicks surviving (log scale)
unimproved
improved
0
4
10
20
3
Age (days)

TABLE 4.4 The mortality rate (percent of chicks dying/day) for stages in the fledging period of lapwing chicks on unimproved and improved grassland with comparative data on arable land. (N = the no. of chicks alive at the start of each period.)

	1986						1987					
Age (days)	Unimproved		Improved		Arable		Unimproved		Improved		Arable	
	n	%	n	%	n	%	n	%	n	%	n	%
0 - 4	497	12.3	109	18.5	101	16.1	76	10.4	27	15.1	54	14.4
5 - 10	292	5.4	48	5.6	50	5.8	49	0.7	14	15.7	29	13.6
11 - 20	209	3.2	34	1.2	35	1.5	47	3.2	5	0	12	0.9
21 - 35	150	0.6	30	0	30	0.2	34	0.2	5	1.6	11	0.7

Productivity

Over the three years of study, a mean of 0.92 chicks per pair fledged from unimproved pastures, but only 0.29 chicks per pair from improved pastures $(t=7.3, df=495, P<0.001)$(Table 4.5). This difference was evident in each of the three years of the study. The productivity of 0.54 chicks per pair on unimproved meadows was significantly higher than the 0.20 chicks per pair on improved meadows $(t=2.50, df=155, P<0.02)$.

Lapwings nesting on unimproved pastures raised significantly more chicks per pair over the three years than those nesting on unimproved meadows $(t=3.17, df=471, P<0.01)$. There was no significant difference in production between improved pastures and improved meadows with an average of 0.25 young fledged per pair.

The breeding success of other waders

All waders breeding on unimproved grassland had similar hatching success, with 59%-69% of pairs hatching chicks (Table 4.6). In contrast, breeding success on improved grassland varied between species. An appreciably smaller proportion of lapwings and curlews produced chicks, the difference being significant for lapwing $(X^2=52.4, df=1, P<0.001)$, whereas redshank hatching success was similar on both grassland types. Breeding snipe were absent from improved land.

Data on the proportion of pairs which fledged chicks was available for lapwing and redshank only. On unimproved grassland, there was no difference in fledging success between the two species. A significantly smaller proportion of lapwing fledged chicks on improved than on unimproved land $(X^2=34.2, df=1, P<0.001)$, but the proportion of pairs of redshank that fledged chicks did not differ significantly.

TABLE 4.5 The mean number of lapwing chicks fledged per pair on different types of grassland. Data includes clutch replacements.

	1985			1986			1987			unweighted		
	n	mean	s.e.	n	mean	s.e.	n	mean	s.e.	n	mean	s.e.
Unimproved pasture	67	1.05	0.10	215	0.72	0.07	67	0.99	0.11	349	0.92	0.05
		***			*			***			***	
Improved pasture	15	0.27	0.18	66	0.35	0.10	24	0.25	0.11	105	0.31	0.07
Unimproved meadow	10	0.42	0.21	65	0.66	0.13	6	0		81	0.60	0.11
											**	
Improved meadow	8	0.12	0.12	27	0.37	0.15	21	0.10	0.10	56	0.23	0.08

Significance levels: * $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$.

TABLE 4.6 The breeding performance of waders nesting on unimproved and improved grassland.
- denotes no data available.
Differences were examined by the chi-squared test.

	percentage of pairs that:									
	a) hatch chicks					b) fledge chicks				
	Unimproved			Improved		Unimproved			Improved	
	n	%		n	%	n	%		n	%
Lapwing	396	69	***	152	35	351	46	***	138	17
Redshank	41	61		13	54	41	44		13	31
Curlew	17	59		13	23	-	-		-	-
Snipe	26	62		-	-	-	-		-	-

Comparative data on the breeding success of lapwing on arable land

Data on lapwing breeding success have been collected for pairs nesting on arable land near to grassland study sites in 1986 and 1987. The summary of these data are given in table 4.7 for the two years combined, except where they differed significantly.

The mean clutch size on arable land did not differ significantly between initial and replacement clutches, or when compared to grassland sites. Overall, 46% of eggs laid hatched, which is significantly higher than on improved grassland, where only 19% of eggs hatched ($t=4.0, df=513, P<0.001$). On arable land, 63% of unsuccessful initial clutches were replaced. This was significantly higher than on improved grassland, where only 30% were replaced ($X^2=8.4, df=1, P<0.001$) and equivalent to unimproved pasture, where 62% were replaced.

Chick survival on arable land showed a pattern closer to that of improved grassland than unimproved. Survival in 1986 (84% per day) among chicks up to four days old, and in 1987 (86% per day) for chicks up to ten days old, was similar to rates on improved grassland but appreciably lower than on unimproved grassland (Table 4.4). In 1986, fledging success on arable land did not differ from that on grassland, with 29% of chicks surviving from hatching to fledge. In 1987, 18% of chicks that hatched on arable land survived. This was similar to the value of 15% obtained for improved grassland, but significantly less than the 43% which fledged on unimproved grassland ($\chi^2=6.1, df=1, P<0.05$).

Over the two years considered, 0.56 chicks per pair fledged. This was significantly lower than the average of 0.86 per pair on unimproved grassland ($t=2.67, df=528, P<0.01$), but significantly higher than the 0.25 chicks fledged per pair on improved grassland ($t=2.48, df=228, P<0.02$).

TABLE 4.7 Breeding parameters for lapwing nesting on arable fields with comparative data for nearby unimproved and improved grassland. Mean values are given with ±1 standard error.

		Arable		Unimproved grassland		Improved grassland	
		n	mean	n	mean	n	mean
clutch size							
a) initial		53	3.74	332	3.73	130	3.61
b) replacement		21	3.71	89	3.47	24	3.90
% hatching success		280	45.6 ± 6.8	1589	38.1 ± 2.2	612	19.2 ± 2.7
% replacement clutches		27	63.0	149	62.0	105	30.4
% fledging success	1986	101	29	494	28	109	28
	1987	54	18	76	43	27	15
productivity		67	0.57 ± 0.11	461	0.88 ± 0.05	161	0.25 ± 0.06

(Clutch size: mean no. of eggs in initial and repeat clutches,
hatching success: the % of eggs laid that hatch,
replacement clutches: the % of failed first clutches that are replaced,
chick survival: the % of chicks surviving from hatching to fledging,
productivity: the mean no. of chicks fledged per pair.)

A significant difference in chick survival existed between years, therefore data for 1986 and 1987 are given separately.

DISCUSSION

The densities of lapwing on improved grasslands in northern England are 69% lower than those on adjacent unimproved fields (Baines in press). The cause of this difference could lie in habitat choice by adults or differential mortality occurring on the two types of fields. The extent to which adults move between improved and unimproved fields has yet to be examined but the existence of a degree of philopatry linked with particular fields has already been detected (Baines in progress). The existence of philopatry suggests that the differences in densities of lapwings on improved and unimproved grasslands could arise from differences in their population dynamics on the two types of fields. Adult mortality rates appear to be low during the breeding season and during this study no indications were obtained that adult survival was appreciably different on the two types of field. It is difficult to envisage differential mortality occurring whilst the lapwings are in flocks and in different areas.

This study has shown that there are appreciable differences in the production of young in the two types of fields. Over three years, the mean production on unimproved land was 0.86 fledglings per pair, whereas the equivalent figure for improved areas was only 0.25 fledglings per pair, a reduction of 71%. The figure for unimproved grassland is comparable to the two year mean of 0.88 chicks fledged per pair for lapwings breeding on a Danish saltmarsh (Ettrup & Bak, 1985), but exceeds that of approximately 0.6-0.7 per pair found by Jackson and Jackson (1975) in the New Forest and is considerably higher than the 0.43 chicks fledged per pair reported by Glutz _et_ _al_. (1975) in Switzerland. Production on improved land was considerably lower than all published figures, with the exception of arable land in Denmark, where, for a time, zero production was recorded (Ettrup & Bak, 1985) and the New Forest between 1976 and 1978, where annual production varied between zero and 0.10 chicks fledged per pair (Jackson & Jackson, 1980).

Calculation of the number of chicks which are needed to fledge to sustain the population indicates that about one chick should be fledged per pair each year. (Based on survival rates of adults of 67% (Haldane 1952, Lack 1954) and first year survival from September to March of 63% (Cramp & Simmons, 1983)). It is not possible to be precise over the exact production required since there are likely to be regional variations in adult survival, and the proportion of lapwings which breed at one year old is inadequately known. It is clear, however, that the annual productivity on improved areas of only 0.25 chicks per pair is inadequate whilst 0.86 on unimproved grasslands approximates to the required levels.

There are differences in fledging success between the two types of fields, but the major difference is related to hatching success, with an average of 24% of eggs hatching on improved and 45% on unimproved grasslands. The food available to lapwings on improved and unimproved fields has been investigated and whilst differences occur, there is evidence of only relatively minor effects on the population dynamics of reproduction (Chapter 5). This conclusion is supported by the fact that hatching success, not fledging success, is the main cause of the differential productivity. Direct observation and the examination of nests where the eggs had disappeared suggested that predation was the major cause of the low hatching success. This aspect is being further investigated.

If differences in productivity cause the differences in densities found on improved and unimproved grasslands, then there must be considerable philopatry or, alternatively, adults selecting areas to breed must prefer unimproved areas. These aspects of the biology of the lapwing remain to be investigated in detail on marginal grasslands.

CHAPTER 5 FACTORS DETERMINING THE BREEDING SUCCESS OF THE LAPWING ON UNIMPROVED AND IMPROVED GRASSLAND

INTRODUCTION

There would appear to be three possible reasons for the reduced density and breeding success of lapwings on improved grassland;

i)Improved grassland may be deficient in food which may reduce its attractiveness as a breeding habitat. For pairs which do breed, reduced food may limit chick growth and ultimately chick or fledgling survival.

ii)Improved grasslands are more intensively managed with the resulting possibility that more clutches may be;

a) destroyed directly by mechanical farming activities, or

b) trampled by livestock which occur at higher grazing densities.

iii)Nests on improved grasslands may be more prone to predation.

These three possibilities are examined in this paper.

METHODS

i)Food availability

The important components of the lapwing diet were identified from stomach contents collected from 16 lapwings killed on the road or through striking overhead wires. These were sorted under a binocular microscope and animal fragments identified.

The effect of land improvement on food availability to lapwing was assessed by sampling the main invertebrate constituents of the lapwing diet in unimproved and improved fields. Unimproved fields were paired with adjacent improved fields.

Three methods of sampling invertebrates were used;

i) *in situ* chemical expellents for earthworms (Lumbricidae) and dipteran larvae (predominantly of the order Tipulidae),

ii) extraction of animals, particularly earthworms and dipteran larvae, from soil samples, and

iii) the use of pitfall traps, in particular for surface active invertebrates.

Samples were taken from unimproved and adjacent improved fields so that, the samples constituted matched pairs, where only the management regimes differed.

Earthworms were sampled from 47 fields in April; 21 unimproved and 26 improved, using the formaldehyde extraction technique (Raw 1959). The effectiveness of the technique is dependent on the effect of soil moisture and temperature on earthworm activity (Evans & Guild 1947, Satchell 1969). During cold or dry conditions, earthworms tend to move deeper into the soil (Gerard 1967) and are less likely to be influenced by formaldehyde. In addition, during dry conditions, *Allolobophora* species do not respond to expellents during their facultative or obligate diapause (Evans & Guild 1947, Grant 1955, Gerard 1967). Nordstrom and Rundgren (1972) found the formaldehyde method to be as efficient as hand sorting when estimating populations of *Lumbricus terrestris*, but inferior to hand sorting when studying *Allolobophora* species, whereas *Dendrobaena* species and *L. rubellus* could be accurately sampled by any method. To ensure adequate sampling of all species, the samples were taken in April, as at this time due to a warming soil, most worms had risen into the top 7.5cm of the soil (Gerard

1967), and as soil moisture was generally high, Allolobophora species were active.

Nine litres of 0.55% formaldehyde were poured over a $0.5m^2$ quadrat placed randomly within the field. The worms that emerged were collected. After ten minutes, or when no more worms emerged, a further application of formaldehyde was applied over the quadrat. Initially, a third treatment was applied after a further ten minutes. The third treatment never produced any worms, so in subsequent samples only two applications were made. The earthworms collected were counted and preserved in alcohol. After one week, the worms were dried on filter paper before weighing. Weight loss due to preservation was not considered (see Satchell 1969).

Tipulid larvae were sampled by a salt extraction technique. Samples were taken from 24 fields in late April/early May; 12 unimproved and 12 improved. Each field was divided into ten equal sized areas and one sample taken from within each area. A sample was taken by hammering a pipe 25cm high and of 10cm diameter into the ground to a depth of 5cm and filling the pipe with brine solution (1kg of sodium chloride dissolved in 3 litres of water). After 15 minutes, the larvae had floated to the surface of the brine and were collected. Soil samples were also taken and the tipulid larvae present extracted using a Berlese funnel. Ten samples, 15cm by 15cm and 10cm deep were, taken randomly from representative areas of each field. Sampling depth was restricted to 10cm as below this depth virtually no tipulid larvae are found (Freeman 1967). Adult tipulids (crane-flies) were collected in pitfall traps (see below).

Surface active invertebrates were sampled using pitfall traps. Pitfall traps allow the collection of large samples of invertebrates and produce many more species than alternative sampling methods (Coulson & Butterfield 1985), they are easy to use (Luff 1975), and they also sample nocturnally active species, which may be overlooked by other sampling techniques. However, pitfall traps are of little use in the direct estimation of populations or in comparing communities (Briggs 1961, Greenslade 1964). A further disadvantage is that the number of animals caught partially reflects the degree of activity of that animal (Greenslade 1961, Mitchell 1963). Nevertheless, Baars (1979) has shown that for Carabidae, pitfall catches allow an adequate estimation of population density and are suitable for assessing relative abundances. As lapwing feed by visual cues, active invertebrates are more likely to be taken, hence pitfall traps were considered an appropriate method.

Ten collecting beakers with a mouth diameter of 4.5cm were sited in representative areas of 12 fields in 1985; 8 unimproved and 4 improved, and 21 fields in 1986; 10 unimproved and 11 improved. The traps were placed in two rows of five with an inter-trap distance of 3m. Animals falling into the traps were preserved in a 2% formaldehyde-detergent solution. Sampling commenced in mid-March and continued to the end of October with trap contents being collected every fortnight. The data collected between mid-March and early July 1986 have been used in this paper as an assessment of the food availability to lapwing throughout the breeding season, whilst data collected between mid-May and early July 1986 have been used to measure food availability during the main chick rearing period.

The density of breeding lapwing in each field were obtained from a minimum of four counts between the beginning of April and the end of May. The number of breeding pairs was taken either as the peak number of nests present at any one time or the mean of the two highest counts of pairs per field if nest counts could not be made. The area of each field was obtained from 1:2500 O.S. maps and the counts of breeding lapwing were converted to the density of pairs/10ha. Similarly, lapwings were censused on their return to the breeding grounds in the first three weeks of March, the pre-breeding period. Densities of birds present in each of the study fields were calculated. The birds present were sexed in the field by plumage differences (Cramp & Simmons 1983) and the pre-breeding distributions of each sex compared.

Between 1985 and 1987, 760 lapwing clutches were studied. In 1986 and 1987 the length and breadth of each egg was measured to 0.1mm and the egg volume calculated using the formula;

$$v = K \, . \, LB^2$$

where L is the egg length, B is the egg breadth at the equator and K is a shape constant (Coulson 1963, Furness and Furness 1981). K was obtained by using eggs from collections and filling them with alcohol from a burette to obtain their internal volumes and relating these values to LB^2. Data on egg volumes were collected from unimproved and improved grassland with comparative data for adjacent or nearby arable fields.

Lapwing chicks were ringed to study individual growth rates. Chicks of unknown age were aged from measurements of chicks of known age. Where possible, chicks were reweighed, on average, every four days. Between the ages of five and thirty days lapwing weight increase was linear. Growth was measured as the mean weight increase per day over this period.

ii)Destruction of clutches by agricultural machinery and by livestock

Nests were found by observing incubating birds, or by systematic searches. Nests were revisited every four days. The cause of clutch failure was recorded. Eggs that were either lost to farm machinery or trampled by livestock were typified by being broken and compressed into the bowl of the nest, with tyre marks, general land compression or hoof prints apparent. Comparative data on the proportion of clutches lost to farming activities on arable land are included.

iii)Loss of clutches by predation

Clutch loss was attributed to predators if either the eggs disappeared during incubation, if large fragments of egg shell remained , or if one or more eggs were taken from the clutch causing desertion of the remaining eggs. Comparative data on the predation of clutches on arable land are included.

RESULTS

i)Food availability

The possibility of reduced food availability to lapwings following improvement was measured by comparing each of the following on unimproved and improved grassland;

i) the relative abundance of important components of the lapwing diet by pitfall trapping,

ii) the mean egg volume of clutches, and

iii) chick growth rates.

Table 5.1 shows the diet of lapwings obtained from samples collected before or after 1 May. Before May 1 the diet was composed largely of fly larvae (Diptera) with beetles (Coleoptera), both adults and larvae, and earthworms (Lumbricidae). Field observations suggested that worms form an important proportion of the overall diet at this time and the 9% of items recorded from stomach analysis is a considerable underestimate. This

TABLE 5.1 Seasonal changes in the diet of lapwings feeding on upland grasslands in the North Pennines, from analysis of stomach contents.

	Before May 1 (9 stomachs) % of animals (n=78)		After April 30 (7 stomachs, 4 from chicks) % of animals (n=124)
Lumbricidae (whole animals)	9		0
Coleoptera (adults)	22	***	80
Coleoptera (larvae)	17	**	4
Diptera (adults)	0		2
Diptera (larvae)	50	***	10
Others	1		5

Significance levels: ** $P < 0.01$, *** $P < 0.001$.

discrepancy was probably due to the rapid digestion of worms and because the presence of chaetae were not converted to "food items" as a satisfactory conversion factor could not be obtained.

After May 1, the diet was mainly adult beetles, the proportion of which increased from 22% to 80% ($X^2=63.6$,df=1,$P<0.001$), with corresponding actual and proportional decreases in the quantity of both beetle and fly larvae taken ($X^2=7.9$,df=1,$P<0.01$ and $X^2=37.1$,df=1,$P<0.001$) respectively. A small number of spiders (Araneae), adults flies and snails (Gastropoda) were also found. No worms were recovered from the samples collected later in the season and this decrease in the use of worms was confirmed by field observations of feeding lapwing. Thus, as the season progressed, there was a shift in emphasis in the lapwing diet from soil invertebrates, principally fly larvae and worms, to surface active invertebrates, particularly beetles.

Improvement of grasslands affected the densities and biomasses of the major invertebrate components of the lapwing diet (Table 5.2). It increased both the density ($t=4.43$,df=44,$P<0.001$) and the biomass ($t=3.95$,df=44,$P<0.001$) of earthworms and increased the biomass of beetles other than carabids ($U=22.0$,$P<0.05$, Mann-Whitney U-test). There were significant decreases in both the number and biomass of spiders caught following improvement, ($U=21.0$,$P<0.05$ and $U=4.0$,$P<0.001$ respectively). The number of carabid beetles caught was similar on both grassland types, but the biomass on improved grassland was 70% lower due to an increase in the proportion of small species ($U=18.0$,$P<0.05$). Improvement did not change the density or the biomass of tipulid larvae but the species composition changed with a marked increase of *Tipula paludosa*.

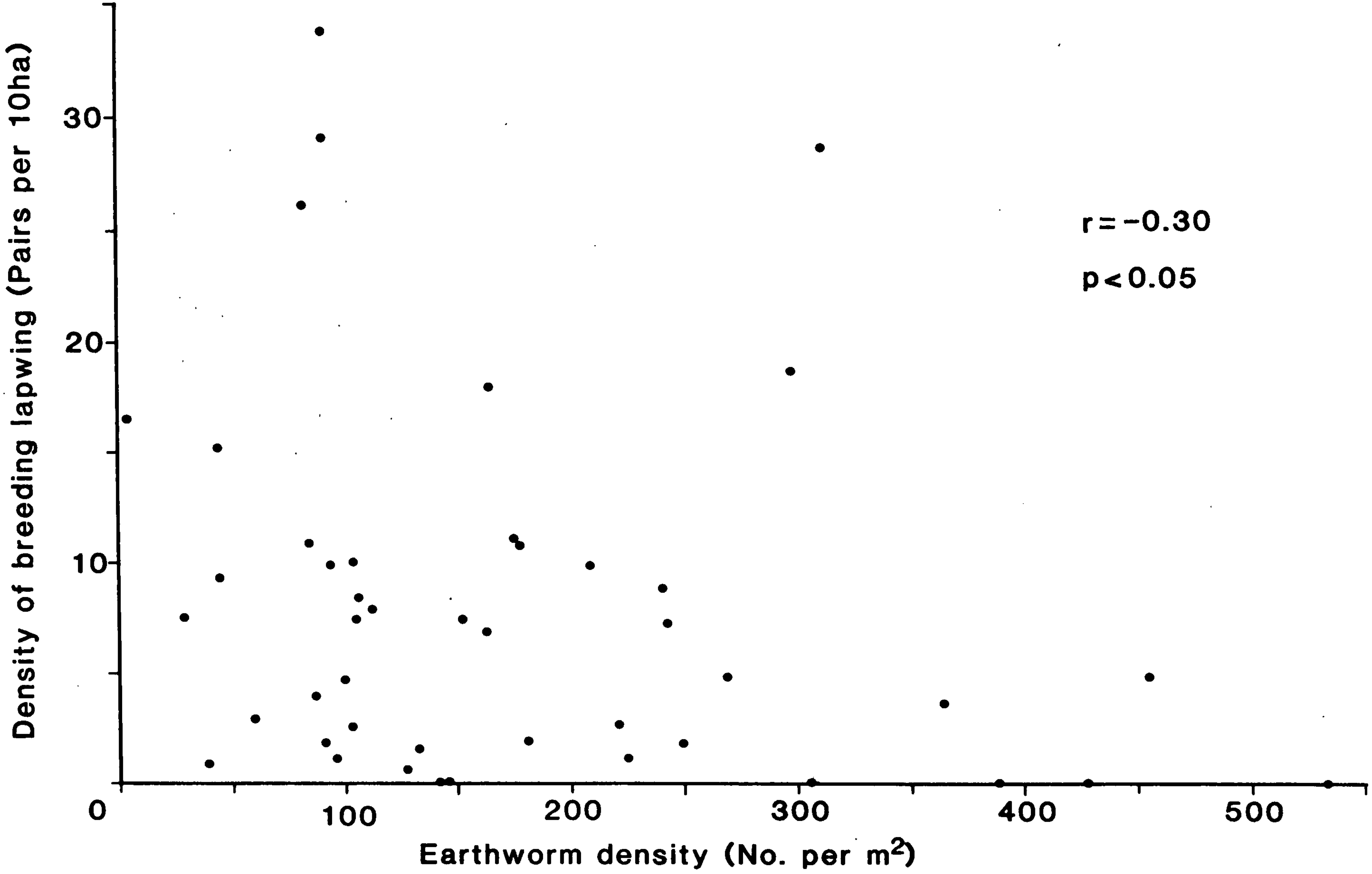
Earthworm densities were found to vary considerably, but overall there was a negative correlation with the breeding density of lapwing ($r=-0.30$,df=43,$P<0.05$) (Fig. 5.1). The highest densities of earthworms

TABLE 5.2 The effect of land improvement on the densities and biomasses of the main invertebrate components of the lapwing's diet. n = the no. of paired samples. Araneae, Carabidae and "Other Coleoptera" represent changes in the quantity of animals caught in pitfall traps.

		% change after improvement			
		Density		Biomass	
	n	%	S.E.	%	S.E.
Lumbricidae	23	+120	12 ***	+146	15 ***
Tipulidae larvae	12	no change		no change	
Araneae	10	-39	17 *	-65	12 ***
Carabidae	10	-10	20	-70	31 *
Other Coleoptera	10	+54	25	+49	24

* $P < 0.05$, *** $P < 0.001$.

FIGURE 5.1 The relationship between the density of earthworms in April and the density of breeding lapwings on upland, marginal grasslands. ($r=-0.30$, d.f.$=43$, $P<0.001$).



Density of breeding lapwing (Pairs per 10ha)
30
20
10
0
100
200
300
400
500
Earthworm density (No. per m²)
r = -0.30
p < 0.05

were found on improved fields where the densities of breeding waders were typically low. Therefore earthworm density was not influencing breeding field selection. However, lapwing distribution in the pre-laying period was markedly different to that in the breeding season, and when lapwing densities in the pre-laying period were considered a strong positive correlation with earthworm densities existed ($r=0.86, df=11, P<0.001$) (Fig. 5.2).

In the pre-laying period, (March 1 - March 21) high densities of lapwing were found on certain improved fields where feeding flocks of up to 50 birds gathered. When the sexual composition of these flocks was examined, 75% of the birds were females, compared to only 36% of birds occupying fields subsequently used extensively for breeding ($X^2 =40.9, df=1, P<0.001$). A few weeks later, these improved fields used for feeding contained either no breeding lapwing or only an occasional pair and could be considered as undefended or "neutral" fields. These "neutral" fields contained high earthworm densities and were probably important for building up reserves for egg production with minimal sexual harrassment.

Observations on individually colour-marked birds indicated that the users of these "neutral" fields nested in surrounding fields. Hence, the size and quality of eggs produced by these birds were not determined by food availability within the field used for breeding, but by the proximity of high quality feeding areas. Each of the study areas had such "neutral" fields frequented by female dominated feeding flocks. Predictably, as females were using the same areas for building up reserves for egg production, no differences in mean egg volume were found in eggs laid on unimproved grassland, improved grassland or on arable land in either 1986 or 1987 (Table 5.3). However, larger eggs were laid on all field types in 1987, the difference being significant for unimproved grassland and arable

FIGURE 5.2. The relationship between earthworm densities in April and the pre-breeding densities of lapwing (1-22 March) on one grassland study area. ($r=0.86$, d.f.$=11$, $P<0.001$).

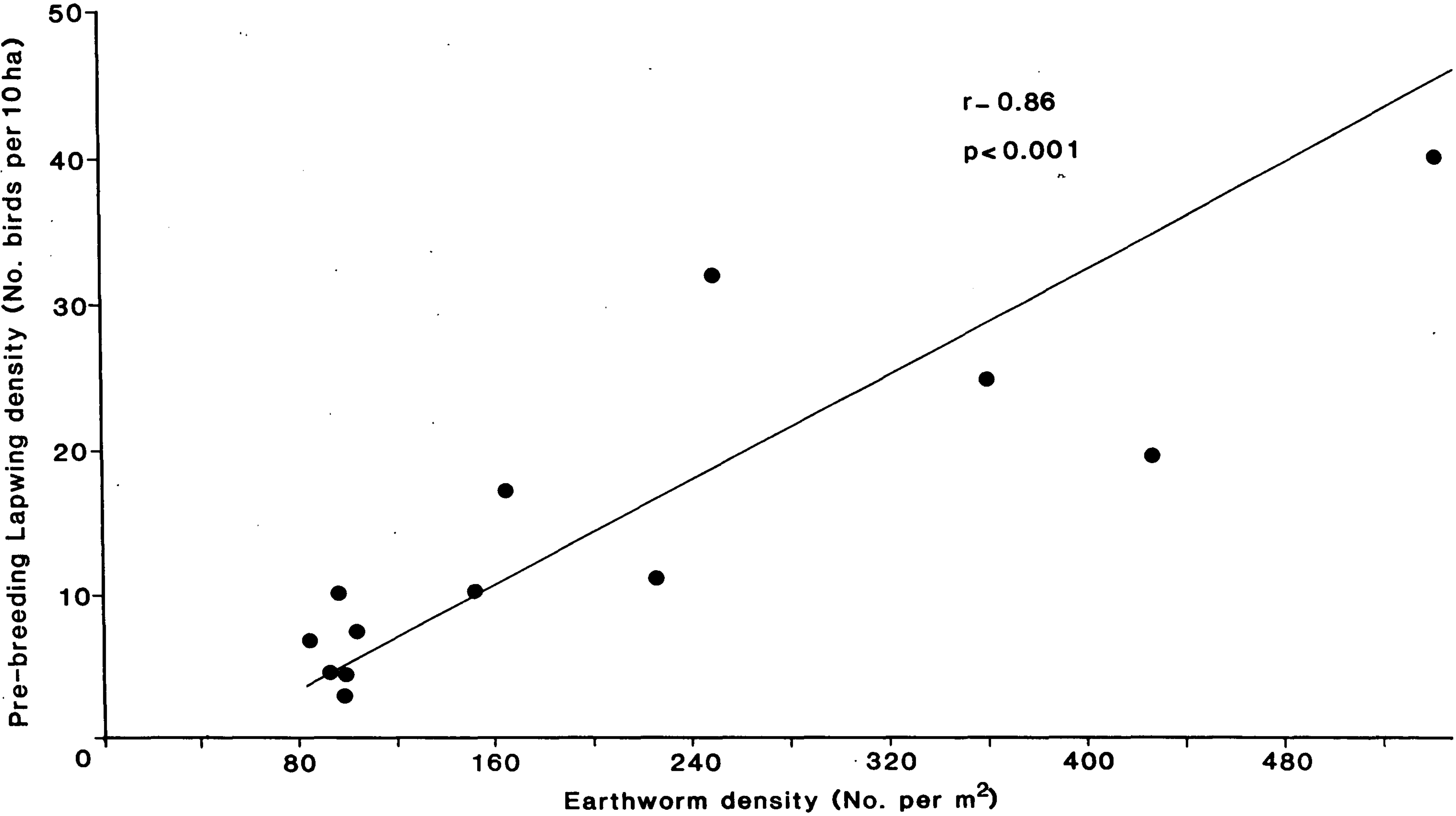

r- 0.86
p< 0.001
Pre-breeding Lapwing density (No. birds per 10 ha)
50
40
30
20
10
0
80
160
240
320
400
480
Earthworm density (No. per m^2)

TABLE 5.3 The volume of lapwing eggs on unimproved and improved grassland and on arable land. (n = the no. of clutches measured) Volume values in cm^3.

	1986				1987		
	n	mean	S.E.		n	mean	S.E.
Unimproved grassland	196	24.15	0.11	***	27	24.96	0.22
Improved grassland	83	23.97	0.15		26	24.50	0.29
Arable land	35	23.80	0.25	**	19	24.86	0.25

**P<0.01, ***P<0.001

land ($t=3.29, df=221, P<0.001$ and $t=3.00, df=52, P<0.01$ respectively).

The change in diet from predominantly soil invertebrates early in the season to mainly surface active invertebrates later in the season suggested that fields containing high numbers of surface active invertebrates, particularly beetles, were better breeding sites, especially for rearing chicks which fed almost exclusively on beetles. The abundance of each of the four principal components of the surface invertebrate fauna; carabid beetles, staphylinid beetles, other beetles and spiders, sampled between mid-May and mid-July, were not significantly correlated with the density of breeding lapwings (Table 5.4). When data on beetles were combined, abundance was significantly correlated with lapwing breeding density on pastures ($r=0.70, df=10, P<0.02$) (Fig. 5.3), but not on meadows. However, in meadows, increasing grass length reduced feeding efficiency, especially when taller than 15cm and such areas are vacated (Klomp 1953). Hence, no significant relationship between beetle abundance and lapwing density was found for meadows.

To investigate food availability to chicks the pastures were divided into two categories according to whether more or less than an arbitrary value of 120 beetles were caught in 10 pitfall traps between mid-May and early July 1986. The growth rates of chicks from the two site types showed no significant difference with weight increases of 5.7g/day in areas of low food availability and 5.3g/day in areas of high food availability. Thus, food availability did not appear to be a factor limiting chick development.

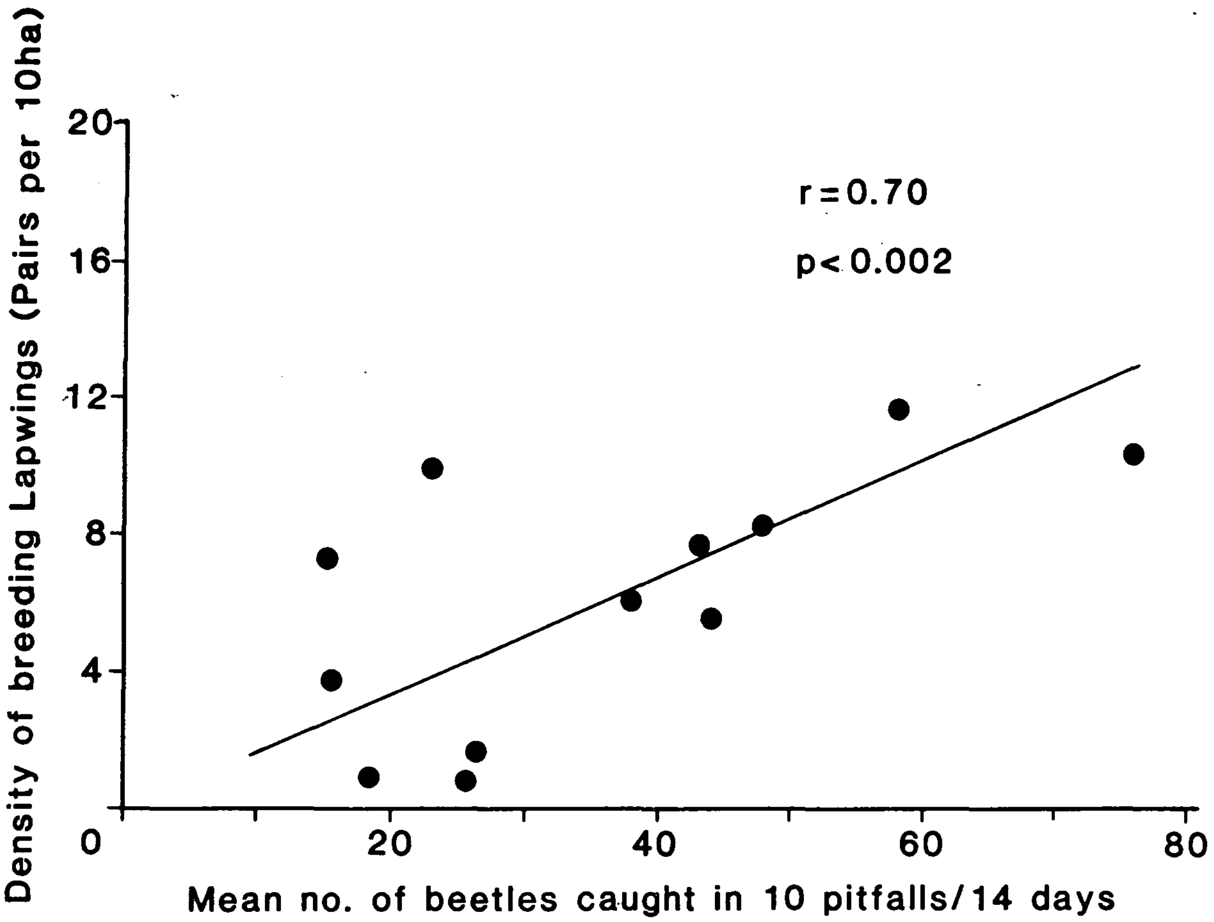
The growth rates of chicks raised on unimproved pastures were then compared with those for chicks reared on improved pasture in 1985, 1986 and 1987 (Table 5.5). Only in 1985, was there a significant difference, with chicks on unimproved pastures growing at 6.1g./day over the linear part of the growth curve and chicks on improved pastures at 5.1g./day

TABLE 5.4 The correlation coefficients between the density of breeding lapwing (pairs/10ha) and the principal components of the surface invertebrate fauna available to feeding chicks. (mean no. of animals/10 pitfall traps per 14 days) on pastures. Samples cover the period mid-May to early July

	r value (n = 10)			
	Carabidae	Staphylinidae	other Coleoptera	Araneae
density of breeding lapwings (pairs/10ha)	0.58	0.38	0.46	0.17
	n.s.	n.s.	n.s.	n.s.

n.s. not significant

FIGURE 5.3. The relationship between beetle abundance between mid May and early July and the density of breeding lapwing on upland, marginal pastures ($r=0.70$, d.f.$=10$, $P<0.02$).



Density of breeding Lapwings (Pairs per 10ha)
20
16
12
8
4
0
20
40
60
80
Mean no. of beetles caught in 10 pitfalls/14 days
r=0.70
p<0.002

TABLE 5.5 The growth rate of lapwing chicks (g./day) over the linear part of the growth curve on unimproved and improved pastures.

	1985			1986			1987		
	n	mean	S.E.	*n*	mean	S.E.	*n*	mean	S.E.
Unimproved pasture	149	6.07	0.17	233	5.06	0.18	72	6.21	0.18
		***							
Improved pasture	72	5.07	0.25	58	5.00	0.16	89	6.11	0.29

***P<0.001.

(t=3.33,df=219,P<0.001). In 1986, growth rates on unimproved areas were significantly lower than in either 1985 or 1987, whilst on improved pastures growth rates were comparable to 1985 but significantly lower than in 1987.

ii) <u>Destruction of clutches</u>.

The second factor considered as a possible cause of reduced breeding success on improved land was that agricultural activities destroyed more lapwing clutches on improved than on unimproved fields. Improved areas were typified by more intensive management (see Study areas). Thus, improved land was worked more frequently and more thoroughly by tractors and tractor-drawn machinery. Therefore, it would be expected that more lapwing clutches on improved land would be destroyed directly by farming activities. Overall, 22% of clutches laid on improved meadows were destroyed by farm machinery compared to 8% on unimproved meadows (X^2=5.46,d.f.=1,P<0.02) (Table 5.6). Meadows are managed more intensively than pastures and may be subjected to land rolling, chain harrowing and spreading of fertilizer, inorganic, organic or both. Improved pastures usually have only inorganic fertilizer applied, whilst unimproved pastures are occasionally limed. This difference in agricultural activity is reflected by the proportion of clutches destroyed by machinery being significantly higher on either unimproved or improved meadows than on their pasture counterparts (X^2 =5.5,df=1,P<0.02 and X^2=7:5,df=1,P<0.01 respectively). Only 6% of clutches on improved pastures and 2% on unimproved were destroyed by machinery.

The year to year variation in the proportion of clutches destroyed by farm machinery reflects differences in the starting date of mechanical activities on the land in relation to the stage of the lapwing breeding cycle. The springs of 1986 and 1987 were wet, rendering farmland unsuitable for machinery until later in the year when most lapwings were incubating

TABLE 5.6 The proportion of lapwing clutches destroyed by farm machinery during rolling, harrowing and fertilizing on different grassland types.

	1985		1986		1987		Total		
	n	%	*n*	%	*n*	%	*n*	%	
Unimproved pasture	131	1.8	191	2.1	25	0	347	1.9	
Improved pasture	26	4.2	76	6.4	7	0	109	5.5	
									**
Unimproved meadow	18	0	67	5.4	11	30.5	96	8.2	
								*	
Improved meadow	15	6.9	31	29.5	32	20.0	78	22.0	
Arable		-	43	4.6	35	20.0	78	11.5	

*P<0.05, **P<0.01

eggs, hence the loss of clutches to agricultural activities was high. Conversely, in 1985, a drier spring, machinery access to land was earlier and before many clutches were laid, hence fewer clutches were destroyed. Only 7% of clutches in improved meadows were lost in 1985, whereas 30% were lost in 1986.

A small proportion of clutches on pasture were trampled by livestock; up to 3% of clutches were destroyed on unimproved pasture and 2% on improved.

iii)Loss of clutches by predation

The third hypothesis to explain differences in breeding success following improvement was differential clutch predation rates. Between 1985 and 1987, 76% of clutches on improved pastures were taken by predators whereas, on unimproved pastures the value was only 47% (X^2 =21.6,df=1,P<0.001). This trend was consistent over each of the three years with the difference being significant in 1985 and 1986, (X^2=6.9,df=1,P<0.01 and X^2=9.3,df=1,P<0.01) (Table 5.7).

No differences in predation levels were found between unimproved and improved meadows. The average predation rate in meadows did not differ significantly from that in unimproved pastures, whereas in improved pastures it was significantly higher (X^2=10.2,df=1,P<0.001).

Observed egg predations were confined to avian predators, namely carrion crows *Corvus corone* and black-headed gulls *Larus ridibundus*. Foxes were present in the study areas but were not thought to be major predators of eggs as no clutch predation was recorded at night (see following section).

TABLE 5.7 The proportion of lapwing clutches taken by predators on different grassland types, 1985-87, and on arable land, 1986-87

	1985		1986		1987		Total	
	n	%	*n*	%	*n*	%	*n*	%
Unimproved pasture	131	50.4	191	48.2	25	11.6	347	46.7
		**		**				***
Improved pasture	26	81.6	76	69.9	7	77.4	109	75.6
Unimproved meadow	18	75.3	67	42.8	11	20.3	96	52.7
Improved meadow	15	61.2	31	37.0	32	52.6	78	51.8
Arable		-	48	19.8	40	26.4	88	24.6

**P<0.01, ***P<0.001

Experimental evaluation of predation

During the first week of May in 1987, the frequency of clutch loss to predators was experimentally assessed using black-headed gull *Larus ridibundus* eggs to simulate lapwing clutches. Five clutches, each containing two gull eggs, were placed randomly in each of 16 unimproved pastures; eight pastures with breeding lapwing and eight without. The same procedure was undertaken on improved pastures. Fields were selected so that all four experimental conditions were either adjacent or in close proximity to each other. This ensured that each set of clutches within a replicate were exposed to similar levels of predators and that the only factors varying were as a result of land management and the presence/absence of breeding lapwings.

The clutches were put out either just before dawn, or just after dusk to avoid the possibility of avian predators being led to the nests, and to ensure that all clutches were exposed for equal day and night-time periods. The experimental nests were constructed by creating a depression in the ground and lining it with dead grass. All clutches were revisited twice daily, at dawn and again at dusk, so enabling predations to be divided into diurnal and nocturnal. Clutches were refound using compass bearings from nearby landmarks and their contents examined from a distance of about three metres, thus overcoming a need for nest markers, which may increase predation (Picozzi, 1975), and the possibility that scent-trails may be followed to the nests. Observations were made twice daily for three days and then for a final time after seven days.

After exposure for one day in areas containing breeding lapwing, five times more clutches were taken by predators on improved than on unimproved pastures (X^2=15.3,df=1,P<0.001) (Fig. 5.4). After 7 days, 36% of the eggs on unimproved pastures had been taken, whereas on the improved pastures 76% had been taken by predators, (X^2=23.5,df=1,P<0.001). In fields which did not contain breeding lapwing 22% of eggs survived one days exposure on unimproved pastures, but only 4% on improved, the difference being significant, (X^2=10.8,df=1,P<0.001). After 7 days, only 2% of the eggs on the unimproved pastures remained intact. On improved pastures all the eggs had been taken by predators. Thus, predation was significantly higher in fields without breeding lapwing (X^2=85.1,df=1,P<0.001).

All the predations during the experiment took place during day-light hours, no predation occurred during the night.

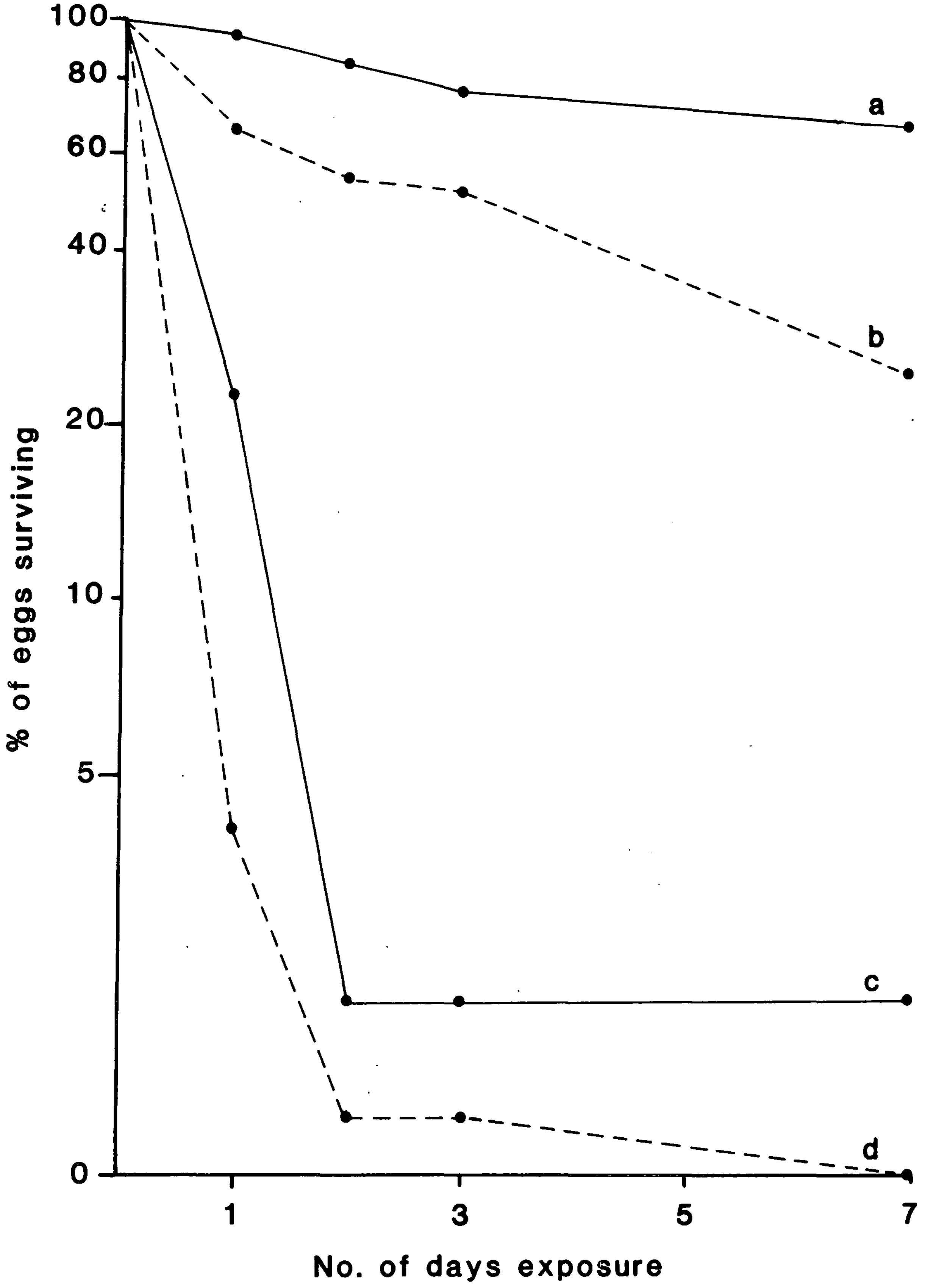
FIGURE 5.4. The survival of simulated lapwing clutches in May 1987 on:

a) unimproved grassland with breeding lapwings present,

b)improved grassland with breeding lapwing present,

c) unimproved grassland with no breeding lapwing, and

d) improved grassland with no breeding lapwing.


100
80
60
40
20
10
5
0
% of eggs surviving
1
3
5
7
No. of days exposure
a
b
c
d

DISCUSSION

Food supplies influence chick survival in several bird species, for example survival of partridge Perdix perdix and pheasant Phasianus colchicus chicks increased with increasing density of prey arthropods, with up to 75% of the variation in chick survival being explained by the variation in arthropod densities (Green 1984, Hill 1985). Similarly, a reduction in invertebrates decreased the growth rates of black duck Anas rubripes and mallard Anas platyrynchos ducklings (Hunter et al. 1984). No significant difference was found in the growth rate of lapwing chicks reared in fields of differing beetle abundance, despite a reliance on beetles, particularly Carabidae, whose biomass had been markedly reduced by improvement. Either food at the lower level of abundance was sufficiently above a threshold level so as not to reduce chick growth, or within a field where beetles were few, there were other invertebrates in sufficient quantities.

The growth rates of partridge chicks are largely determined by weather conditions and their subsequent effect on food availability (Green 1984). The effect of variation in the weather on partridge chick survival is almost as great as that of the preferred insects (Potts 1986). Green (1984) found that cold conditions resulted in chicks being brooded for longer periods, especially if it was also wet, thus the time available for foraging was reduced and became more critical. This would be particularly crucial in areas where invertebrates were initially not as plentiful. Low temperatures also render invertebrates less active (Varley et al. 1973). As feeding is largely by visual cues (Burton 1974, Metcalfe 1985) invertebrate inactivity lowers food availability (Avery & Krebs 1984). Hence in 1986, a cold, wet spring, the growth rates of lapwing chicks were significantly reduced relative to 1985 and 1987. Wet conditions, with comparatively warmer temperatures, as found in 1987, keep earthworms active (Nordstrom 1975), relatively near to the surface (Gerard 1967, Rundgren 1975) and therefore, available to feeding chicks. Only in 1985, when conditions were drier, was there a significant difference in growth rates between chicks reared on unimproved and improved fields. Drying conditions provide less suitable feeding conditions for newly hatched chicks (Jackson & Jackson 1980) by reducing invertebrate surface activity (Potts 1986) and by making the ground too hard for sub-surface probing. Improved fields, being better drained, are more susceptible to drought than unimproved fields. Under conditions of drought, especially towards the end of the breeding season, food may become limiting with chick mortality increased through starvation or through having to move to alternative foraging areas (Baines, in prep.). Only under drought conditions does food appear to limit chick development and ultimately survival. Consequently, food availability was not an important factor limiting production.

Improved fields were managed much more intensively than unimproved. Harrowing and rolling were practised more on improved meadows than on unimproved. These activities cover the whole field surface, therefore all clutches may be destroyed. Pastures are usually only fertilized. The wheels of tractors and fertilizer spreaders do not cover all the land surface, therefore not all clutches are liable to be crushed. For this reason, loss of clutches is not an important factor limiting productivity on pastures. Most clutches were destroyed relatively early within the breeding season leaving sufficient time for clutches to be replaced. However, in improved meadows, rapid grass growth leads to conditions unsuitable for breeding lapwing, thus curtailing the breeding season on this habitat (Lister 1964). Hence, lower productivity on improved meadows is attributable to more intensive management resulting in more clutches lost to agricultural activities and the production of a faster growing grass sward that leaves insufficient time for replacement clutches to be laid.

The effect of predators on ground-nesting birds is well documented (Brykjedal 1980, Elliot 1985, Erikstad et al. 1982, Picozzi 1975, Potts 1986). Schrank (1974) found that waterfowl nesting within denser vegetation had higher hatching success. Jones and Hungerford (1972) and Dwernychuk and Boag (1972) showed that simulated duck clutches were afforded greater protection from predators by thicker vegetation, with egg loss being inversely correlated with the amount of overhead cover. Many wader species nest in open habitats with little or no vegetation cover and rely on egg crypticity. Skeel (1983) found that whimbrel Numenius phaeopus nesting in a hummock-bog area, with a complex and irregular habitat structure enhancing crypticity, lost fewer clutches to predators than those nesting on more uniform habitats which rendered clutches more conspicuous to predators. In this study, clutch predation was lower on unimproved pastures than on any other grassland type. Unimproved pastures have a greater vegetative and physical diversity than improved pastures. Tussock forming rushes and grasses along with several species of sedge, grass and moss combine with unvegetated areas to create a disruptive background mosaic. Physically, the topography is more undulating, often with an irregular surface due to the presence of hummocks. Within this habitat, clutches and incubating birds tend to be less obvious to predators. Conversely, improved pastures tend to be more uniform, the vegetation is more homogeneous and lacks the structural diversity to be found in unimproved pastures. The vegetation does not have a disruptive effect on nest detection, and eggs are more conspicuous to aerial predators, hence predation is greater. This has been clearly supported by the experimental study on predation of clutches, with approximately twice as many clutches on improved pastures being taken by predators as on adjacent unimproved fields.

Higher densities of lapwing were found in unimproved pastures, 54 pairs/100ha, than on improved pastures, 14 pairs/100ha (Baines, in press). Higher densities may give more effective protection from predators through joint efforts in detecting and chasing a predator (Goransson _et al_. 1975, Skeel 1983) but Elliot (1985) found that the rate of predation of lapwing clutches was similar at all nesting densities. The experimental study demonstrated the importance of other lapwings in the same field as an important factor in reducing egg predation. After one day, approximately six times more clutches were taken by predators in fields without breeding lapwing than in fields where breeding lapwing were present.

Reductions in mammalian predators resulted in increases in hatching success of ducks (Balser _et al_. 1968, Duebbert & Kantrud 1974, Duebbert & Lokemoen 1980). Reductions in avian predators, particularly corvids increased the hatching success of willow ptarmigan _Lagopus lagopus_ and black grouse _Lyrurus tetrix_ (Parker 1984) and partridge _Perdix perdix_ (Potts 1986). Myrberget (1972) suggested that corvid predation on willow ptarmigan eggs may lead to reduced numbers. In this study, clutch predation on improved areas, chiefly by corvids, resulted in insufficient fledgling production to maintain the population at existing levels and has probably been largely responsible for the 63% reduction in lapwing densities on improved pastures.

CHAPTER 6 CHANGES IN THE SPECIES COMPOSITION OF THE INVERTEBRATE FAUNA ASSOCIATED WITH GRASSLAND IMPROVEMENT

METHODS

i)Sampling

Sampling methods are descibed in chapter 5.

ii)Soil moisture, organic content, pH and water-tables.

In April 1986, four 5cm diameter soil cores were taken to a depth of 15cm in 40 unimproved and 30 improved fields to determine soil moisture and soil organic content. The cores were combined 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 furnace at 450°C for four hours and subsequently reweighed. This loss of weight represented the organic content of the soil. Small sub-samples of the cores were mixed with distilled water to determine the soil pH.

Data on the water-tables of 11 improved fields, which had been drained, and 11 adjacent unimproved fields, which had not been drained, were collected between May and July 1985. Within each field, a hole of 7.5cm diameter was drilled into the soil to either bedrock, or, if bedrock was not reached, one metre, using an auger. The depth of the water column below ground level was measured every 14 days. The values of each 14 days were combined to give monthly water table depths.

iii)Species identification and nomenclature.

Tipulids from 15 sites sampled in 1986 were identified according to Coe, Freeman and Mattingly (1950) with nomenclature following Kloet and Hincks (1945). Spiders collected from 12 sites in 1985 and 21 sites in 1986 were identified according to Locket and Millidge (1951,1953) and Locket, Millidge and Merrett (1974), with nomenclature following Roberts (1985,1987). Carabid beetles collected from 8 sites in 1985 were identified according to Lindroth (1974), the nomenclature following Kloet and Hincks (1970). Earthworms were not identified to species.

iv)Classification and Ordination of the sites

Sites were classified according to pitfall trap data collected for all invertebrate taxa and for species of spider using two-way indicator species analysis (TWINSPAN) (Hill 1979a). TWINSPAN is a divisive polythetic method of classification based on the ordination method of reciprocal averaging (Hill 1973, 1974). It was used in preference to agglomerative methods as it uses the overall structure of the data at the outset and as a result higher levels of hierarchy are relatively insensitive to the details of the clustering at the lower end. TWINSPAN classifies both samples and species and constructs ordered two-way tables to exhibit the relationship between them. To account for differing numerical abundance five levels of pseudospecies were assigned (Hill *et al.* 1975). Ordination of the classified sites was carried out by detrended correspondence analysis (DECORANA) (Hill 1979b, Hill & Gauch 1980). DECORANA ordinated the sites along four axes, using abundance figures and species lists derived from pooling fortnightly trap catches from each site. All species/groups trapped were incorporated into the analysis.

v)Analysis of vegetation architecture.

To assess the importance of vegetation structure to the spiders, four 0.25m^2 quadrats were taken at random points within the area encompassed by each set of pitfall traps used in 1986. A presence/absence assessment of ten vegetation forms at three heights above the ground was made within each quadrat. The vegetation forms were as follows; *Juncus effusus*, *Juncus squarrosus*, other *Juncus* species, ericaceus shrubs, sedges *Carex*, tussock forming grasses, non-tussock forming grasses, herbs, moss, lichens and bare ground. Presence/absence of the above were noted at three height categories; <8cm, 8-20cm and >20cm. A score of one was given for each presence and zero for absence. The scores were summed to give an overall site total.

RESULTS

The improvement of upland grasslands resulted in several changes to the physical nature of the soil; soil moisture was reduced by 24% (t=6.40,df68,P<0.001) and soil organic content by 38% (t=6.62,df68,P<0.001), whereas pH was increased by 8% (t=2.86,df68,P<0.01)(Table 6.1). Land drainage during improvement lowered the water-table. By May, the median depth of the water-table was 22cm lower (59%) on improved than on unimproved sites, (T=0,P<0.02, Wilcoxon's test for matched pairs). The difference in water-tables was 35cm by July (T=0,P<0.001).

TABLE 6.1 The percentage moisture content, organic content and pH of unimproved and improved grassland soils sampled in April 1987.

		% soil moisture			% organic content			pH		
	n	$\bar{x}$		s.e.	$\bar{x}$		s.e.	$\bar{x}$		s.e.
Unimproved	40	49.1		1.5	22.5		1.2	5.0		0.1
			***			***			*	
Improved	30	37.2		1.1	13.9		0.5	5.4		0.1

* $P < 0.05$, *** $P < 0.001$

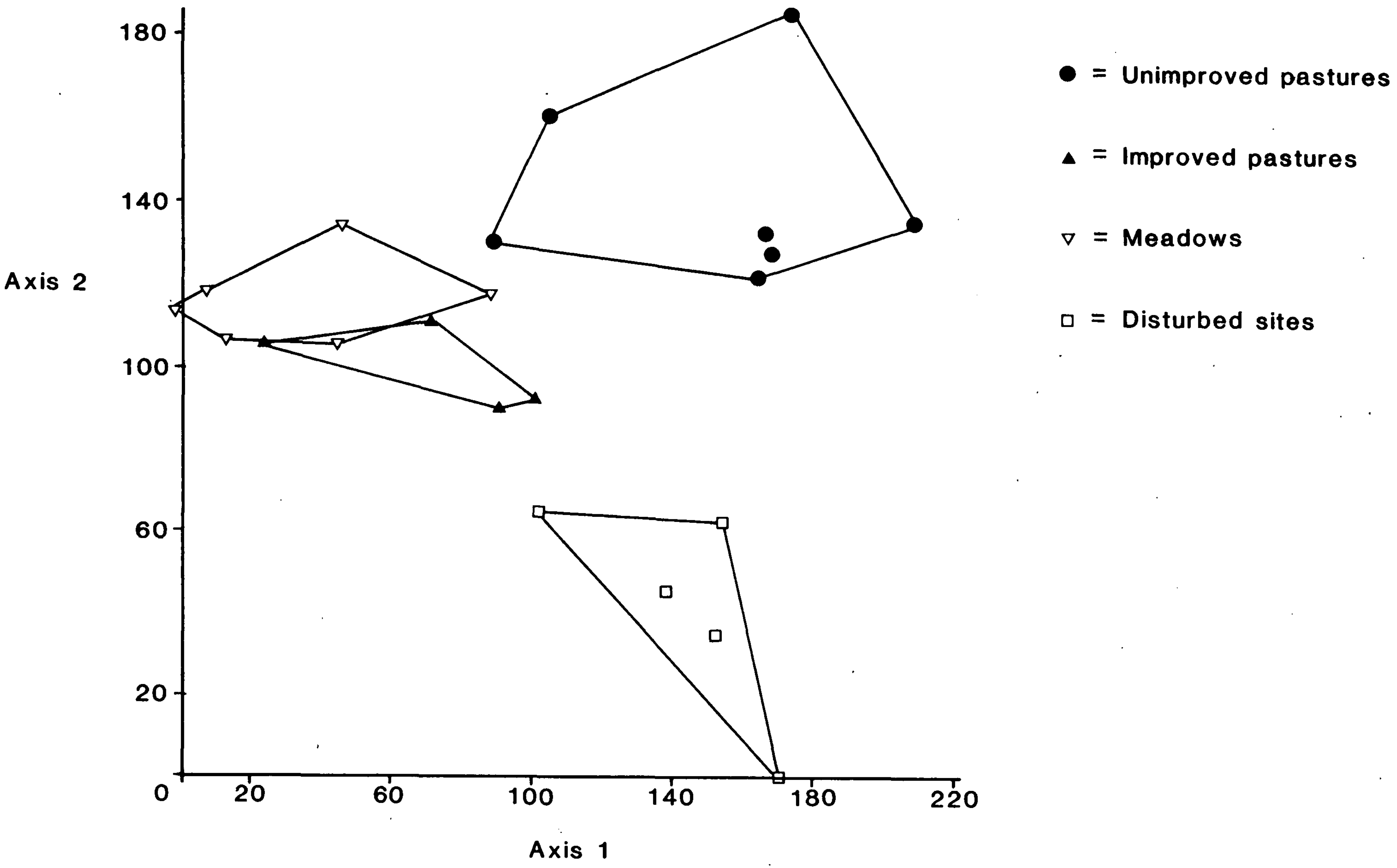
General invertebrate communities

Classification of sites according to their invertebrate faunas by TWINSPAN analysis to level 2 produced four communities reflective of management regimes; cereal and recently disturbed sites (ie. recently ploughed and reseeded), improved pastures, unimproved pastures and meadows. The classified sites were ordinated using DECORANA. Eigenvalues, giving an indication of the community variation explained by each axis were 0.362, 0.159, 0.063 and 0.036, for the first to fourth axes respectively. Most of the accountable variation lay in axes 1 and 2. These axes are represented graphically (Fig. 6.1).

Earthworms

Improvement resulted in significant increases in both the density and biomass of earthworms. A mean of 107 worms $/m^2$ were extracted from unimproved fields, whereas on improved fields, the corresponding density was 235 worms $/m^2$, an increase of 120%. (t=4.38,df45,$P<0.001$)(Table 6.2). Earthworm biomass increased by 146%,(t=3.93,df45,$P<0.001$), and there was little overall difference in worm size between the two field types. Earthworm density and biomass were negatively correlated with soil organic content and soil moisture, biomass showed a better correlation with soil organic content (r=-0.52,df=45,$P<0.001$)(Fig. 6.2) and soil moisture (r=-0.59,df=41,$P<0.001$) than density.

FIGURE 6.1. DECORANA ordination plot (Axis 1 v Axis 2) of 21 upland grassland sites and 2 cereal sites sampled in 1986 according to their invertebrate faunas. Polygons enclose all sites within each TWINSPAN group. Disturbed sites are those which have been recently ploughed and include cereal fields and reseeded grassland.



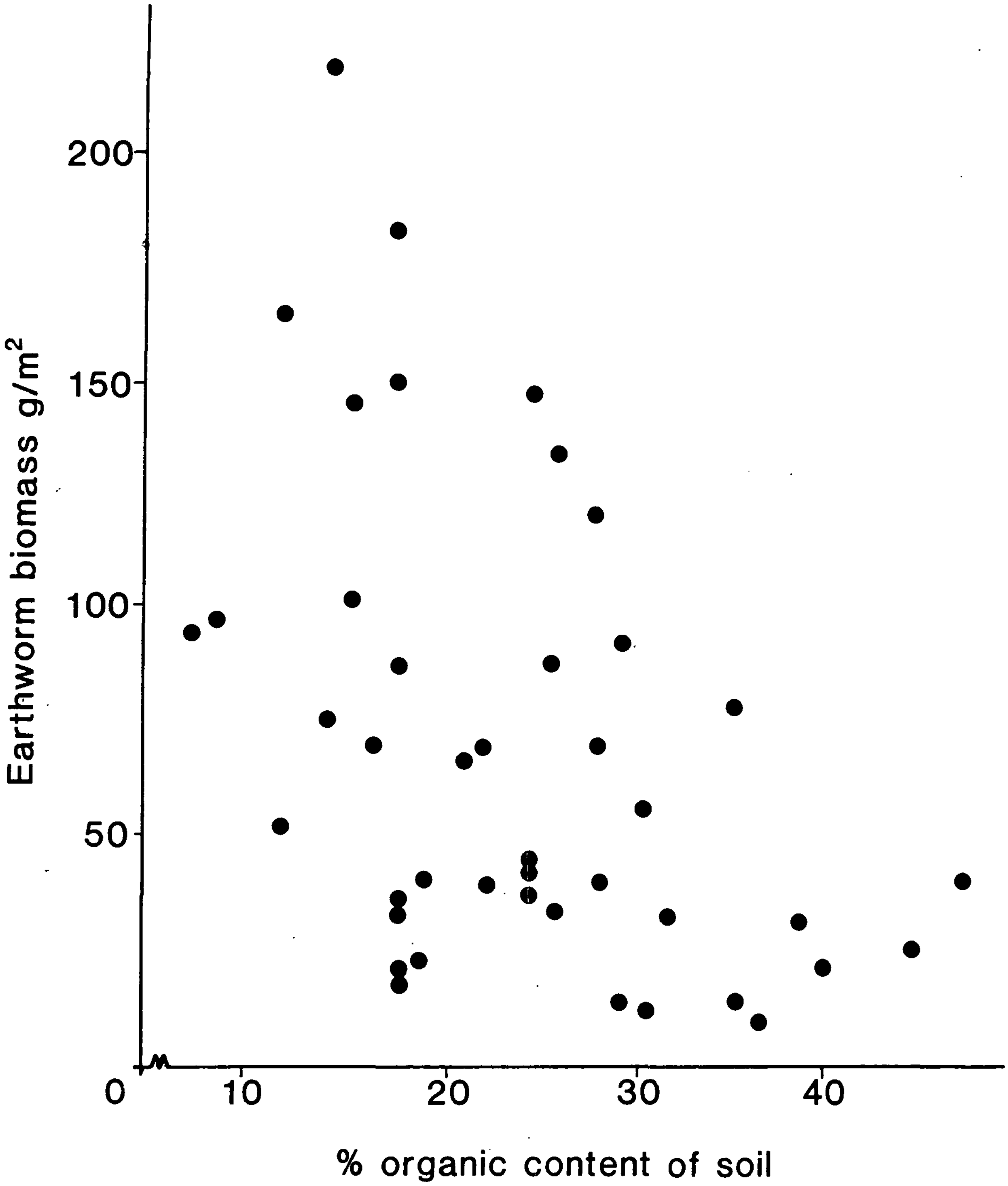
180
140
100
60
20
0
Axis 2
20
60
100
140
180
220
Axis 1
● = Unimproved pastures
▲ = Improved pastures
▽ = Meadows
□ = Disturbed sites

TABLE 6.2 The densities (no./m²) and biomass (g/m², wet weight) of earthworms on unimproved and improved grassland sampled by formaldehyde extraction in April 1987.

	density			biomass		
	(n)	mean	s.e.	(n)	mean	s.e.
Unimproved	(21)	107	15	(21)	41	8
		***			***	
Improved	(26)	235	25	(26)	101	13

*** $P < 0.001$

FIGURE 6.2. The relationship between soil organic content and earthworm biomass for 47 upland grassland sites sampled in April 1987 ($r=-0.52$, d.f.=45, $P<0.0001$).


Earthworm biomass g/m²
200
150
100
50
0
10
20
30
40
% organic content of soil

Tipulidae

There was no significant difference in the density of tipulid larvae between unimproved and improved grassland, with a mean of 26 larvae /m^2on unimproved, compared to 23 /m^2on improved (Table 6.3). On pastures, larvae occurred at a density of 36 /m^2, significantly higher than the mean of 13 larvae /m^2recorded from meadows (t=3.40,df21,P<0.01).

Although improvement did not affect the density of tipulid larvae there was a significant reduction in species richness with a mean of 6.2 species per unimproved site, including adult flies, compared to 1.7 species per improved site (t=3.63,df13,P<0.01). Considering all sites, 16 species were found on unimproved fields, whereas only 6 species were found on their improved counterparts (Table 6.4). Only Tipula paludosa and Nephrotoma appendiculata were represented by more than five animals on improved grassland. T. paludosa was the most abundant species on both unimproved grassland, where it formed 40% of the catch, and on improved grassland, where 84% of the tipulids caught were T. paludosa, a significantly higher proportion than on unimproved grassland (X^2 =126,d.f.=1,P<0.001). The proportion of tipulids caught that were T. paludosa was negatively correlated with soil moisture content (r=-0.73,df=10,P<0.01) (Fig. 6.3). N. appendiculata was only found on improved grassland. The proportion of Tipula pagana, the larvae of which feed on moss, was significantly reduced on improved fields relative to unimproved (X^2=39.1,d.f.=1,P<0.001), whereas Molophilus spp. Erioptera trivialis, E. lutea, E. diuturna, Tipula fusca, T. luna, T. oleracea were all absent from improved fields.

The number of cranefly species per site was positively correlated with soil moisture content (r=0.76,df11,P<0.01)(Fig. 6.4).

TABLE 6.3 The densities of tipulid larvae per m^2 sampled by salt extraction on different grassland types in April/May 1987.
(n = no. of fields sampled)

	Pastures			Meadows		
	n	mean	s.e.	n	mean	s.e.
Unimproved	(6)	42.2	5.6 ***	(7)	11.7	5.1
Improved	(6)	29.0	9.7	(4)	14.5	5.5
Totals	(12)	35.6	5.7 **	(11)	12.7	3.6

** $P < 0.01$, *** $P < 0.001$

TABLE 6.4 The species composition of the Tipulidae caught in pitfall traps on unimproved and improved grassland in 1986.

	Unimproved (n = 523 animals)		Improved (n = 238 animals)	
	no. caught	% of total	no. caught	% of total
Tipula paludosa	210	40	200	84
Tipula pagana	89	17	2	1
Molophilus spp.	47	9	0	0
Erioptera trivialis	46	9	0	0
Tipula fusca	38	7	0	0
Tipula varipennis	23	4	3	1
Trichyphona immaculata	18	3	2	1
Tipula oleracea	17	3	0	0
Erioptera lutea	10	2	0	0
Nephrotoma appendiculata	0	0	26	11
Nephrotoma maculata	0	0	5	2
Others	25	6	0	0

Six other species were found on unimproved grassland comprising 1% or less of the total catch: Dicranomyia modesta, Erioptera diutarna, Limnophila neigeni, L. pulchella, Pilaria nemoralis and Tipula luna.

FIGURE 6.3. The relationship between percentage soil moisture and the proportion of the Tipulidae comprised by *Tipula paludosa* sampled by pitfall traps at 13 upland grassland sites in 1986 ($r=-0.74$, d.f.$=11$, $P<0.01$).

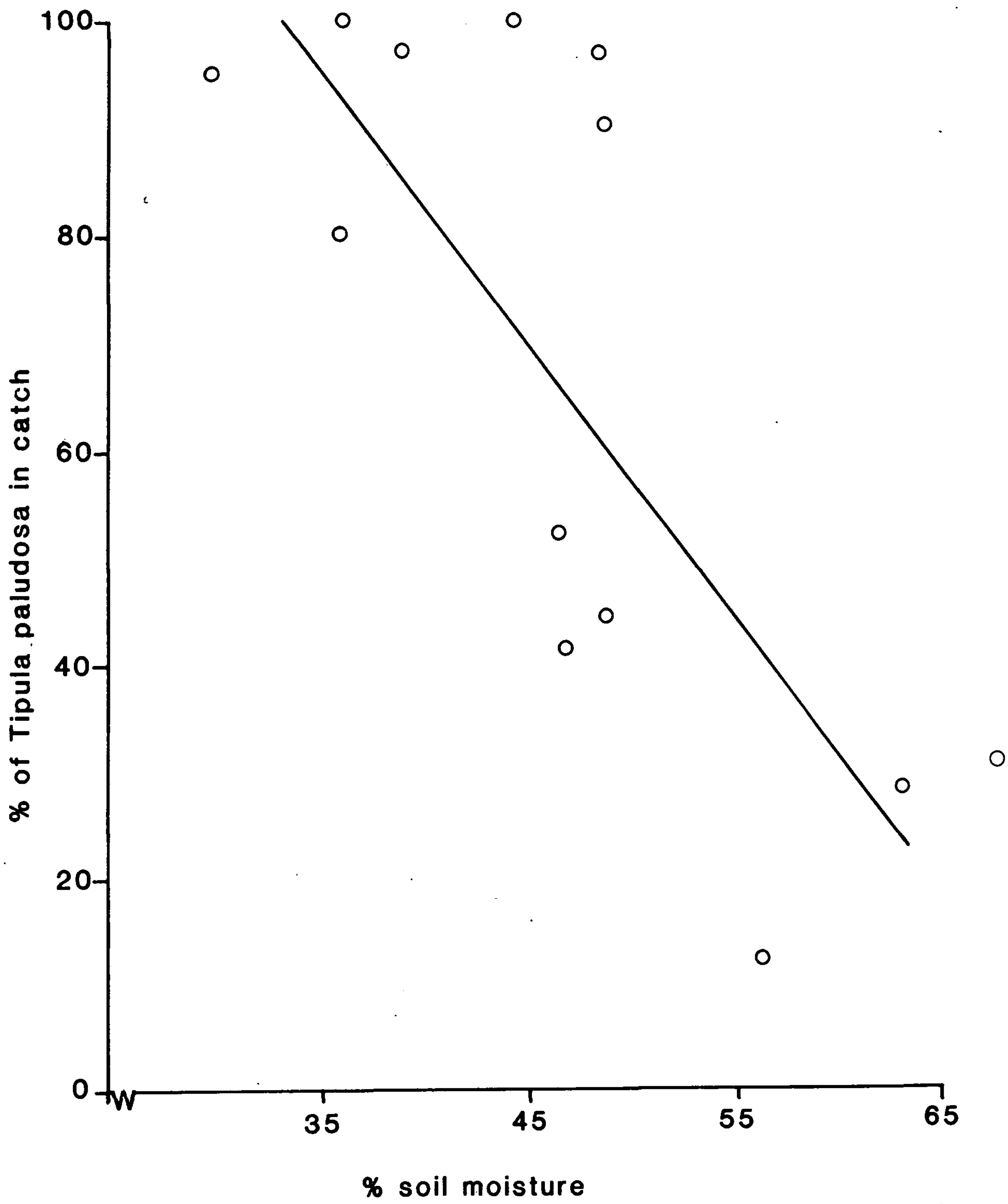
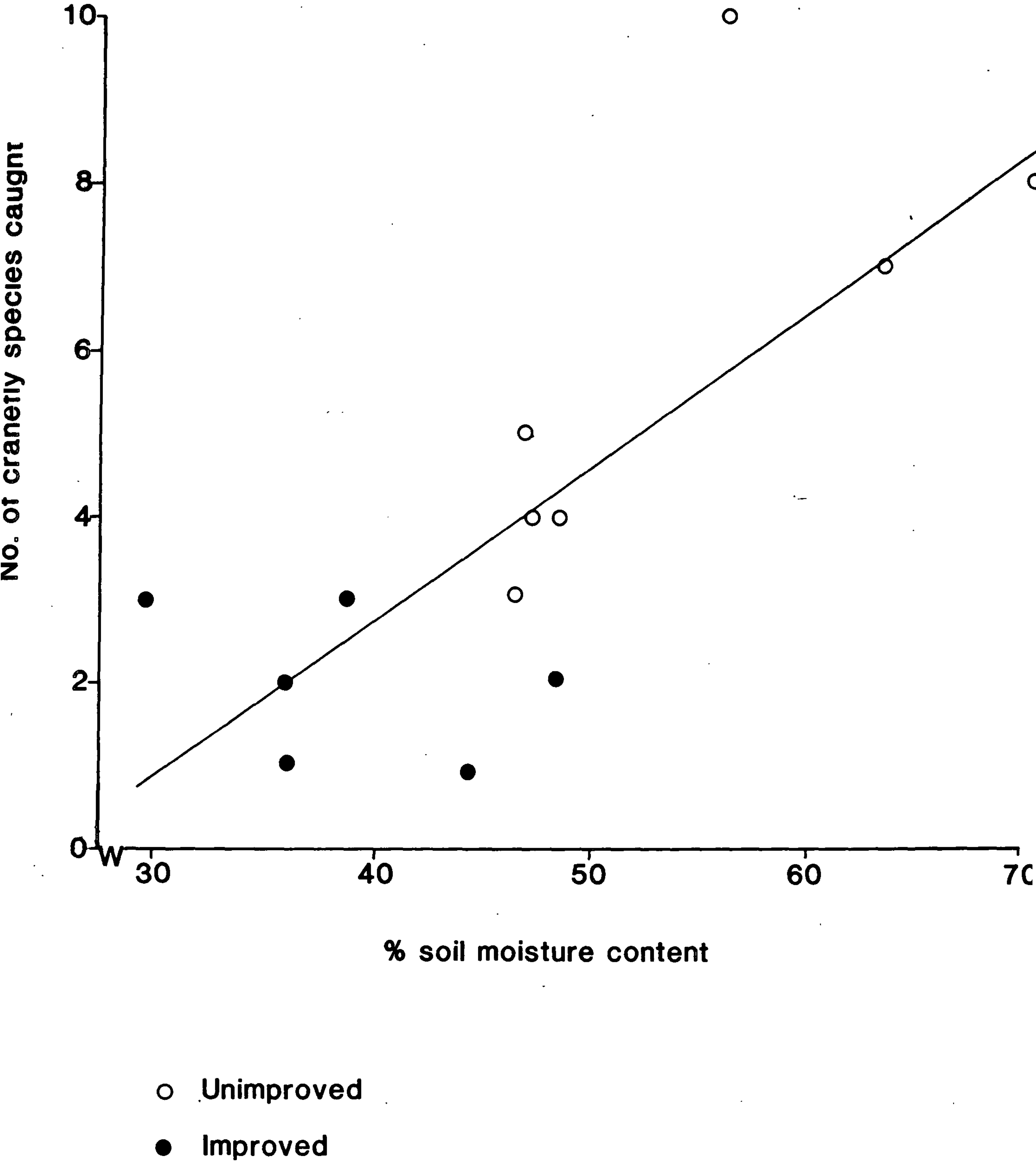

100
80
60
40
20
0
W
35
45
55
65
% of Tipula paludosa in catch
% soil moisture

FIGURE 6.4. The relationship between the number of species of cranefly (Tipulidae) caught in pitfall traps and the percentage soil moisture at 13 upland grassland sites in 1986 ($r=+0.76$, d.f.$=11$, $P<0.01$).


10
8
6
4
2
0
W
30
40
50
60
7
No. of cranefly species caught
% soil moisture content
○ Unimproved
● Improved

Araneae

Classification of the spider catches to level 1 by TWINSPAN split sites into those which had been improved and those which were unimproved. Beyond level 1 sites could not be conveniently split further according to land management and the spider fauna of improved pastures was not discernable from that of meadows, either unimproved or improved. The classified sites were ordinated by DECORANA. Eigenvalues for axes 1 to 4 were 0.610, 0.286, 0.054 and 0.030. Most of the variation was represented in axes 1 and 2 and these are presented graphically in Fig. 6.5.

In both 1985 and 1986, significantly more species of spider were found on unimproved than on improved grassland (t=3.76,df10,P<0.01 and t=5.76,df19,P<0.001 respectively)(Table 6.5). More species were found in 1985 than in 1986 with an average of 28 and 19 species respectively on unimproved fields and 23 and 10 species respectively on improved fields. Species diversity, using the Margalef diversity index (Margalef 1951) was significantly higher on unimproved grassland than on improved grassland in each of the two years (t=4.15,df10,P<0.002 and t=4.92,df19,P<0.001 respectively)

The relative similarity of sites in terms of spider species composition was measured in 1986 using the Sorensen quotient of similarity (Sorensen 1948) (QS=2j/a+b, where 'a' is the number of species caught on site 'A' and 'b' is the number of species caught on site 'B' and 'j' represents the number of joint occurences). The QS for meadows was 0.68, significantly higher than the 0.60 for unimproved pastures (t=2.22,df54,P<0.05) or the 0.58 for improved pastures (t=2.78,df36,P<0.01). Thus the species composition of meadows varied less than than that of pastures.

FIGURE 6.5. DECORANA ordination plot (Axis 1 v Axis 2) of 21 upland grassland sites sampled in 1986 according to their spider faunas. Polygons enclose all sites within each TWINSPAN group.

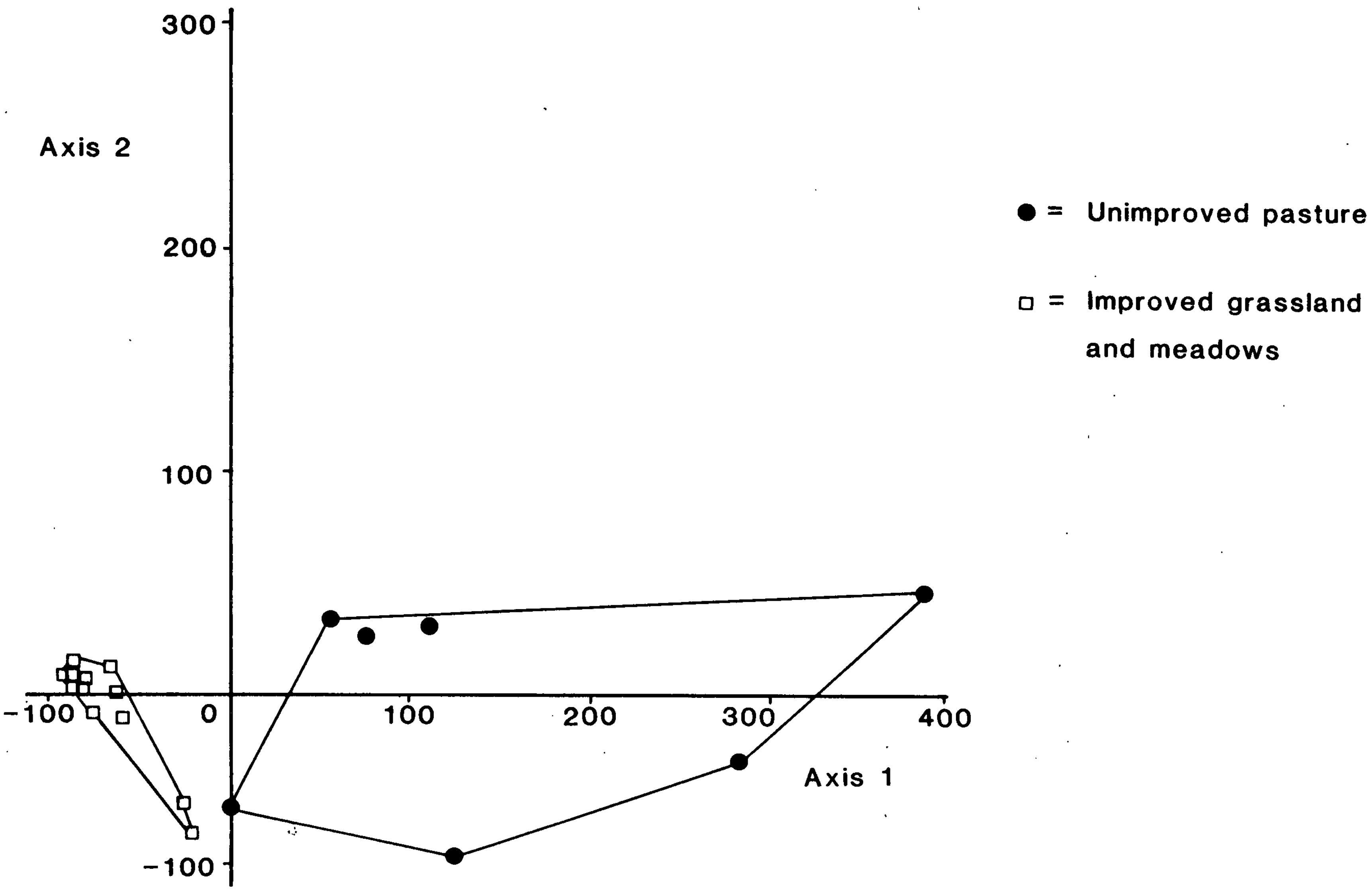

Axis 2
300
200
100
0
−100
100
200
300
400
Axis 1
● = Unimproved pasture
□ = Improved grassland and meadows

TABLE 6.5 The species richness (mean no. of species) and the diversity (Margalef 1951) of the spider fauna of unimproved and improved grassland in 1985 and 1986.

	1985					1986				
		no. of species.		diversity.			no. of species.		diversity.	
	n	$\bar{x}$	s.e.	$\bar{x}$	s.e.	n	$\bar{x}$	s.e.	$\bar{x}$	s.e.
Unimproved	8	28.1	1.1	3.9	0.2	8	19.1	1.3	3.3	0.3
		**		***			***		***	
Improved	4	22.5	1.0	2.8	0.2	13	10.0	0.9	1.6	0.1

** $P < 0.01$, *** $P < 0.001$

Over the two years 1985 and 1986, 71 species representing 9 families were caught on unimproved grassland, whereas only 41 species from five families were caught on improved grassland (Table 6.6). Linyphiidae were the most numerous family and constituted 76% of the species found on unimproved grassland (n=54) and 71% of those on improved grassland (n=29). The only other family which made up more than 5% of the species on either grassland type were the Lycosidae with 10% on unimproved grassland and 17% on improved grassland (n=7 species on each habitat type).

The numerical composition of the spider fauna was significantly different between unimproved and improved grassland (X^2 =963,df=5,P<0.001). On improved grassland, 94% of the spiders caught were linyphiids, a significantly higher proportion than on unimproved grassland where 85% of the spiders were linyphiids (X^2=642,df=1,P<0.001). Alternatively, lycosids represented 11% of the spider fauna on unimproved areas, but only 2% on improved grassland (X^2=897,df=1,P<0.001). In 1985, unimproved sites had on average 21 species of Linyphiidae, whereas only 16 species were found on improved sites (t=3.38,df10,P<0.01) (Table 6.7). In 1986, fewer linyphiids were caught, but significantly more species were still found on unimproved fields, with 13 species as opposed to 8 species on improved fields (t=4.20,df19,P<0.001). There was no significant difference in the number of species of Lycosidae on unimproved or improved grassland in 1985, but in 1986 an average of 4 species were found on unimproved fields compared to 1.5 species on improved fields (t=5.71,df19,P<0.001).

TABLE 6.6 The species and numerical composition of the spider fauna on unimproved and improved grassland in 1985 and 1986.

	1985				1986				TOTAL			
	% species		% individuals		% species		% individuals		% species		% individuals	
	Unimp	Imp	Unimp	Imp	Unimp	Imp	Unimp	Imp	Unimp	Imp	Uimp	Imp
	(n=59)	(n=41)	(n=12232)	(n=8327)	(n=48)	(n=26)	(n=3899)	(n=3715)	(n=71)	(n=41)	(n=16131)	(n=12042)
Dysderidae	1.7	0	+	0	0	0	0	0	1.4	0	+	0
Amaurobiidae	1.7	0	+	0	0	0	0	0	1.4	0	+	0
Gnaphosidae	3.4	0	+	0	2.1	0	0.5	0	2.8	0	0.1	0
Thomisidae	1.7	4.9	+	0.2	4.2	0	0.9	0	2.8	4.9	0.3	0.1
Lycosidae	12.1	17.1	6.3	2.4	14.6	19.2	17.7	0.6	9.9	17.1	11.0	2.2
Aglenidae	1.7	0	+	0	0	3.8	0	+	1.4	2.4	+	+
Theridiidae	1.7	2.4	+	0	2.1	0	0.3	0	1.4	0	0.1	0
Tetragnathidae	3.4	2.4	2.6	5.0	4.2	7.7	4.4	0.5	2.8	4.9	3.2	3.5
Linyphiidae	75.9	73.2	90.9	92.5	72.9	69.2	76.3	98.9	76.1	70.7	85.2	94.3

+ = < 0.1%

TABLE 6.7 The mean number of species of Linyphiidae and Lycosidae caught on unimproved and improved grassland in 1985 and 1986.

	1985					1986				
		Linyphiidae		Lycosidae			Linyphiidae		Lycosidae	
	n	$\bar{x}$	s.e.	$\bar{x}$	s.e.	n	$\bar{x}$	s.e.	$\bar{x}$	s.e.
Unimproved grassland	8	21.1	1.1	5.1	0.3	8	12.6	1.1	3.8	0.3
		**					***		***	
Improved grassland	4	16.3	3.9	4.8	0.5	13	7.8	0.5	1.6	0.3

** $P < 0.01$, *** $P < 0.001$

Spiders from the families Amaurobiidae, Dysderidae, Gnaphosidae and Theridiidae were not found after grassland improvement. Overall, 42% of the species found on unimproved grassland were confined to such areas, whereas all species found on improved grassland were also found on unimproved grassland (Table 6.8).

The species richness of a site was positively correlated with the complexity of vegetation structure or vegetation architecture ($r=0.82, df=19, P<0.001$) (Fig. 6.6). Both the number of species of Linyphiidae and the number of species of non-Linyphiidae were positively correlated with a diverse vegetation architecture ($r=0.81, df=19, P<0.001$ and $r=0.73, df=19, P<0.001$ respectively). The diversity of vegetation architecture was positively correlated with soil moisture and soil organic content ($r=0.78, df=17, P<0.001$ and $r=0.81, df=17, P<0.001$ respectively). Therefore site species richness was also positively correlated with these two environmental parameters.

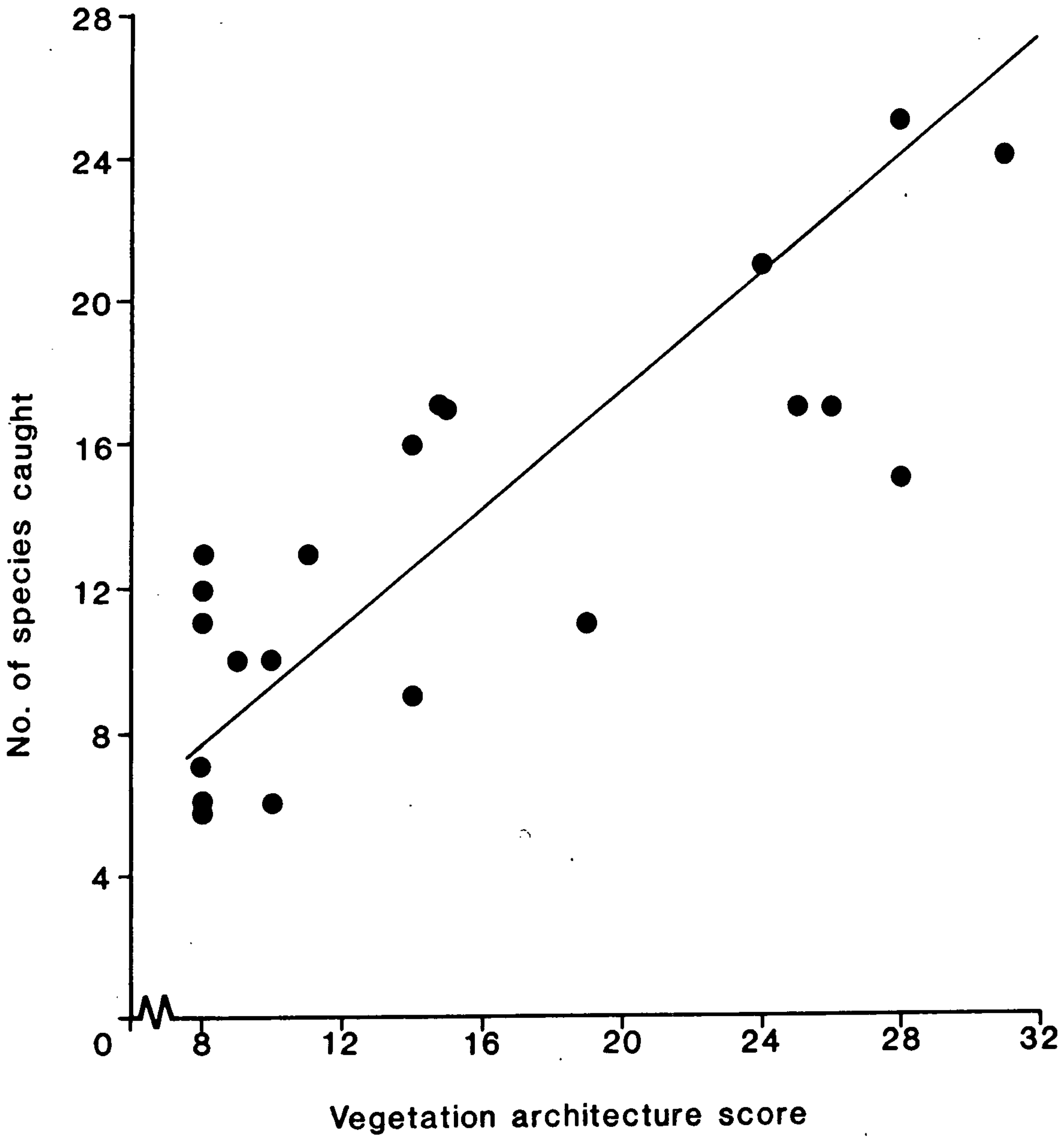
<u>Carabidae</u>

There was no change in the number of carabid beetles caught following land improvement, but biomass decreased by 70% (see Table 5.2), indicating that a greater proportion of smaller species was present on improved areas. Species composition of the carabid community was only assessed for eight sites; four unimproved and four improved, thus detailed statistical analysis was not possible. Both the mean number of species caught and the species diversity tended to be higher for unimproved sites, with a mean of 16 species and 13 species, and a diversity of 2.8 and 2.3 on unimproved and improved sites respectively (Table 6.9).

TABLE 6.8 The number of species of spider found exclusive to unimproved or improved grassland in 1985 and 1986.

	1985 (n=63 spp)		1986 (n=49 spp)		Total (n=71 spp)	
	Unimp	Imp	Unimp	Imp	Unimp	Imp
Lycosidae	1	0	2	0	1	0
Linyphiidae	24	2	17	0	23	0
Others	8	1	6	1	6	0
Total	33 (52%)	3 (5%)	25 (52%)	1 (2%)	30 (42%)	0

FIGURE 6.6. The relationship between the complexity of vegetation structure and the number of species of spider caught in pitfall traps at 21 upland grassland sites between March and October 1986 (r=0.82,d.f.=19,P<0.001).



No. of species caught
28
24
20
16
12
8
4
0
8
12
16
20
24
28
32
Vegetation architecture score

TABLE 6.9 The species richness and diversity of the carabid fauna of unimproved and improved grassland in 1985, (n=4 for each grassland type).

	Unimp. grassland		Imp. grassland	
	$\bar{x}$	range	$\bar{x}$	range
No. of species	16.3	(14-18)	12.8	(12-15)
Species diversity	2.8	(2.0-3.2)	2.3	(2.0-3.0)

The following species, *Pterostichus nigrita*, *P. diligens*, *Elaphrus riparius*, *Patrobus assimilis* and *P. atrorufus*, assigned typical wet habitat species by Houston (1970) and Butterfield and Coulson (1983), constituted 54% of the carabid fauna of unimproved grassland, a significantly higher proportion than the 33% on improved grassland (X^2=88.8,df=1,$P<0.001$). Representatives from typically dry grassland communities were either absent or present in low numbers, as although four of the sites sampled had been improved, they still tended to be quite wet.

Other Coleoptera

Helophoridae were the most numerous beetle on both grassland types. On improved grassland, they were approximately five times more numerous than the next most frequently caught group, the Carabidae, whereas on unimproved grassland, numbers of helophorids were in the same order of magnitude as carabids. When the composition of the beetle fauna on unimproved and improved grasslands were compared, Helophoridae were omitted due to their abundance swamping the importance of less frequently caught families as proportions of the catch composition.

Grassland improvement resulted in a significant change in the composition of the beetle fauna ($X^2=406, df=7, P<0.001$) (Table 6.10). Staphylinidae and Carabidae together comprised 83% and 87% of the beetles caught on unimproved and improved grassland respectively. Carabidae formed a significantly higher proportion of the fauna of unimproved than of improved grassland ($X^2=34.5, df=1, P<0.001$), whereas, the percentage of staphylinids in the catch was significantly higher on improved areas ($X^2=76.1, df=1, P<0.001$). The only other beetle family contributing to over 5% of the fauna was the Parnidae, with 11% of beetles on unimproved grassland belonging to this group, a significantly higher proportion than on improved grassland ($X^2=211, df=1, P<0.001$). On improved land, Curculionidae (4%), Chrysomelidae (4%) and Scarabaeidae (3%) all comprised a significantly higher proportion of the beetle community than on corresponding unimproved land ($X^2=8.2, df=1, P<0.01$, $X^2=65.2, df=1, P<0.001$ and $X^2=46.1, df=1, P<0.001$ respectively).

TABLE 6.10 Composition of the Coleoptera fauna of unimproved and improved grassland as sampled by pitfall traps (March-October 1986). Helophoridae have been excluded from the analysis.

	Unimproved (n=2490 beetles)			Improved (n=2846 beetles)	
	n	%		n	%
Staphylinidae	773	31.0	***	1214	42.7
Curculionidae	63	2.5	**	113	4.0
Scarabaeidae	12	0.5	***	86	3.0
Sphaeridiidae	5	0.2		4	0.1
Carabidae	1302	52.3	***	1258	44.2
Chrysomelidae	11	0.4	***	106	3.7
Elateridae	25	1.0		16	0.6
Silphidae	2	0.1		0	0
Parnidae	276	11.1	***	45	1.6
Byrrhidae	19	0.8		0	0
Histeridae	2	0.1		3	0.1

** $P < 0.01$, *** $P < 0.001$

DISCUSSION

The effects of improvement of upland grassland on the density, biomass and species diversity of the major invertebrate groups are summarized see table 5.2. Whilst the density and biomass of earthworms increased by 120% and 146% respectively following improvement, spider numbers and biomass were reduced by 39% and 65% respectively. There was no change in the numbers of carabid beetles caught but biomass decreased by 70%. Neither the density or the biomass of tipulids were affected. Improvement reduced the mean species diversity of spiders by 46%, carabid beetles by 8% and tipulids by 62%.

Earthworm densities have been shown to be limited by food availability (Svendsen 1957, Boyd 1957,1958, Curry 1976, Edwards & Lofty 1977), soil moisture (Olsen 1928, Madge 1969, Edwards & Lofty 1977) and pH (Edwards & Lofty 1975, Standen 1984). Applications of dung increased densities of earthworms both on peat soils (Svendsen 1957) and on mineral soils, with up to a three fold increase on pasture plots and a fifteen fold increase on arable plots receiving 3.5 tonnes of manure /ha (Edwards & Lofty 1977). In addition, Bengston (1975) found that in Iceland, numbers of deep burrowing species were positively affected by well drained, cultivated soils supplied with manure and fertilizers.

The improvement of upland grassland resulted in more fertile soils due to increased inorganic fertilization, whilst increased aeration and reduced waterlogging following drainage allowed greater breakdown of accumulated organic layers (Coulson & Butterfield 1978). The organic content of the soil was reduced by 38% and as a result of increased microbial breakdown, more food is made available to earthworms.

Mean soil pH was significantly raised from 5.0 on unimproved to 5.4 on improved land due to the breakdown of acidic humus layers in drier, more aerobic conditions, and by the direct application of lime to the grassland. Thus, improvement raised soil pH into the optimum pH range stated for most worms of 5.0-6.0 (Edwards & Lofty 1977). Improvement by land drainage resulted in a mean April soil moisture of 37%, 24% lower than on equivalent undrained areas, and a July water-table 40% lower. Earthworms favour soils which are not waterlogged and improvement brought soil moisture nearer the 12-30% moisture range found by Olsen (1928) to be favoured by most earthworms.

The density of tipulid larvae did not change following grassland improvement, but there was a marked reduction in the number of species present from an average of 6 species on unimproved fields to a fauna dominated solely by *Tipula paludosa* on improved fields. This is in agreement with Coulson (1959), who found that Tipulidae were most abundant in wet habitats, with relatively few species in better drained areas. Land drainage, with resultant moisture loss and a lowered water-table appear responsible for the reduction in species richness on improved areas.

The larvae of *Tipula pagana* feed on mosses (Coulson pers. comm.) and the loss of this species, and possibly others, from improved areas may be due to a loss of specific food plants following drainage. The affinity of some larvae to specific food plants is questionable. Freeman (1967) showed in food trials, that there were no differences in food selection between carr, woodland soil and moss-dwelling tipulids. It is unlikely that inter- or intra-specific competition for food is an important component in population regulation due to a wide range of food items consumed.

An alternative explanation for the reduced number of species of Tipulidae on improved areas is that due to reduced moisture from better drainage, sites may be no longer suitable for successful oviposition and that for species with low desiccation tolerances, excessive mortality may occur in the egg or first instar stages.

Decreased site wetness and more intensive management regimes reducing the complexity of vegetation structure are the major factors accounting for the reduced number of species and reduced abundance of spiders on improved grassland relative to unimproved. Several species of lycosids, in particular *Pardosa pullata* and *Pirata piraticus* (Norgaard 1951, Cherrett 1964, Coulson & Butterfield 1986) and *Pardosa amentata* (Rushton *et al*. 1987) are very sensitive to low humidities. The proportion of lycosids in the spider community of improved grassland was only a fifth of that on unimproved sites. It would appear that land improvement, in reducing humidity by lowering the water-table and changing the vegetation composition has rendered such habitats less favourable to several species of Lycosidae.

The architecture of the plant community and its associated microclimate probably constitutes one of the most important factors influencing the types of spider and their numerical abundance (Duffey 1962). The more complex the vegetation form, the greater the degree of possible stratification and hence physical niches (Allee *et al*. 1949, Cherrett 1964, Duffy 1978). This is particularly relevant to the Linyphiidae, which, in this study constituted 76% of the spider fauna, due to their reliance on structural components of the vegetation for supporting webs. Overall, 46% fewer species of linyphiid were found on improved fields where the complexity of the vegetation architecture had been reduced by reseeding and the application of inorganic fertilizer. Sward uniformity was enhanced further by intensive sheep grazing. Grazing reduces the numerical abundance of spiders by 44% on upland limestone grassland (Cherrett 1964). Boyd (1960) found a similar reduction of 37% on machair grassland in Tiree.

CHAPTER 7 COMPARATIVE AND SEASONAL ABUNDANCE OF INVERTEBRATES ON UNIMPROVED AND IMPROVED GRASSLAND

METHODS

The data presented are from pitfall trap catches made in 1986. Details of sampling procedure are given in chapter 5. Ten unimproved sites were sampled from March 15. Sampling was continued until July 21 at five of the sites and until October 24 at the five remaining sites. Similarly, of the eleven improved sites sampled, five sets of traps were in the field from March 15 to July 21 and six from March 15 to October 24. The traps were emptied every fourteen days.

The mean number of invertebrates /site and their biomass (dry weight) for the period March 15 to July 21 was calculated for eleven invertebrate groups or taxa by summing the fortnightly catches. The biomass of the catch was obtained by drying a sample at least 30 animals from up to four length classes (<4mm, 4-8mm, 9-16mm and >16mm) within each taxa to constant weight in a drying oven at 100 °C and weighing the animals to the nearest 0.1mg. Differences between invertebrate catches on unimproved and improved grassland were tested for significance using the Mann-Whitney U-test.

Seasonal distribution patterns were compared using data from March 15 to October 24. A conversion factor of 2.0 was applied to catches on unimproved sites sampled after July 21 and a similar value of 1.8 to improved sites to account for the fewer sites sampled later in the season. Catch data were represented as the number of animals caught per fourteen day period as a percentage of the total during the entire sampling period. The standard deviation (s.d.) of the mean percentage of animals caught in each fourteen day catch period over the whole catching season was calculated to illustrate the variation of catch size with season. A lower standard deviation represented less variation in catch size on different dates.

RESULTS

The invertebrates most commonly caught in pitfall traps, excluding Acarina and Collembola, were beetles (Coleoptera). Beetles comprised 44% of the fauna caught in pitfall traps. Over half of the beetles caught belonged to the Helophoridae, the remainder were chiefly Carabidae and Staphylinidae. Spiders (Araneae) made up 34% of the catch, of these, the vast majority were the web-spinning Linyphiidae with only relatively few Lycosidae and "others". Overall, 17% of the catch were Diptera . The most frequently caught dipterans were adult dung-flies (Scathophagidae) and craneflies (Tipulidae). Comparatively few representatives of the Lepidoptera, Opiliones, Mollusca or Hymenoptera were caught, and these, together with other miscellaneous invertebrate groups comprised the remaining 5% of the catch.

The mean number of spiders caught per site during the period March 15 - July 21 was 39% lower on improved than on unimproved grassland ($U=21.0$, $P<0.05$, Mann-Whitney U-test) and their biomass 65% lower ($U=4.0$, $P<0.001$)(Table 7.1). This difference was attributable to significantly fewer non-linyphiid spiders, both lycosids (97% fewer) and others (93% fewer), on improved fields ($U=0.5$, $P<0.001$ and $U=1.0$, $P<0.001$ respectively). There was no significant difference in either, the quantity, or the biomass of linyphiids caught between unimproved and improved grassland.

TABLE 7.1 The mean number and mean biomass of invertebrates caught in ten pitfall traps between 15 March and 21 July 1986 on each of ten unimproved grassland and eleven improved grassland sites. The differences between the two grassland types are expressed as the percentage changes following improvement. The significance of the differences were tested using the Mann-Whitney U-test.

	Mean number caught/site			Mean biomass (g)		
	Unimproved	Improved	% change	Unimproved	Improved	% change
ARANEAE						
Lycosidae	70	2	-97 ***	0.25	0.01	-96 ***
Linyphiidae	383	284	-26	0.22	0.15	-32
others	27	2	-93 ***	0.02	0.001	-95 ***
TOTAL	469	288	-39 *	0.48	0.17	-65 ***
COLEOPTERA						
Staphylinidae	61	103	+69	0.23	0.43	+87
Helophoridae	182	514	+182	0.16	0.62	+288
Carabidae	104	94	-10	2.19	0.65	-70 *
others	49	22	-53 *	0.15	0.21	+29
larvae	48	90	+88	0.43	0.66	+53
TOTAL	439	320	+87	3.17	2.46	-22
DIPTERA						
Tipulidae	13	3	-73	0.25	0.04	-84
others	152	281	+85	0.31	0.76	+145
TOTAL	165	284	+72	0.56	0.80	+43
MISC. GROUPS	60	5	-91 ***	0.15	0.01	-93 ***
TOTAL	113	1398	+23	4.40	3.44	-22

* $P < 0.05$, *** $P < 0.001$

Overall, there was no significant difference in the number or biomass of beetles caught between the two grassland types. Analysis to family level showed that improvement resulted in a 70% lower biomass of carabid beetles (U=18.0, $P<0.05$). Despite this appreciable difference in biomass, there was no significant difference in the number of carabids caught per site. This illustrates that improvement resulted in a change in species composition, with fewer larger species such as *Carabus violaceus*, *C. problematicus* and *Pterostichus nigrita* present after improvement, but a corresponding increase in smaller species.

Numbers of staphylinid and helophorid beetles tended to be higher on improved than on unimproved land, with increases of 69% and 182% respectively, but not significantly. The "other" beetles were 53% less numerous on improved grassland (U=17.0, $P<0.02$), but there was no significant difference in mean biomass. This was largely due to large numbers of relatively small beetles on unimproved fields, chiefly the wet-loving Parnidae, whereas larger species, belonging to the Scarabaeidae, were present on improved fields.

There was no significant difference between the numbers or biomass of adult Diptera caught on unimproved and improved grassland; Tipulidae tended to be more numerous on unimproved fields, whilst dung-flies (Scathophagidae) tended to be more commonly caught on improved fields, but neither trend was significant.

Other invertebrates, chiefly Mollusca, Diplopoda, Chilopoda, Opiliones and Hymenoptera, all decreased following improvement, and when combined for analysis, were 91% fewer on improved than on unimproved grassland (U=4.5, $P<0.001$) and had a biomass 93% less (U=9.0, $P<0.001$).

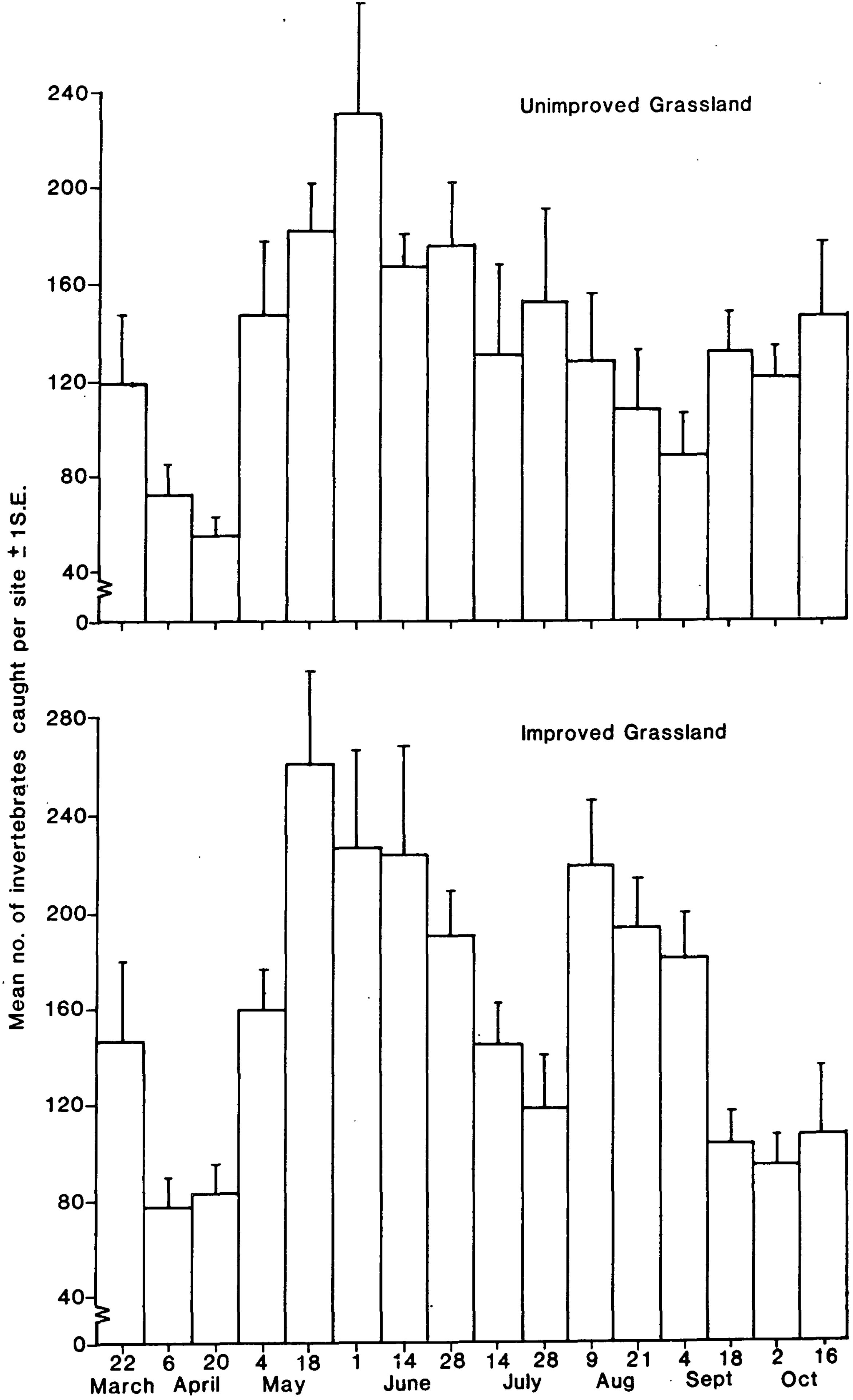
The seasonal distribution pattern of the total invertebrate catch in pitfall traps (excluding Acarina and Collembola) for unimproved and improved grassland is given in Figure 7.1. On both grassland types, peak catches were in May, although the maximum on improved land was in mid-May, two weeks earlier than on unimproved land. Peak catch sizes were similar, with an average of 230 invertebrates /10 pitfall traps per fourteen days on unimproved grassland and 260 invertebrates /10 traps on improved grassland.

Following the peak catch, the number of invertebrates caught on improved fields sharply declined to 118 per 10 traps before reaching a second peak in mid-August (218 animals /10 traps). No similar peak was found on unimproved grassland and consequently, over the six weeks comprising the peak, significantly more invertebrates were caught on improved than on unimproved grassland ($t=5.17$, d.f.=28, $P<0.001$). On unimproved grassland, catch size decreased more steadily than on improved grassland until September. In mid-September, there was a small, second peak in the number of invertebrates caught, (maximum of 146 animals /10 traps) which lasted until the end of the sampling period in October. During this period, significantly more animals were caught on unimproved than on improved grassland ($t=2.04$, d.f.=31, $P=0.05$). There was no difference in the total number of invertebrates caught over the whole sampling period between unimproved and improved grassland, with a mean of 2150 animals/10 traps and 2500 animals/10 traps respectively.

Of note is the period in April when particularly cold weather suppressed invertebrate activity and resulted in small pitfall catches. This emphasises that pitfall catches reflect invertebrate activity and not overall abundance.

The seasonal distribution of abundance patterns of five of the invertebrate groups sampled are presented in Figs. 7.2 to 7.4. The pattern of abundance of lycosid spiders was similar on both unimproved and improved grassland with peak catches from early June to mid-July (Table 7.2).

FIGURE 7.1. The mean number of invertebrates caught on ten unimproved and eleven improved grassland sites sampled between March and October 1986. Error bars indicate one standard error of the mean. Catches are based on ten pitfall traps per site.



Mean no. of invertebrates caught per site ± 1S.E.
Unimproved Grassland
240
200
160
120
80
40
0
Improved Grassland
280
240
200
160
120
80
40
0
22
6
20
4
18
1
14
28
14
28
9
21
4
18
2
16
March
April
May
June
July
Aug
Sept
Oct

TABLE 7.2 The peaks of abundance of nine groups of invertebrates sampled by pitfall traps on unimproved and improved grassland between 15 March and 4 October 1986. A peak is defined as a period when more than ten percent of the total catch for the study period were trapped within fourteen days. The standard deviation (s.d.) of the percentage of animals caught per fourteen day period over the whole catching period is presented as a measure of variation in the catch size with season.

	Unimproved grassland		Improved grassland	
	s.d.	peaks	s.d.	peaks
ARANEAE				
Lycosidae	6.5	Jun 07 - Jul 21	10.5	May 24 - Jul 21
		Sep 11 - Sep 25		Aug 28 - Sep 11
Linyphiidae	3.1	May 24 - Jun 21	4.6	Aug 02 - Sep 11
COLEOPTERA				
Staphylinidae	2.1	Oct 09 - Oct 24	6.3	Jun 07 - Jul 07
Helophoridae	6.7	Mar 15 - Mar 30	5.2	Mar 15 - Mar 30
		Apr 27 - Jun 07		Apr 27 - Jun 21
Carabidae	2.1	Sep 25 - Oct 09	3.6	Jun 07 - Jul 07
				Sep 25 - Oct 09
others	7.8	May 10 - Jun 30	4.4	Sep 11 - Oct 09
larvae	3.7	Mar 15 - Mar 30	5.0	Mar 15 - Mar 30
DIPTERA				
Tipulidae	8.1	Aug 14 - Sep 18	13.5	Aug 14 - Sep 11
		Oct 09 - Oct 24		
other Diptera	4.7	May 10 - Jun 07	6.8	May 10 - Jun 07

Conversely, for linyphiid spiders, the seasonal abundance patterns were significantly different between unimproved and improved grassland (X^2=1181, df=15, P<0.001). On unimproved areas, catches peaked between May 24 and June 21, but on adjacent improved areas, there was only a minor increase in the percentage of spiders caught over this period, with the main peak occurring between August 2 and September 11 (Fig. 7.2). Of the four most commonly caught linyphiid spiders, comprising 67% of the grassland linyphiid fauna, Oedothorax fuscus, Centromerita concinna and Erigone atra all had distinct spring peaks of capture, whilst E. dentipalpis, the most common of the four, had a bimodal distribution. When the data were divided into catches of Erigone dentipalpis on unimproved and on improved grassland, two peaks of abundance, a late spring peak (June 7 - 21) and a late summer peak (August 2 - 14), were evident on improved grassland, whereas on unimproved grassland, there was only one main peak in spring (May 24 - June 21) (Fig. 7.2).

Within the Coleoptera, both the Staphylinidae and the Carabidae showed significantly different seasonal trends between catches on unimproved and improved grassland (X^2 =531, df=15, P<0.001 and X^2=195, df=15, P<0.001 respectively) (Fig. 7.3). Over 40% of the staphylinid beetles caught on improved grassland were caught in a four week peak between June 7 and July 7, compared to only 12% during the same period on unimproved grassland. On unimproved areas, the abundance of staphylinids tended to be relatively uniform thoughout spring and summer, with catch numbers showing a sharp peak in the autumn (October 9 - 24). No similar peak was apparent on improved areas during the autumn. Carabidae, had a main peak in spring (June 7 - July 7) on improved fields, with a smaller secondary peak in autumn (September 25 - October 9). On unimproved fields, the seasonal pattern of abundance was much more uniform, with no pronounced peaks of abundance.

FIGURE 7.2. The seasonal distribution of Linyphiidae in pitfall traps catches on unimproved (n=4066 animals) and improved grassland (n=8662 animals) between March and October 1986.

The seasonal distribution of *Erigone dentipalpis* is illustrated as a specific example.

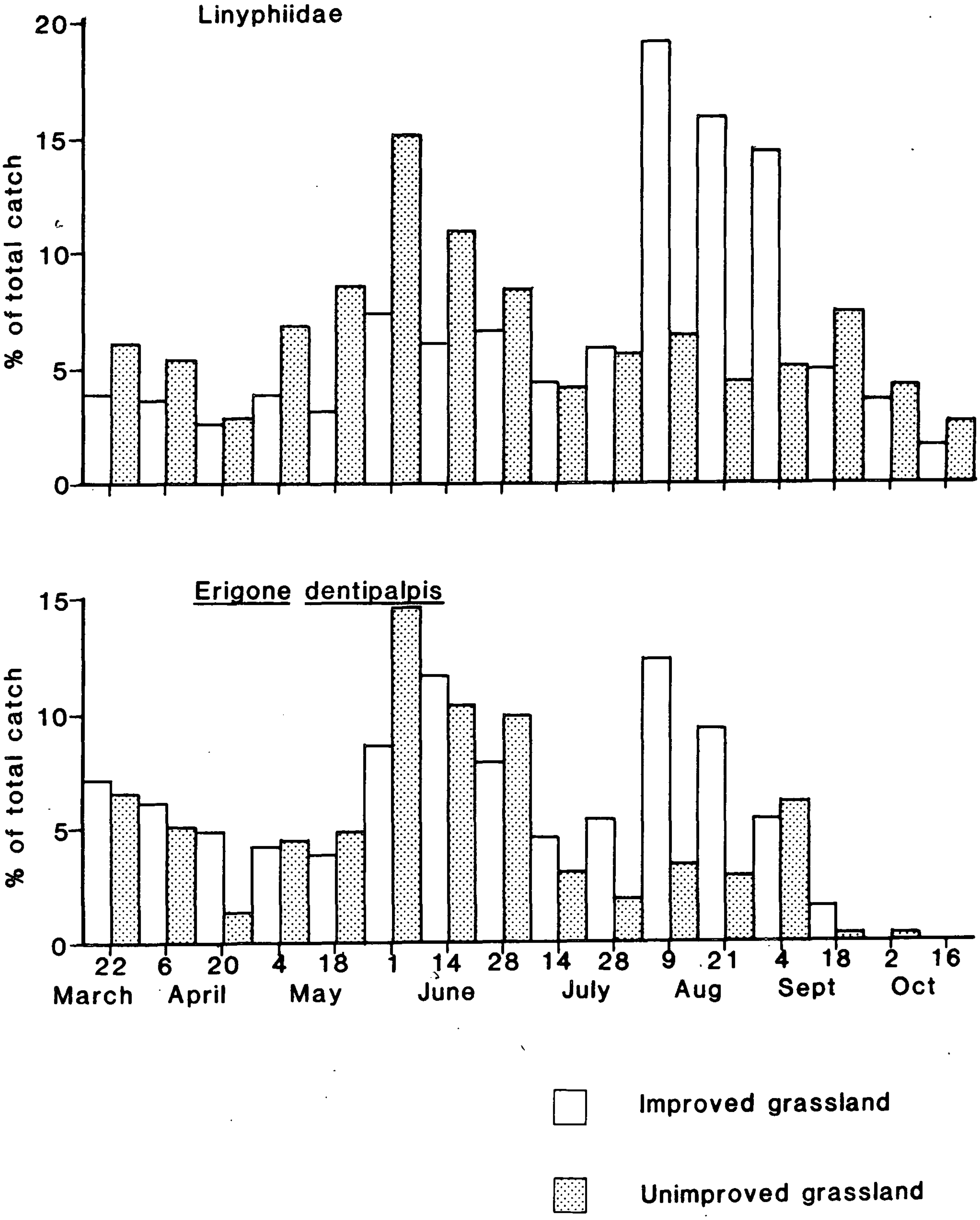
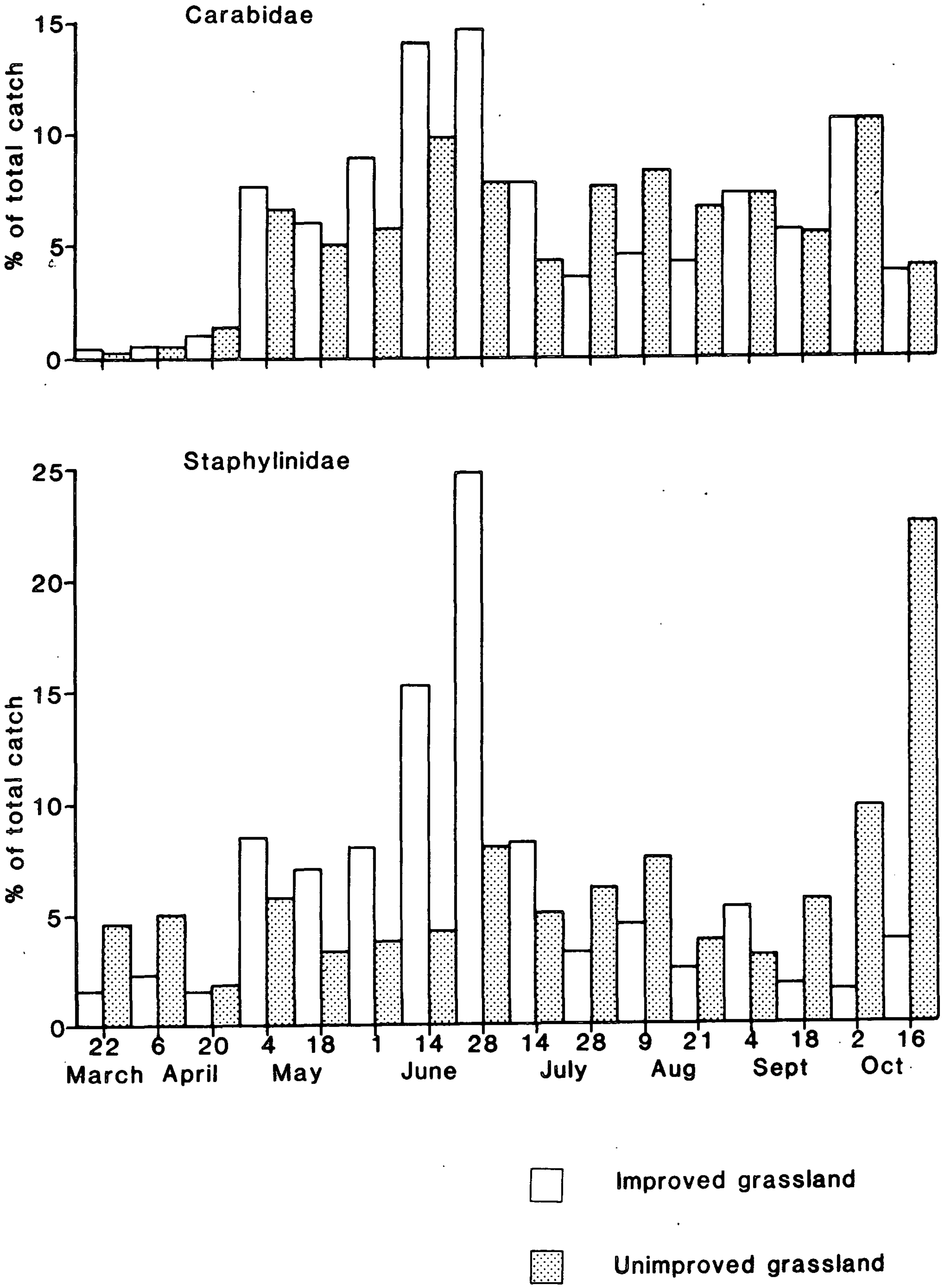

Linyphiidae
Erigone dentipalpis
% of total catch
20
15
10
5
0
22
6
20
4
18
1
14
28
14
28
9
21
4
18
2
16
March
April
May
June
July
Aug
Sept
Oct
Improved grassland
Unimproved grassland

FIGURE 7.3. The seasonal distribution of Carabidae and Staphylinidae in pitfall trap catches on unimproved (n=1942 and 1997 animals respectively) and improved grassland (n=1153 and 1222 animals respectively) between March and October 1986.


Carabidae
% of total catch
15
10
5
0
Staphylinidae
% of total catch
25
20
15
10
5
0
22
6
20
4
18
1
14
28
14
28
9
21
4
18
2
16
March
April
May
June
July
Aug
Sept
Oct
Improved grassland
Unimproved grassland

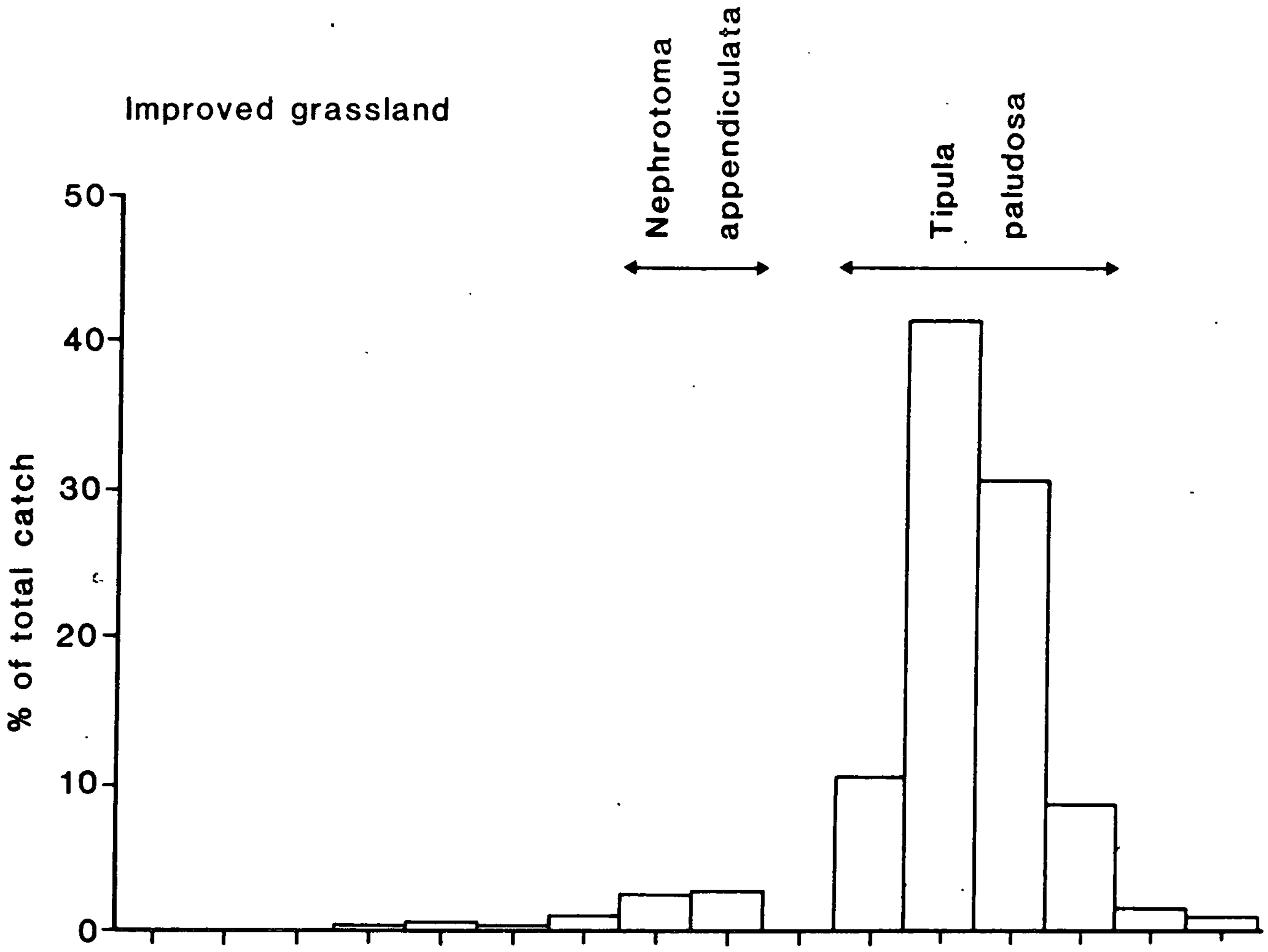
There was no significant difference in the seasonal catch distributions of either adult helophorid beetles, or beetle larvae between the two grassland types. Both adult helophorids and beetle larvae (principally Nebria (Carabidae) larvae) peaked in March.

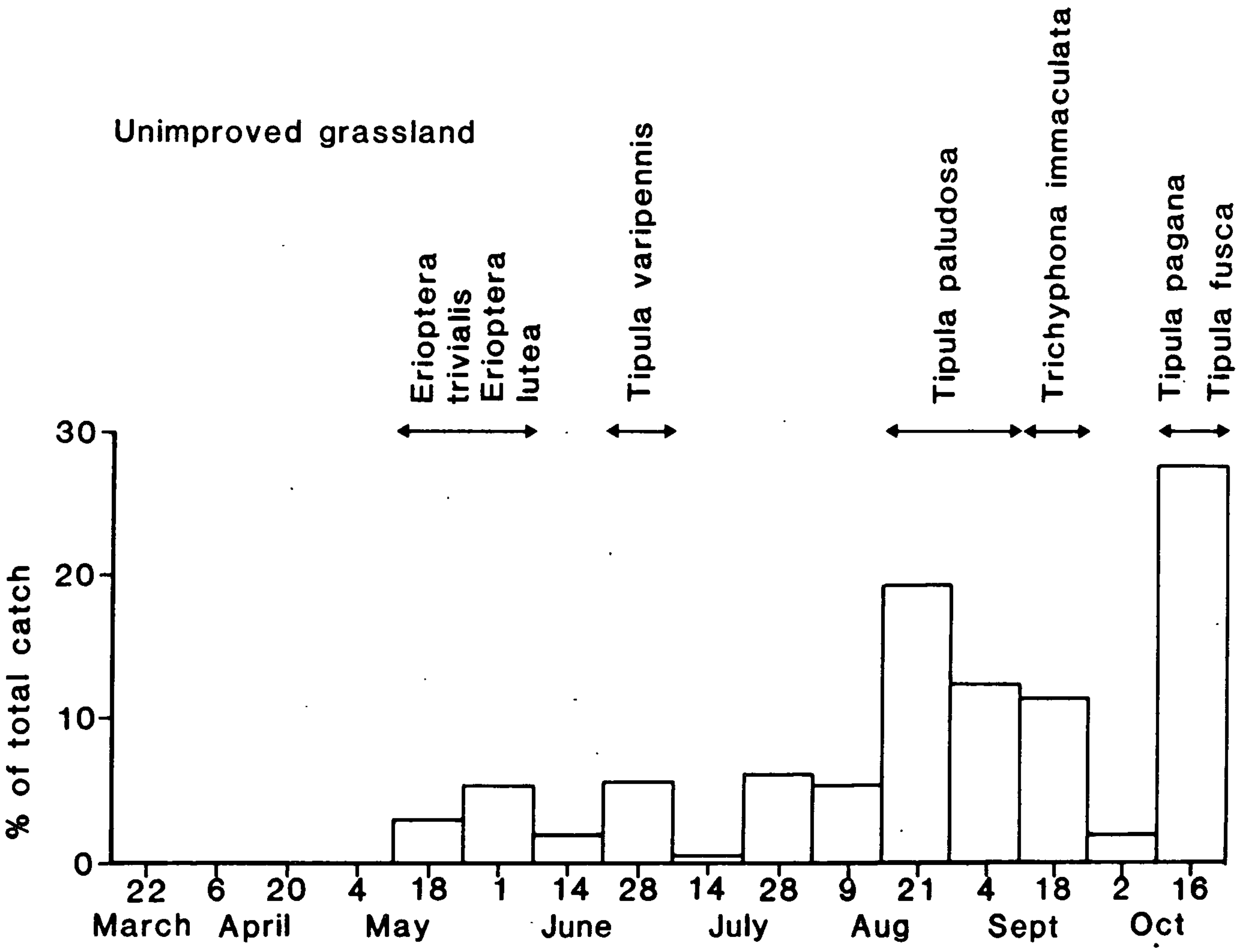
On unimproved grassland, Tipulidae showed several peaks of abundance resulting from several species with differing adult emergence periods (Fig. 7.4) Two major peaks existed, the first (August 14 - September 25), being attributable to the emergence of Tipula paludosa (August 14 - September 11) and Trichyphona immaculata (September 11 - 25). The second major peak (October 9 - October 24), resulted from the emergence of T. pagana and, to a lesser extent, T. fusca. On improved grassland, there was only one peak (August 14 - September 11) and was attributable to T. paludosa, during this period 83% of the tipulids sampled from improved grassland were caught.

The variation (s.d.) in catch size with season was, with the exception of Helophoridae and beetles in the "other" category, lower on unimproved grassland than on corresponding improved areas (Table 7.2).

FIGURE 7.4. The seasonal distribution of Tipulidae in pitfall trap catches on unimproved (n=537 animals) and improved grassland (n=655 animals) between March and October 1986.

The species comprising the principal peaks are noted.


Improved grassland
Nephrotoma appendiculata
Tipula paludosa
% of total catch
50
40
30
20
10
0


Unimproved grassland
Erioptera trivialis
Erioptera lutea
Tipula varipennis
Tipula paludosa
Trichyphona immaculata
Tipula pagana
Tipula fusca
% of total catch
30
20
10
0
22
6
20
4
18
1
14
28
14
28
9
21
4
18
2
16
March
April
May
June
July
Aug
Sept
Oct

DISCUSSION

Vegetation changes and the reduction in soil moisture are largely responsible for the significantly fewer spiders, the lower biomass of carabid beetles and fewer Parnidae on improved grassland. As discussed in chapter 6, lowered humidity resulting from a reduced layer of leaf litter and drier soils on improved grasslands appear responsible for the relative lack of lycosids and the fewer species of tipulids following improvement. Vegetational changes, especially the removal of tussock vegetation by reseeding or by increased applications of inorganic fertilizer, appear vital in explaining reductions in both the number of species and individuals comprising the invertebrate fauna. Ford (1937), making measurements of temperature and humidity in Bromus tussocks, concluded that their high humidity was important to their fauna as protection from drought. Luff (1966), showed that the density of the arthropod fauna of tussocks in winter was more than twice that of the intervening grass areas. This increased density was caused both by the presence of more species, and by an increase in the average number of specimens per species. Decreased complexity of vegetation architecture by tussock removal following improvement resulted in significantly fewer species of spiders, particularly the web-spinning linyphiidae (see chapter 6).

Earthworms were the only invertebrate group to significantly increase following improvement, but appreciable increases were found for scarabaeid beetles and Diptera belonging to the Scathophagidae as a result of increased applications of dung, often in the form of slurry, to improved fields. Helophorid beetles were more numerous on improved fields, particularly the meadows. This increase was associated with more bare, muddy areas favoured by these beetles early in spring following intensive cattle grazing in the previous autumn.

In accordance with the findings of Williams (1959), the overall invertebrate activity increased from March onwards to peak in late May/June, with a secondary peak in the autumn. Within this general pattern, differences in the phenology of linyphiid spiders, carabid and staphylinid beetles and craneflies (Tipulidae) existed between unimproved and improved grassland. These differences are as a result of differing species compositions, with individual species having different peaks of either activity or emergence.

Pearson and White (1954) found that pitfall trapping collected more male spiders than females. This male activity was associated with seeking the more static females during the copulation period (Williams 1962, Merrett 1967). These bursts of activity usually begin early in spring and peak in late June (Pearson & White 1954, Williams 1962, Merrett 1967, Vlijm & Kessler-Geschiere 1967, Edgar 1971 and Christophe & Blandin 1977). Pearson and White (1954) and Williams (1962) showed a temporal succession in lycosid spiders on moorland and in woodland respectively. Large numbers of _Trochosa terricola_ in April were followed by _Tarentula pulverulenta_ and, a little later in June, by the _Lycosa_ species. A secondary peak in the autumn, was found by Williams (1962), Vlijm and Kessler-Geschiere (1967), and in this study, and was due to a build up of activity by juveniles. The species composition of lycosid spiders on unimproved and improved grassland were similar resulting in similar seasonal patterns of abundance.

This was not the case with the Linyphiidae, where a June peak on unimproved grassland resulted from coincidental peaks of _Oedothorax fuscus_, _Centromerita concinna_, _Erigone dentipalpis_ and _E. atra_. On improved grassland, linyphiid numbers peaked in autumn. The difference resulted from fewer of the principal spring peaking species on improved land, and more Erigone dentipalpis, which on improved land exhibited a bimodal distribution, with a minor peak in June and a main peak in August (Fig. 7.2) Similar results for those found on improved grassland were found by Pearson and White (1954) on moorland in Wales, and by Sudd (1972) on the East Yorkshire coast, with Erigone atra and E. dentipalpis having activity peaks in August.

Tipton (1960) showed that many Carabidae require a high humidity. In Nebria brevicollis, low humidities during July/August are avoided by entering a diapause (Greenslade 1965), as it has been shown that dormant stages are more tolerant to harsh environmental conditions than active stages (Birch & Andrewartha 1942). Diapause may regulate the life-cycle to synchronize adult emergence (Lees 1955), or to ensure that larvae appear when conditions are most suitable for them (Andrewartha 1952).

Many of the grassland species of carabids can be divided into "wet" and "non-wet" species (Lindroth 1949, Williams 1959, Greenslade 1961 and Murdoch 1967). In wet habitats, rising water-tables in autumn and winter prevent breeding as eggs and larvae are not adapted to withstand innundation. Thus, species with a winter larval stage are selected against in wet habitats (Murdoch 1967). Lindroth (1949) found that 91% of "wet" species (n=124) had their larval stage in summer, while 42% of "non-wet" species (n=164) had winter larvae. Similarly, Greenslade (1961) found that 63% (n=24) of the non-wet species he studied had winter larvae. Typical wet species include Elaphrus cupreus, Loricera pilicornis, Pterostichus nigrita, P. strenuus and Agonum obscurum. All these species have peak spring abundances in pitfall catches as a result of reproductive activity, they have summer larvae and adults emerge in the autumn and overwinter in this stage (Greenslade 1965, Murdoch 1967). Non-wet species include Nebria brevicollis, Patrobus atrorufus and Pterostichus madidus. These species are typified by having peak catches of adults during their autumn breeding season and overwintering as larvae, a second peak occurs in spring when the next generation emerges (Williams 1959). A significantly higher proportion of "wet" species were found on unimproved grassland than on corresponding improved grassland.

The seasonal distribution pattern of carabid catches on unimproved and improved grassland were similar. The spring peak of activity was more pronounced than the autumn peak on improved grassland, whereas on unimproved grassland, the distribution of animals throughout the trapping season was more uniform with only slight peaks in spring and autumn. The phenology of all beetle larvae combined was remarkably similar on both grassland types. Large, early-spring peaks corresponding to the "non-wet" larval overwintering species, principally Nebria brevicollis, and smaller, but distinct, summer peaks corresponding to larvae of the "wet" species were found on both unimproved and improved fields. In the Staphylinidae, there were clear differences following land improvement, with a strong spring peak on improved grassland, probably attributable to dung associated species, and an equally sharp peak in autumn on unimproved grassland, suggesting a division between "wet" and "non-wet" species.

The life-cycles of most members of the Tipulidae are completed in one year. The egg and first two larval stages are brief, but 25 weeks are spent as an overwintering third instar larvae by Tipula paludosa (Coulson 1962). The adults live for a few days only. Consequently, their emergence needs to be highly synchronized. Coulson (1962) found that 67% of Tipula subnodicornis emerged within 11 days, whilst the same proportion of T. paludosa emerged over 23 days. It is this synchronized emergence of each species which causes the differences in seasonal distribution patterns of craneflies between unimproved and improved grassland. More species are found on unimproved areas, with the result that there are more peaks of emergence than on comparable unimproved areas. An analagous situation is found on moorland, where there is a marked difference in abundance and seasonal distribution of tipulids between alluvial grassland and *Juncus squarrosus* dominated peat areas (Coulson & Whittaker 1978). The vast spring emergence on peat areas was caused by *Tipula subnodicornis* and *Molophilus ater* (Coulson 1959, Nelson 1965). In contrast, the insects associated with mineral soils showed a much more even distribution of emergence spread over spring, summer and autumn, with peaks of *T. varipennis*, *T. paludosa* and *T. pagana*.

CHAPTER 8 GENERAL DISCUSSION

Krebs (1978) made two fundamental observations concerning populations of animals and plants. First, that abundance varies from place to place. There are some "good" habitats, where a species is, on average, common and some "poor" habitats, where it is, on average, rare. This situation is evident when considering breeding waders on upland grasslands. The marginal farmland habitat is a mosaic, broadly comprised of unimproved and improved fields in close proximity to each other. These adjacent areas have high and low densities of waders on a microhabitat scale. Lapwing densities on the traditionally managed unimproved grasslands, "the good habitat", are up to 71% higher than on areas of grassland that have been recently improved, "the poor habitat," whilst densities of curlew and redshank were up to 81% and 82% higher respectively. Snipe, on the other hand, were virtually excluded from such improved areas. The second observation was that no population goes on increasing without limit. The problem is to find out what prevents unlimited increase in low and high density areas.

Food availability often limits populations. Lack (1954) considered this to be the case in most vertebrate populations and that it operated through density-dependent changes in mortality. Lack stated that starvation does not appear to be a frequent cause of death in songbird nestlings, but in species with asynchronous hatching such as the swift (*Apus apus*) (Lack & Lack 1951) and raptorial birds (Brown 1976), starvation was a more common cause of nestling mortality. This was illustrated for the tawny owl (*Strix aluco*) by Southern (1970), who showed that correspondingly greater numbers of young were fledged with increasing rodent prey populations. However, an asymptote was reached when no more young were produced regardless of how much higher rodent abundance rose. At the other extreme, when rodents were excessively scarce, owls failed to breed. Similar effects were found at Barrow, Alaska, in pomarine skuas (Stercorarius pomarinus), snowy owls (Nyctea scandica) and short-eared owls (Asio flammeus), whose principal diets were lemmings (Lemmus trumucronatus) (Pitelka et al. 1955). Partridge chicks rely on insect food, with insects comprising 95% of items eaten during the first two weeks after hatching (Ford et al. 1938). Reduced insect availability following spraying of arable fields with herbicides (Southwood & Cross 1969, Sotherton 1980) resulted in increased chick mortality. When strips of fields were left unsprayed, chick mortality decreased (Rands 1986). Similarly, evidence from radiotracking red grouse (Lagopus lagopus) has shown that growth and survival rates of chicks are improved if a higher density of food is available (Hudson 1986).

In this study on lapwings, food availability during the breeding season was not found to be a major factor in population regulation. Only under adverse weather conditions of intense heat or cold did food become limiting. Such periods are reflected by the patterns of invertebrate abundance in 1986 (Fig. 7.1). A cold spell during early-April, resulting in snow-cover for about two weeks, caused a reduction in invertebrate activity and availability. This was reflected by significantly fewer animals being caught in pitfall traps. Such an April cold spell in Finland (Vespalainen 1968) and in Sweden (Marcstrom & Mascher 1979) resulted in high lapwing mortality, with up to 87% reduction in the local populations. Death was due to starvation and average weight losses at death were 35-45%. In this study, high mortality amongst lapwings was noted during the 1986 cold spell and several clutches were abandoned. Following ammelioration of the weather, clutch sizes were reduced, and this is reflected by the lower clutch size and smaller eggs found that year relative to other years.

Birds which live in a seasonally varying environment, face the problem of fitting their cycle into the seasonality. Within the breeding season, birds tend to synchronize the chick stage with periods of maximum food availability (Lack 1954, 1968). The main period of lapwing chick development coincided with peak invertebrate activity, and a study of growth rates over this period did not reveal evidence of a food shortage. However, chicks from late or replacement clutches appeared to be limited by food availability during a hot, dry spell in July and August 1986. Invertebrate catches over this period were significantly reduced. This reduction was attributable partly to hot, dry weather reducing invertebrate activity and partly to low beetle availability, the period concerned falling between the spring and autumn peaks of activity and emergence. Jackson and Jackson (1980) found that in drought conditions lapwing chick growth rates were significantly reduced, they took longer to fledge and mortality was higher. Such effects were also found in this study, and food availability to chicks under dry conditions are currently being investigated further. Drought conditions in the uplands, where soils are usually of a high moisture content and where water-tables are usually high, are probably representative of conditions frequently found in drier, lowland areas of eastern Britain where rainfall is lower and soils are better draining. Thus, food shortage may be an important factor limiting chick survival in arable fields and drier grasslands. Under drought conditions, many chicks of both lapwing and redshank were forced to move to wetter fields, usually those where drainage was less efficient resulting in the retention of wetter patches. Here, food appeared more readily available if such wet areas occurred. Food availability has been shown to influence the distribution of meadow pipits (<u>Anthus pratensis</u>) breeding on moorland areas (Coulson & Whittaker 1978). Breeding is synchronised with the emergence of <u>Tipula subnodicornis</u> from the peat areas. The first brood is fed almost exclusively on this insect. The second brood, in July, is fed almost entirely on insects collected from stream sides and mineral grassland. Nests are concentrated on blanket bog, but in close proximity to grassland areas in order to utilize both food sources. Houston (1970) found that five species of carabid beetle and the common frog (*Rana temporaria*) showed similar movements from bog to grassland in summer in search of food.

The second major factor to be discussed that frequently limits populations is that of predation. Ricklefs (1973) states that predation is the prime mover of energy through the community and defines the links in the food chain. Predators may regulate both the numbers and distribution of their prey, for example, the introduction of the ladybird (*Rodolia cardinalis*) into California virtually eradicated the cottony-cushion scale insect (*Icerya purchasi*), a pest of the citrus industry (DeBach 1964). Alternatively, there are cases where predators and herbivores have no apparent effect on each other. Such a case is illustrated by the introduction of the weevil *Apion ulicis* to New Zealand in an attempt to control the abundance of gorse (*Ulex europaeus*). Despite eating up to 95% of the gorse seeds produced, it had no appreciable impact on numbers of the plant (Miller 1970). Animals that are long-lived and have low reproductive rates, ('k' strategists) tend to invest heavily in avoiding predation, whilst animals that are short-lived and have high reproductive rates, ('r' strategists) tend to maximise their production of offspring at the risk of increasing their own vulnerability to predators. A high level of investment is put into reproduction by 'k' strategists. In the case of ground nesting birds such as the golden plover *Pluvialis apricaria*, a clutch of eggs may constitute up to 73% of the females body weight (Ratcliffe 1976). The eggs are protected from predators by either the incubating hen being camouflaged, or the eggs being cryptically marked. The chicks that hatch are also cryptically coloured and the level of parental protection is high.

The large eggs of nidifugous species of bird provide food for several mammalian and avian predators, and nearly all eggs lost are attributable to predation. The analysis of causes of clutch loss in partridges from 15 studies in Europe and North America showed two important causes: predation and mowing (Potts 1980). In Sussex, mowing resulted in the loss of many pheasant clutches, but only 2% of partridge clutches per annum. However, 80% of clutch losses were attributable to predators (Potts 1986). Similarly, in this study, 88% of lapwing clutch losses were due to predators. The chief egg predators were, in both cases, carrion crows. In addition, fox predation of sitting hens was common in partridges.

Fewer partridge nesting sites due to hedgerow removal tended to concentrate the remaining birds. The resulting high numbers of nests in only a small proportion of the habitat attracted a high probability of predation leading to density dependent clutch predation. However, predation of lapwing clutches does not occur in a density dependent manner. Elliot (1985) found that nest predation has a prime importance in influencing lapwing breeding dispersion. Group nesting enhanced the effectiveness of active response to potential avian predators, but not to mammalian predators such as foxes, and once one nest in a group had been found then subsequent predations on the remaining nests were higher in grouped than in single nests. To combat this, more than the expected number of lapwing nests were 30-100 metres apart from the next nest. The ability of lapwings to reduce egg predations has been experimentally demonstrated by Goransson et al. (1975) and in this study by observing predation rates on simulated lapwing clutches within differing densities of breeding lapwing. Other bird species use the aggressive nature of breeding lapwing to their advantage by nesting in their vicinity and thus receiving increased protection from predators (Campbell 1974, Drycz et al. 1981).

Nesting loss may vary both locally and annually, largely as a result of differences in predation (Lack 1946). Beintema and Muskens (1987) found predation levels to vary between years and regions, but for lapwing and black-tailed godwit (Limosa limosa) the patterns varied together. Variations in predation of these species were found to be significantly linked with vole abundance, the preferred food of many predators that also eat wader eggs. In addition, Dunn (1977) found that weasel predation on tit (Parus) spp. nestlings was higher when rodent densities, an alternative weasel prey, was low. Differential levels of predation on ground nesting birds may also exist within nesting habitats. The importance of overhead nesting cover in reducing the number of clutches taken by predators has been shown for wildfowl (Schrank 1974) and for gamebirds (Rands 1986), whilst for waders nesting in habitats where there is little or no vegetation cover, the cryptic marking of eggs is important (Skeel 1983). As discussed in previous chapters, grassland improvement has rendered clutches on improved pastures more conspicuous to predators and 62% more clutches were taken by predators than on corresponding unimproved pastures. Differential levels of predation between unimproved and improved pastures were also demonstrated experimentally. Too few chicks were fledged from improved fields to replace adult losses and the density of lapwing has declined, seemingly through clutch predation.

A line of evidence frequently used to support the arguement that prey numbers are regulated by predators is that prey often increase dramatically when their predators are removed. Such an experiment is currently being conducted by the Game Conservancy Trust on the edge of Salisbury Plain. Predatory corvids and mammals were removed from one area, with an equivalent area being left as a control. Only the results for the first year following control are available, but show fewer nest losses in the predator reduced area (Potts 1986). Potts reports of a similar study conducted over ten years in France by Frank (1970), where the number of partridges shot in the predator reduced area were twice those in the control. Similar responses were observed for hares (Lepus europaeus) and pheasants. In the U.S.A., differing results were obtained from two predator removal experiments. In the first, ruffed grouse (Bonasa umbellus) populations showed improved nesting success when predators were removed, but there was no difference in chick mortality, nor did the population increase (Edminster 1939). The second example is that of the californian vole (Microtus californicus). Here, population declines were similar both before and after predator control and the carnivores were feeding on a doomed prey surplus (Pearson 1966).

An increased density of prey can lead to individual predators switching diet and taking proportionally more of that prey species. Above the point of individual satiation, predators can only respond to increasing prey density through an increase in the number of predators, either by immigration (Pitelka et al. 1955) or by population growth (Hollings 1959). Even though lapwing densities on improved grassland appear to be regulated by clutch predation, chiefly from carrion crows, it is unlikely that an increase in lapwing numbers would result in an increase in predator density. This is due to crows being generalist predators and lapwing eggs account for only a small proportion of the overall diet (Holyoak 1968). In addition, crows cannot aggregate into areas where lapwing densities are high as they are territorial (Erikstad et al. 1982). Similarly, a decrease in predator abundance following a decline in lapwing numbers is equally unlikely. At high densities of breeding lapwing, both random and specialized egg predators can reduce breeding success sufficiently to cause population declines, whereas at the resulting lower densities predation will be more random and either keep densities low or further reduce them.

If differences in lapwing productivity caused the reduced densities on improved grassland then a high degree of philopatry may exist. Many species of birds and mammals are faithful to their natal area; 86% of blackbirds (Turdus merula) breed within 3km of their natal area (Greenwood & Harvey 1976), whereas 50% of common terns (Sterna hirundo) (Austin 1949) exhibit natal fidelity. In the herring gull (Larus argentatus), 77% of males returned to their natal part of the colony, but only 54% of females did likewise (Chabrzyk & Coulson 1976). In many other species, including the kittiwake (Rissa tridactyla) (Wooller & Coulson 1977), blackbird (Greenwood & Harvey 1976), swallow (Hirundo rustica) (Davies 1976), and great tit (Parus major) (Greenwood et al. 1979) males were more philopatric than females. A high degree of philopatry is frequently only shown by one of the sexes. In birds, it is usually the male, as it is males which establish the territories and attract the females. In the lapwing, the limited evidence available suggests that a high proportion of chicks return to breed in their natal areas, and usually to the same field within which they were reared. Of these birds, 64% were males, (n=25).

High nitrogen use early in the season on improved fields intensifies the green colour of the fields. Klomp (1953) showed that lapwings tended to avoid green surfaces, therefore birds exhibiting philopatry and breeding area fidelity are less likely to settle on improved fields.

Alternatively, if recruitment to the breeding population on improved areas is not largely through philopatry, the differences in density found between unimproved and improved grasslands must be due to breeding adults preferring unimproved areas in which to breed. Skeel (1983) found that the return rates of whimbrels were higher to bog habitats, where nesting success had been high, than to sites where nesting success was comparatively low. Movement to new areas probably accounted for much of the lower return rate. It has been found in many species that breeding dispersal is influenced by reproductive performance the previous year (Harvey et al. 1979, Greenwood 1980). Thus, more frequent dispersal would be expected from improved grassland where breeding success was lower. In intra-specific competition for nest sites, poorer quality birds that fail to obtain a territory on unimproved grassland may be relegated to the less preferred improved habitats. This situation is analagous to the findings of Coulson (1968), where better birds bred in the middle of colonies, and Errington (1946) and Jenkins et al. (1964), who showed that in prey species that displayed strong territorial behaviour, the examples given being the musk-rat (Ondatra obscurus) and the red grouse repectively, weaker animals are forced into marginal habitats by intra-specific competition. Within the marginal habitats, mortality through predation is higher than in the animals that occupy optimal habitats.

Philopatry, breeding site preference, and the degree to which adults move between improved and unimproved fields has yet to be fully examined. The roles of these factors in accounting for the differences in breeding density between the two field types require further study.

Ground nesting birds are particularly vulnerable to changes in land management. The decline of the corncrake (Crex crex) in mainland Britain has been attributed to the change in mowing time associated with the shift from hay-making to silage production (Cadbury 1980). Smith (1983) showed that lapwing numbers in the lowland grasslands of England and Wales were higher in areas of less intensive grassland management. The problem of wader nest losses to trampling by stock has been studied in the meadows of

The Netherlands by Beintema (1982). About 40% of lapwing nests, 60% of snipe nests and 72% of redshank nests were trampled at a stocking density of one cow/hectare. He also showed that high stocking densites early in the year prevented the successful relaying of clutches. Although nest trampling was not a problem in this study, high stocking densities may explain the low proportion of unsuccessful lapwing clutches that were replaced on improved pastures.

Associated with increased stocking densities is a higher degree of mechanization, with increased use of tractors to undertake a greater range of tasks such as liming, fertilizing, nitrogen injecting and multiple mowing. Lapwings appear able to sustain their numbers where the scale of agricultural activity is low, but where intensification following land improvement has taken place, many lapwing nests were destroyed by tractors and rollers, whilst earlier mowing may destroy many curlew nests. On improved areas, particularly improved meadows where farming is most intensive, lapwing populations tend to be limited by agricultural activities.

There has been a marked shift in the timing of the breeding season in waders in The Netherlands, seemingly in response to earlier mowing and grazing (Beintema et al. 1985). Breeding commences one or two weeks earlier than at the start of the century. This effect could be attributable to either sufficient food for egg formation being available earlier in the season, or may be genetically determined by selection through nesting success, as nest loss through agricultural activities increases later in the season.

APPENDIX TO GENERAL DISCUSSION

Selection of study fields

This study has compared paired sets of fields; those which have been improved, with those which have not been improved (see chapter 2). Ideally, an experimental approach would have been preferable, with fields being improved at random from initially unimproved areas. Unfortunately, such experiments can only be considered in much longer term research as the full effects of improvement are not felt for several years. On time scale alone, such investigations were beyond the scope of this study.

With finite financial resources available for land improvement, despite subsidies, it is unlikely that fields are improved entirely at random. In most instances, the proportion of land that is improved on a given farm will reflect;

i) the suitability of land for improvement; those fields which are easiest to improve are most likely to be selected for improvement. Such fields may be more amenable to improvement by being naturally better draining, or by having deeper, more nutrient rich soils, or by having a more favoured aspect relative to prevailing weather conditions. Alternatively, those fields which are naturally more favourable to agriculture and would require minimal improvement may remain "unimproved." Instead, resources may be chanelled towards improving the agriculturally poorer fields, thus maximising the effects of land improvement. This factor is a discernible source of bias in the selection of study fields. Despite this potential bias, the magnitude of the changes in both the physical and vegetational make-up of a field following improvement are large and usually greatly exceed differences caused by aspect or location. Thus it is considered that the comparisons made between improved fields and neighbouring unimproved fields are essentially valid and the differences real. The locality of a field may also render it more attractive to potential improvement by being nearer to the farm, or to access tracks for machinery or leading stock.

ii) the availability of capital to finance improvement; on some farms all suitable land has been improved, whereas on neighbouring farms, where land may be equally suitable for improvement, financial restrictions or lack of desire to improve land may result in only relatively few fields being improved. Where suitable comparisons were not available under the same land ownership, it was often possible to pair unimproved and improved fields of an initially similar nature along farm boundaries, with each field in the pair being under different ownership.

Site fidelity and philopatry

Of 15 marked adult birds that were seen throughout the 1986 breeding season, 10 (67%) returned in 1987. Adult mortality has been estimated at 33% per annum (Haldane 1952, Lack 1954). This value probably overestimates mortality but nevertheless suggests that virtually all adults must be site faithful. Of these 10 birds, 7 returned to the same territories occupied the previous year and the remaining three moved to adjacent fields. Insufficient data were available to give figures for chick philopatry, but observations on ringed chicks recaptured as adults suggested that many chicks returned to breed in their natal fields. Providing that one sex, the one which selects the breeding area, is strongly philopatric, then the differences found in the densities of lapwing on unimproved and improved fields could arise solely from the differences in breeding success. The test of the importance of the roles of philopatry and habitat imprinting in determining lapwing breeding densities would be whether chicks reared in unimproved fields would return to those fields even if they had been improved, or whether they would preferentially select alternative unimproved areas.

Lapwing population trends with respect to agricultural change

The lapwing has been the subject of two national British Trust for Ornithology (B.T.O.) surveys, in 1937 (Nicholson 1938) and in 1960-61 (Lister 1964). Lister (1964) found regional variations since the 1937 survey, with areas that had returned to cereal production, for example, the east of England, showing declines, whereas the reverse was true for pastoral areas.

The annual Common Bird Census (C.B.C.) returns subsequent to the 1961 survey have shown a continued decline of lapwings in cereal areas, particularly those counties south and east of Gloucestershire, Warwickshire and Leicestershire, and an increase in sheep farming areas, which are mainly in the north and west (O'Connor & Shrubb 1986). These trends have persisted despite stabilization of the arable-pasture balance and probably reflect a decline in spring tilled land in preference to autumn sown crops. Lapwings show a strong preference for spring tillage (Lister 1964, Shrubb 1988) but autumn tillage tends to be strongly avoided due to the height and density of the crop at the start of the breeding season (O'Connor & Shrubb 1986, Shrubb 1988). Increased density and eveness of plants in autumn sown cereals apparently resulted in a decrease in lapwing densities on a Sussex farm studied by Shrubb from a mean of 6.5 pairs /100 ha in 1961-1965 to 3.5 pairs in 1975-80 and 1.5 pairs in 1981-85 (O'Connor & Shrubb 1986). Thus in intensively farmed cereal areas, declines of lapwing are attributable to conditions becoming unsuitable and general avoidance of such areas. This differs from the situation found on marginal grassland in this study, where breeding lapwing still persist in reasonable densities on the less favoured improved areas, but fail to produce sufficient chicks to maintain the population on such fields.

The changes in arable land uses make the populations of lapwing on grasslands increasingly important. The increase in lapwing observed in sheep farming areas may possibly be due to a regional shift in distribution, away from cereal areas (O'Connor & Shrubb 1986).

Preliminary results of the 1987 B.T.O. Lapwing Survey showed differences in the distribution and density of lapwing in England and Wales, with high concentrations in Lancashire, parts of Yorkshire, Cumbria and Co. Durham and few birds in S.W. England and many parts of Wales (Shrubb 1988). The B.T.O. survey showed similar results to those found in this study. Within grassland areas, significantly more lapwings bred in rough grassland than expected, whereas fewer were found breeding on improved grassland. Here too, predation of clutches may be one of the predominant factors reducing fledgling production. In addition, in drier areas, particularly in the east of the country where rainfall is considerably less, chick mortality through reduced foraging success may be increased (Jackson & Jackson 1980).

A sharp decline between 1962 and the mid 1980's in the lapwing C.B.C. index was supported by the 1987 survey. When counts of 27 areas, each of 80ha or more, covered in the 1961 survey (Lister 1964) were repeated, a 68% decrease was apparent from 577 pairs in 1961 to 183 pairs in 1987 (Shrubb 1988). This is comparable to the 69% lower lapwing density on improved grassland relative to unimproved found in this study in northern England.

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SUMMARY

1. Since the 1940's, agricultural improvement of upland grasslands has progressed rapidly, with 31% of rough grassland being lost between 1949 and 1981. The impact on breeding wading birds was assessed in the years 1985-87 by comparing the densities and distribution of waders using unimproved and improved grassland in the Eden Valley and Alston, Cumbria and in Teesdale, Co. Durham.

2. Improvement resulted in the virtual disappearance of snipe. In other waders, the improvement of pastures resulted in marked declines; 71% in lapwing, 81% in redshank and 82% in curlew, whilst the improvement of meadows resulted in less severe decreases of 42%, 58% and 32% respectively. The proportion of fields occupied by breeding waders underwent similar reductions.

3. Following improvement, breeding waders do not appear to have redistributed themselves between improved and unimproved fields. Instead there has been a marked overall decline in the number of waders in areas where improvement has taken place.

4. Wader densities found on marginal grasslands were higher than those reported for lowland grasslands, with lapwing densities 12 times, redshank 4 times, snipe 6 times and curlew 25 times higher.

5. The absence of snipe from improved areas can be explained entirely by land drainage reducing soil moisture and its associated effects on vegetation composition, particularly _Juncus_. Reductions in curlew following

improvement appear to be associated with vegetation changes and more intensive farming practices, whereas redshank seem relatively unaffected providing wet areas persist nearby.

6. Data on the breeding success of lapwings were obtained from a study on 637 clutches between 1985 and 1987, 474 on unimproved and 193 on improved grassland to identify possible reasons for the reduced densities of breeding lapwing on improved fields. In addition, comparative data were collected from 93 clutches on arable land.

7. First clutches were significantly larger on unimproved grassland with a mean of 3.73 eggs, compared to 3.61 eggs on improved grassland. In contrast, replacement clutches were larger on improved areas (3.90 eggs) than on unimproved (3.47 eggs).

8. On average, 40% of eggs laid by lapwings on unimproved pastures hatched compared to only 17% on improved pastures. No significant difference in hatching success was found between unimproved and improved meadows with 32% and 22% of eggs hatching respectively.

9. Overall, 73% of unsuccessful first clutches laid by lapwings were replaced on unimproved pastures, whereas on meadows and improved pastures up to 32% only were replaced.

10. Survival rates of lapwing chicks increased with age from hatching to fledging. Survival of small chicks was significantly higher on unimproved areas than on comparative improved areas. In 1986, 28% of chicks fledged from both unimproved and improved grassland, whereas in 1987, 43% of chicks

survived to fledge from unimproved fields, a significantly higher proportion than the 15% from improved fields.

11. Production by lapwings on unimproved land (0.86 chicks fledged per pair) was sufficient to replace adult losses and so maintain numbers, whereas on improved land, production was too low (0.25 chicks fledged per pair) to maintain existing breeding densities.

12. As the season progressed, there was a change in the lapwing diet from soil invertebrates, principally tipulid larvae and earthworms, to surface active beetles, particularly Carabidae and Curculionidae.

13. Lapwing breeding densities were negatively correlated with the densities of earthworms, but positively correlated with beetle abundance. Earthworm and lapwing densities were correlated in the pre-laying period. Feeding flocks of lapwing on improved, "neutral" fields (fields with no breeding lapwing, or lapwing at a low density) in the pre-laying period were 75% female, but only 36% of birds occupying the breeding fields at this time were female.

14. No significant differences were found in the volume of lapwing eggs laid on unimproved grassland, improved grassland or on arable land. A difference in egg volume was found between 1986 and 1987.

15. In 1986, there was no difference in lapwing chick growth rates between areas of low or high beetle abundance suggesting that food was not a limiting factor in chick production that year. In 1985, the growth rate of chicks averaged 6.1g/day on unimproved pastures, significantly higher than

the average of 5.1g/day on improved pastures. The year in question was relatively dry. In 1986 and 1987, there was no significant difference in growth rates between chicks on unimproved and improved areas. Under conditions of drought, food for chicks may become limiting, especially on improved fields.

16. Loss of lapwing clutches to agricultural activities was higher on improved than on unimproved land and higher on meadows than on pastures. On improved meadows, the higher proportion of clutches lost to agricultural activities and the low proportion of clutches that were replaced accounted for the reduced breeding success observed.

17. Overall, 76% of lapwing clutches on improved pastures were taken by predators compared to only 47% on unimproved pastures. Observed predators of eggs were carrion crows Corvus corone and black-headed gulls Larus ridibundus. Increased predation on improved land, as a result of reduced nest crypticity, chiefly accounted for the lower breeding success on improved pastures relative to unimproved pastures.

18. The predation hypothesis was tested using black-headed gull eggs to simulate lapwing clutches. Predation rates were higher on improved pastures than on unimproved and also on fields where no lapwings were nesting.

19. Hatching success on unimproved areas was similar for lapwing, curlew, redshank and snipe. On improved areas, redshank hatching success was relatively high, with 54% of pairs producing chicks compared to 35% for lapwing and 23% for curlew.

20. Fledgling production on improved land was insufficient to maintain the lapwing population at its existing level without recruitment from unimproved areas and has probably caused the reduction in lapwing densities found on improved land.

21. Grassland improvement resulted in reductions in soil moisture and organic content by 24% and 38% respectively, whilst drainage lowered the water-table 35cm on improved land by July. Soil pH increased by 8%.

22. Invertebrates were sampled by three methods: *In situ*; chemical expellents for earthworms and dipteran larvae, extraction of animals from soil samples, principally for earthworms and dipteran larvae, by Berlese funnels, and pitfall traps for sampling surface active invertebrates.

23. Classification of sites according to their invertebrate fauna by TWINSPAN analysis recognized four communities reflective of management regimes; cereal and recently disturbed sites, improved pastures, unimproved pastures and meadows.

24. Increased soil nutrients, drier soils and a higher pH following improvement resulted in significant increases in earthworm density and biomass by 120% and 146% respectively.

25. Grassland improvement did not affect the density of tipulid larvae, but resulted in a 62% reduction in species diversity. *Tipula paludosa* was the most numerous species on both grassland types and accounted for 40% of the catch on unimproved grassland and 84% on improved grassland. The number of species of cranefly was positively correlated with soil moisture content.

26. On improved grassland, Tipulidae showed several peaks of abuncance resulting from species having different adult emergence periods. The two main autumn peaks were largely attributable to Tipula paludosa and T. pagana. On improved grassland, there was only one main peak, that of T. paludosa.

27. There was no significant difference in the number or biomass of Diptera caught between unimproved or improved grassland.

28. Classification of the spider catches by TWINSPAN analysis split sites into two groups; those which had been improved and those which were unimproved. Improvement reduced the species diversity by 46% with 71 species being found on unimproved grassland compared to only 41 on improved. The spider species richness of a site was positively correlated with the complexity of vegetation architecture, which in turn was correlated with soil moisture and soil organic content.

29. Significant reductions in the numbers and biomasses of spiders following improvement were attributable to significantly fewer non-linyphiid spiders, both lycosids (97% fewer) and other groups (93% fewer) on improved fields.

30. Linyphiid spiders reached peak abundance in June on unimproved grassland, on improved grassland the peak occurred in August. Erigone dentipalpis, the most commonly caught linyphiid, exhibited two peaks of abundance on improved grassland, a late spring peak and a late summer peak, whilst on unimproved grassland, there was only a spring peak. Lycosid spiders reached peak abundance in June on both unimproved and improved

grassland.

31. The Helophoridae were the most numerous family of beetle found on either grassland type. Excluding Helophoridae from the analysis, Staphylinidae and Carabidae comprised 83% and 87% of the beetles caught on unimproved and improved grassland respectively.

32. Staphylinidae, Curculionidae, Scarabaeidae and Chrysomelidae all formed a significantly higher percentage of the beetle fauna on improved land than on corresponding unimproved land, whilst the reverse was true for Carabidae and Parnidae.

33. There was no significant difference in either the quantity or biomass of beetles between unimproved and improved grassland. The significantly higher numbers of Parnidae and higher biomasses of Carabidae were balanced by more Staphylinidae, Scarabaeidae and Helophoridae on improved grassland.

34. On unimproved grassland, the abundance of staphylinids reached a sharp peak in spring, with catches in Autumn being relatively low, whereas on unimproved grassland, catch sizes were relatively uniform until a late autumn peak. Carabidae exhibited a pronounced spring peak and a secondary autumn peak on improved land, whereas on unimproved land, the distribution of catches was more uniform and without distinct peaks.

35. Although the number of carabid beetles caught did not change following land improvement, the species composition did change, reducing the biomass by 70% indicating that a greater proportion of smaller species were present on improved sites. Both the mean number of of carabid species caught and

the species diversity tended to be higher for unimproved sites. A significantly higher proportion of "wet" habitat carabids were present on unimproved than on improved grassland.

36. Other invertebrates, mainly Mollusca, Diplopoda, Chilopoda and Opiliones, were reduced in number by 91% and biomass by 93% following grassland improvement.

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Appendix 1.

The sub-study areas comprising the two principal study areas surveyed for breeding waders, and from which data on the nesting success of the lapwing was obtained, are listed below. A four figure grid reference is given to the centre of each area.

Eden Valley	Teesdale
Asby Mask NY6912	Langdon Beck/Harwood NY8531
Breaks Hall NY7114	Alston NY7346
Blackmoor Green NY8115	
Little Musgrave NY7513	
Seavy Rigg NY8117	
Stainmore NY8512	
Tebay NY6505	

Appendix 2.

The sites sampled by pitfall traps in 1985 and 1986. A six figure grid reference is given to the centre of each field

1985			
Aisgill:	SD775974.	SD775975	
Blackmoor Green:	NY814156.	NY816156	
Foreshieldgrain:	NY756474.	NY756475	
Haska Rigg:	NY860124		
Hazel Bank:	NY812158.	NY813158	
Howburn:	NY707428.	NY708430.	NY707432
New Hall:	NY722175		
Seavy Rigg:	NY815176.	NY817177	
Soulby Grange:	NY738119.	NY735116.	NY735114
Wrenside:	NY836099.	NY835103	

1986			
Ashfell:	NY753058		
Blackmoor Green:	NY817163.	NY814162	
Breaks Hall:	NY719138.	NY713143.	NY715143
Dona Close:	NY706106.	NY704116	
High Crossgill:	NY749398.	NY748400	
Little Musgrave:	NY746129.	NY744124	
Mousegill:	NY855115		
New Hall:	NY722175.	NY722177	
Mazonwath:	NY693065		
Riddlesay:	NY759099		
Swathburn:	NY699125.	NY697126.	NY703128
Turkeytarn:	NY693132.	NY694122.	NY695118