

The Roles of Predation, Food and Agricultural Practice in Determining the Breeding Success of the Lapwing (*Vanellus vanellus*) on Upland Grasslands

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Source: *Journal of Animal Ecology*, Vol. 59, No. 3 (Oct., 1990), pp. 915-929

Published by: British Ecological Society

Stable URL: <https://www.jstor.org/stable/5022>

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THE ROLES OF PREDATION, FOOD AND  
AGRICULTURAL PRACTICE IN DETERMINING  
THE BREEDING SUCCESS OF THE LAPWING  
(*VANELLUS VANELLUS*) ON UPLAND GRASSLANDS

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SUMMARY

(1) Lapwing breeding densities decreased by 74% on pastures and 56% on meadows following agricultural improvement of upland grasslands. Fledgling production was 63% lower on improved relative to unimproved areas. Three possible hypotheses to account for these decreases have been examined: (i) increased predation of clutches; (ii) a reduction in invertebrate food and/or its availability; (iii) a greater destruction of clutches by agricultural machinery and/or trampling by livestock.

(2) Overall, 76% of clutches on improved pastures were taken by predators compared to only 47% on unimproved pastures. Increased predation largely accounted for the reduced breeding success on improved pastures relative to unimproved pastures.

(3) Although land improvement resulted in decreases in several of the invertebrate groups upon which lapwings feed, reduced food availability had only minor effects on breeding success.

(4) Clutch destruction during agricultural activities was almost four times higher on improved than on unimproved land and over five times higher on meadows than on pastures. On improved meadows, the higher proportion of clutches destroyed and the low proportion of clutches that were replaced accounted for the reduced breeding success.

(5) The predation hypothesis was tested using simulated lapwing clutches. After 1 day of exposure to predators, almost twice as many 'clutches' were taken by predators on improved pastures as on unimproved.

(6) Fledging production on improved land was insufficient to maintain numbers at current levels without recruitment from unimproved areas and this has probably caused the reduction in lapwing densities on improved land.

INTRODUCTION

Since the 1940s, agricultural improvement of upland grasslands (grassland immediately below the wall separating moor from enclosed fields) has progressed rapidly with 31% of rough grassland being lost between 1949 and 1981 (Sydes 1990). Wet and rough grazing areas have been drained, sometimes reseeded and, subsequently, they have received increased levels of inorganic fertilizers. In addition, previously non-productive agricultural areas above the moor wall have been brought into production by ploughing and reseeded with competitive grass mixes.

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These agricultural improvements to rough grazing areas in the north Pennines have caused the virtual disappearance of snipe *Gallinago gallinago* L. from improved land and marked reductions in the density and proportion of improved fields used by redshank *Tringa totanus* L., curlew *Numenius arquata* L. and lapwing *Vanellus vanellus* L. (Baines 1988). Lapwing breeding densities decreased by 74% on pastures and 56% on meadows following agricultural improvement. Fledgling production by these lapwings was 63% lower on agriculturally improved land than on adjacent unimproved land. The difference mainly arose through a 50% lower hatching success on improved fields. Whilst there were also differences in fledging success these were small (Baines 1989).

Three possible reasons for the reduced density and breeding success of lapwings on agriculturally improved grassland are examined in this paper. (i) A large proportion of lapwing clutches are taken by predators. Beintema & Muskens (1987) and Galbraith (1988) in his study on agricultural land in Scotland found predation to be the main cause of egg loss. The hypothesis is examined that there may be different levels of egg predation between different types of grassland and that nests on improved grasslands may be more vulnerable to predators. (ii) Improved grassland may be deficient in food, which may reduce its attractiveness as a breeding habitat or reduce chick growth rates and survival. (iii) In Dutch meadows, many clutches were destroyed by agricultural activities, notably mowing and trampling by cattle. In Scotland, Galbraith (1988) found that on intensively farmed arable fields, egg loss was a major factor limiting productivity. As improved grasslands are more intensively managed, more clutches may be destroyed by farm machinery, or trampled by livestock, which occur at higher grazing densities.

## STUDY AREAS

Two main study areas were used: the Eden Valley and Upper Teesdale. Eight study subareas at the head of the Eden Valley near Brough, Kirkby Stephen and Tebay, Cumbria (within National Grid squares NY60, 61, 71 and 81) formed the Eden Valley study area. Two subareas near Alston, Cumbria and Langdon Beck, Co. Durham (within National Grid squares NY74, 82 and 83) were used in Upper Teesdale.

Each subarea contained between twenty and eighty-five fields (75–325 ha). Fields were classified into two broad categories: 'improved' or 'unimproved' dependent on changes in the intensity of their management. Fields where management intensity had been increased were termed agriculturally 'improved'. Improvement was accomplished by using government grants to underdrain fields, followed by (i) replacement of the existing semi-natural vegetation with competitive grass mixes by ploughing and subsequent reseeding and annual applications of inorganic fertilizer, or (ii) increasing fertilizer applications to existing grasslands to encourage more nutritious grass species. This has allowed increases in stocking density which, in turn, can alter both the vegetation composition and structure (Hewson 1977; Anderson & Yalden 1981). Consequently, agriculturally improved fields were typically bright green with a restricted number of plant species and a uniform vegetation architecture.

Conversely, 'unimproved' fields were more extensively managed and the intensity of their management had not been markedly increased or, in some cases, had been reduced, resulting in the reverting of once improved areas to rough grassland. As a result, unimproved fields supported fewer stock or had lower grass yields than their improved counterparts. Typically, they appeared greenish-brown, were richer in plant species and had a more complex vegetation structure. Tussock-forming rushes (*Juncus*) and grasses

grew alongside several species of sedge (*Carex*), grass and moss, which together with unvegetated areas, combined to create a diverse vegetation mosaic. Physically, the topography was more undulating, often with an irregular surface due to the presence of hummocks.

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

## METHODS

### *Food availability*

Components of the lapwing diet were identified from stomach contents collected from twelve adult lapwings and four chicks found dead, either killed on roads or through striking overhead power wires in the study area.

The effect of land improvement on food availability to lapwing was assessed by sampling the main invertebrate constituents of the lapwing diet (reviewed in Cramp & Simmons 1983). Invertebrate samples were taken from adjacent pairs of improved and unimproved fields and used to infer changes following land improvement.

Earthworms were sampled from twenty-three unimproved and twenty-three improved fields in April using the formaldehyde extraction technique (Raw 1959). Nine litres of 0.55% formaldehyde were poured on the ground within a 0.5 m<sup>-2</sup> quadrat placed randomly within the field. The worms that emerged were collected. After 10 min, or when no more worms emerged, a further dose of formaldehyde was applied. Initially, a third treatment was made after a further 10 min, but as it never produced any worms, in subsequent samples only two applications were made. The earthworms collected were counted and weighed (wet weight).

Tipulid larvae were sampled by salt extraction. Samples were taken from twelve unimproved and twelve improved fields in late April/early May. Each field was divided visually into ten equal-sized areas and one sample taken from within each area. A cylinder 25 cm high and 10 cm diameter was hammered into the ground to a depth of 5 cm and filled with brine solution (1 kg of sodium chloride dissolved in 3 l water). After 15 min, the larvae which floated on the surface of the brine were collected.

Surface-active invertebrates were sampled using pitfall traps. This was considered an appropriate method of sampling invertebrate availability to feeding lapwings, as the number of animals caught in traps partially reflects the degree of activity of that animal (Greenslade 1961). Lapwing feed by visual cues, therefore active invertebrates are more likely to be taken. The traps were sited in representative areas of ten unimproved and ten improved fields. Ten collecting beakers with a diameter of 4.5 cm were placed in two rows of five with an inter-trap distance of 3 m. 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 represent the relative food availability to

lapwing throughout the breeding season, whilst data collected between mid-May and early July 1986 measured food availability during the main chick rearing period.

#### *Lapwing densities*

Lapwings were censused on their return to the breeding grounds in the first 3 weeks of March, the pre-breeding period. The density of birds feeding in each of the study fields was calculated for one study subarea. The birds present were sexed in the field by plumage differences (Cramp & Simmons 1983) and the pre-breeding distributions of each sex compared.

The density of breeding lapwings was obtained from a minimum of four counts of lapwing in each field between the beginning of April and the end of May. The area of each field was obtained from 1:2500 OS maps and the counts of breeding lapwing were converted to the density of pairs per 10 ha.

#### *Egg volume*

Between 1985 and 1987, 760 lapwing clutches were studied. Nests were found by seeing incubating birds, or by systematic searches. Nests were revisited every 4 days. In 1986 and 1987 the length and breadth of each egg was measured to an accuracy of 0.1 mm and the egg volume calculated using the formula

$$V = K LB^2$$

where  $V$  is the volume,  $L$  is the egg length,  $B$  is the egg breadth at the maximum diameter and  $K$  is a shape constant (Coulson 1963; Furness & Furness 1981). By using eggs from collections and filling each with alcohol from a burette to obtain the internal volume and relating these values to  $LB^2$  a constant  $K_3$  0.464 was obtained. Data on egg volumes were collected from unimproved and improved grassland with comparative data from adjacent or nearby arable fields.

#### *Clutch loss*

Clutch loss was the major cause of differential breeding success between unimproved and improved pastures and the cause of clutch failure was recorded in detail. Eggs that were either lost to farm machinery or trampled by livestock were usually broken and compressed into the bowl of the nest, with associated tyre marks, general land compression or hoof prints apparent. 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, apparently causing desertion of the remaining eggs.

Many of the clutches were found during incubation, and hatching failure was calculated following Mayfield (1961, 1975). Comparative data on the percentage of clutches lost to farming activities and predation were obtained for arable land.

#### *Growth of chicks*

Lapwing chicks were ringed, many within a day of hatching to study individual growth rates. Unringed, older chicks were aged from head and bill and wing-length measurements compared with those of chicks of known age. Where possible, chicks were reweighed, on average, every 4 days. Between the ages of 5 and 30 days, the increase in chick weight was linear with age. Growth was measured as the mean weight increase per day over this period.

TABLE 1. The proportion of lapwing clutches taken by predators on different grassland types 1985–87, and on arable land 1986–87

	1985		1986		1987		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
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

\*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

## RESULTS

### *Loss of clutches by predation*

The first hypothesis to explain differences in breeding success following improvement was differential clutch predation rates. Over the 3 years, 76% of clutches on improved pastures were taken by predators whereas, on unimproved pastures the value was only 47% ( $\chi^2 = 21.6$ , d.f. = 1,  $P < 0.001$ ). This trend was consistent over each of the 3 years with the difference being significant in 1985 and 1986 ( $\chi^2 = 6.9$ , d.f. = 1,  $P < 0.01$  and  $\chi^2 = 9.3$ , d.f. = 1,  $P < 0.01$ ) (Table 1).

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 ( $\chi^2 = 10.2$ , d.f. = 1,  $P < 0.001$ ). Over the 2 years 1986–87, predation of clutches on arable land was significantly lower than on any of the grassland types, with only 25% of clutches being taken by predators.

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

### *Food availability*

The possible effects of reduced food availability to lapwings following improvement were investigated by comparing each of the following on unimproved and improved grassland: (i) the relative abundance of important components of the lapwing diet; (ii) the mean egg volume of clutches; and (iii) chick growth rates.

### *Components of the diet*

Analysis of stomachs collected before 1 May showed that the diet was then composed largely of fly larvae (Diptera) with beetles (Coleoptera), both adults and larvae, and earthworms (Lumbricidae) (Table 2). 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 probably a considerable underestimate. This 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.

TABLE 2. Seasonal changes in the diet of lapwings feeding on upland grasslands in the North Pennines, from analysis of stomach contents

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

\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

After 1 May, the diet was mainly adult beetles, the proportion of which increased from 22% to 80% ( $\chi^2 = 63.6$ , d.f. = 1,  $P < 0.001$ ), with corresponding actual and proportional decreases in the quantity of both beetle and fly larvae taken ( $\chi^2 = 7.9$ , d.f. = 1,  $P < 0.01$  and  $\chi^2 = 37.1$ , d.f. = 1,  $P < 0.001$ ), respectively. A small number of spiders (Araneae), adult 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. 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.

#### *Relative abundance of invertebrates*

Improvement of grasslands affected the densities and biomasses of the major invertebrate components of the lapwing diet (Table 3). It increased both the density ( $t = 4.43$ , d.f. = 44,  $P < 0.001$ ) and the biomass ( $t = 3.95$ , d.f. = 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

TABLE 3. The effect of land improvement on the densities and biomasses of the main invertebrate components of the lapwing's diet. *n* = the number of paired samples. Araneae, Carabidae and 'Other Coleoptera' represent changes in the quantity of animals caught in pitfall traps

	<i>n</i>	% change after improvement			
		Density		Biomass	
		%	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

\*  $P < 0.05$ ; \*\*\*  $P < 0.001$ .



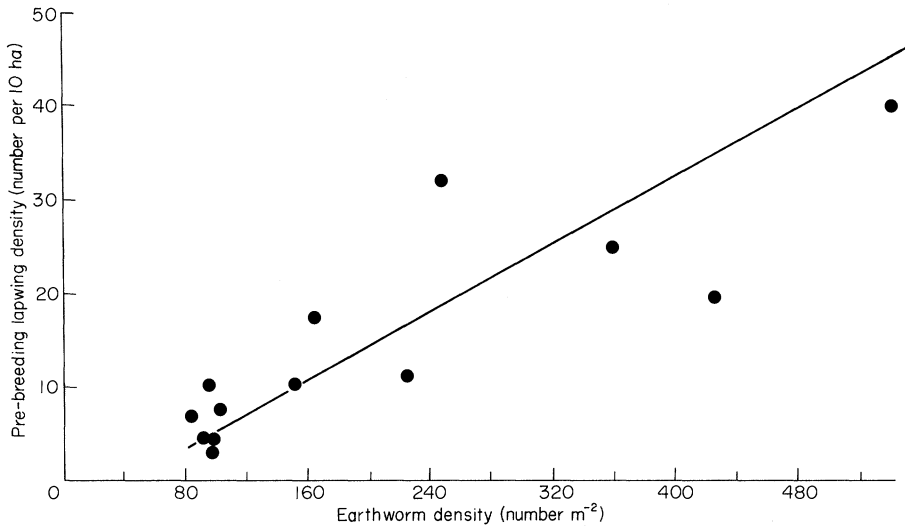


FIG. 1. The relationship between earthworm densities in April and the pre-breeding densities of lapwing (1–22 March) on one grassland study area ( $r=0.86$ , d.f. = 11,  $P<0.001$ ).

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 increased proportion of small species. Improvement did not change the density or the biomass of tipulid larvae but the species composition changed with a marked increase of *Tipula paludosa* Meigen.

#### *Distribution of lapwing with respect to food availability*

When lapwing densities in the pre-laying period were considered, a strong positive correlation with earthworm densities existed ( $r=0.86$ , d.f. = 11,  $P<0.001$ ) (Fig. 1). In the pre-laying period (1–21 March) high densities of lapwing were found on certain improved fields where feeding flocks of up to fifty birds gathered. Overall, 75% of these birds were females ( $n=145$ ), compared to only 36% of birds occupying fields subsequently used extensively for breeding ( $n=130$ ) ( $\chi^2=40.9$ , d.f. = 1,  $P<0.001$ ). 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 necessarily determined by food availability within the field used for breeding, but by the proximity of high quality feeding areas. Each of the study had such 'neutral' fields frequented by female dominated feeding flocks. However, a few weeks later, these improved fields used for feeding contained either no breeding lapwings or only an occasional pair and could be considered as undefended or 'neutral'. 'Neutral' fields contained high earthworm densities (248–534  $m^{-2}$ ) and were probably important for building up reserves for egg production with minimal sexual harassment.

Lapwing distribution in the breeding season was markedly different from that in the pre-laying period. Earthworm densities varied considerably, but overall there was a negative correlation with the breeding density of lapwing ( $r=-0.30$ , d.f. = 43,  $P<0.05$ ) (Fig. 2). The highest densities of earthworms were found on improved fields where the densities of breeding waders were typically low. It would appear that earthworm density



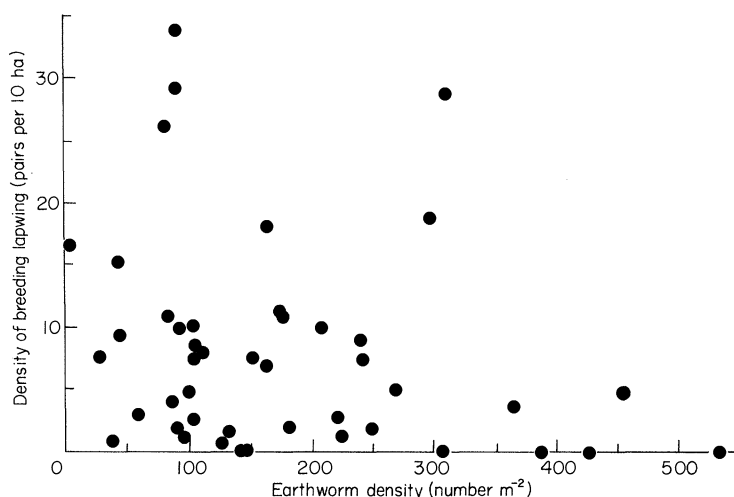


FIG. 2. The relationship between the density of earthworms in April and the density of breeding lapwing on upland, marginal grassland ( $r = -0.30$ , d.f. = 43,  $P < 0.05$ ).

did not influence breeding field selection and that other factors, e.g. availability of arthropods, moisture content of the soil, and vegetation type and structure, are more important.

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 main components of the surface invertebrate fauna sampled from pastures between mid-May and mid-July, were not significantly correlated with the density of breeding lapwings; carabid beetles ( $r = 0.57$ , d.f. = 10), staphylinid beetles ( $r = 0.38$ , d.f. = 10), other beetles ( $r = 0.46$ , d.f. = 10) and spiders ( $r = 0.17$ , d.f. = 10). When data on beetles were combined, abundance was significantly correlated with lapwing density on pastures ( $r = 0.70$ , d.f. = 10,  $P < 0.02$ ) (Fig. 3), but not on meadows. However,

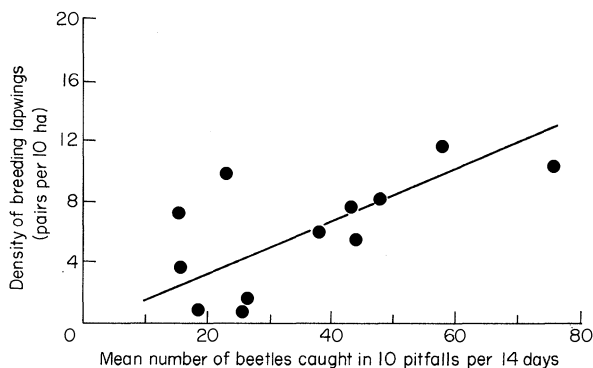


FIG. 3. The relationship between beetle abundance between mid-May and early July and the density of breeding lapwing on upland, marginal pastures ( $r = 0.70$ , d.f. = 10,  $P < 0.002$ ).

TABLE 4. The volume of lapwing eggs (cm<sup>3</sup>) on unimproved and improved grassland and on arable land (*n* = number of clutches measured)

	1986				1987		
	<i>N</i>	Mean	S.E.		<i>n</i>	Mean	S.E.
Unimproved grassland	196	24.15	0.11	***	27	24.95	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

\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

in meadows, increasing grass length reduces feeding efficiency, especially when taller than 15 cm and such areas are vacated (Klomp 1953); therefore, food abundance in meadows was not considered because few chicks feed there.

#### *Egg volumes*

Predictably, as females were using the same 'neutral' fields for building up reserves for egg production (see previous section), there were no within-year differences in mean egg volume between eggs laid on unimproved grassland, improved grassland or on arable land (Table 4). However, larger eggs were laid on all field types in 1987, the difference being significant for unimproved grassland and arable land ( $t = 3.29$ , d.f. = 221,  $P < 0.001$  and  $t = 3.00$ , d.f. = 52,  $P < 0.01$ , respectively).

#### *Chick growth rates*

The possibility of lowered food availability to lapwing chicks following improvement was investigated by measuring chick growth rates. The fields used by chicks were divided into two categories according to whether more or less than the median value of 120 beetles were caught in ten pitfall traps between mid-May and early July 1986. The growth rates of chicks from each of the two categories of site showed no significant difference with mean weight increases of  $5.7 \pm 0.2$  g day<sup>-1</sup> ( $n = 88$ ) in areas of low food availability and  $5.3 \pm 0.2$  g day<sup>-1</sup> ( $n = 92$ ) 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 compared with those for chicks reared on improved pasture in 1985, 1986 and 1987 (Table 5). Only in 1985, a dry year, was there a significant difference, with chicks on unimproved pastures growing at  $6.1$  g day<sup>-1</sup> over the linear part of the growth curve, and chicks on improved pastures at  $5.1$  g day<sup>-1</sup> ( $t = 3.33$ , d.f. = 219,  $P < 0.001$ ). In 1986, a wet, cool year, 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.

#### *Destruction of clutches*

The third 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 was expected that more lapwing clutches on improved land would be destroyed directly by farming

TABLE 5. The growth rate of lapwing chicks ( $\text{g day}^{-1}$ ) over the linear part of the growth curve on unimproved and improved pastures

	1985			1986			1987		
	<i>n</i>	Mean	S.E.	<i>n</i>	Mean	S.E.	<i>n</i>	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

\*\*\*  $P < 0.001$ .

activities. Meadows are managed more intensively than pastures and are often subjected to land-rolling, chain-harrowing and spreading of fertilizer (inorganic, organic or both). Improved pastures usually have only inorganic fertilizer applied, whilst unimproved are occasionally limed. Table 6 shows that overall, 22% of clutches laid on improved meadows were destroyed by farm machinery compared to 8% on unimproved meadows ( $\chi^2 = 5.46$ , d.f. = 1,  $P < 0.02$ ). The proportion of clutches destroyed by machinery on both unimproved and improved meadows was approximately four times higher than on their pasture counterparts ( $\chi^2 = 5.5$ , d.f. = 1,  $P < 0.02$  and  $\chi^2 = 7.5$ , d.f. = 1,  $P < 0.01$ , respectively). Only 6% of clutches on improved and 2% on unimproved pastures were destroyed by machinery. Over the 2 years 1986 and 1987, 12% of clutches on arable land were lost to agricultural activities.

The year-to-year variation in the proportion of clutches destroyed by farm machinery reflected 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 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 pastures were trampled by livestock; up to 3% of clutches were destroyed on unimproved pastures and 2% on improved.

### Experimental evaluation of predation

The results from the previous three sections clearly show that predation of clutches is the principal factor involved in reducing the density and breeding success of lapwings on improved pastures. This conclusion was experimentally tested.

During the first week of May 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 sixteen 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.

TABLE 6. The proportion of lapwing clutches destroyed by farm machinery during rolling, harrowing and fertilizing on different grassland types

	1985		1986		1987		Total	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
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

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

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, for 3 days and for a final time after 7 days, so enabling any predation to be divided into diurnal and nocturnal. Clutches were

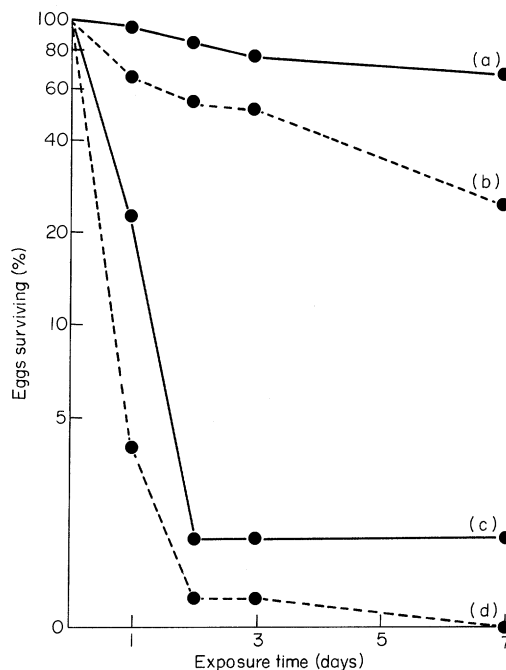


FIG. 4. The survival of simulated lapwing clutches in May 1987 on: (a) unimproved pastures, with breeding lapwings present; (b) improved pastures with breeding lapwings present; (c) unimproved pastures with no breeding lapwing; and (d) improved pastures with no breeding lapwing.

relocated using compass bearings from nearby landmarks and their contents examined from a distance of about 3 m, 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.

After exposure for 1 day to predators in areas containing breeding lapwing, five times more clutches were taken on improved than on unimproved pastures ( $\chi^2 = 15.3$ , d.f. = 1,  $P < 0.001$ ) (Fig. 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 ( $\chi^2 = 23.4$ , d.f. = 1,  $P < 0.001$ ). In fields which did not contain breeding lapwing, 22% of eggs survived 1 day's exposure on unimproved pastures, but only 4% on improved ( $\chi^2 = 10.8$ , d.f. = 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 pressure was significantly higher in fields without breeding lapwing ( $\chi^2 = 85.1$ , d.f. = 1,  $P < 0.001$ ) due to the lack of birds to harass and exclude potential clutch predators.

All predation during the experiment took place during daylight hours, no predation occurred during the night.

## DISCUSSION

### *Predation*

The effect of predators on ground-nesting birds is well documented (Picozzi 1975; Brykjedal 1980; Erikstad, Blom & Myrberget 1982; Elliot 1985; Potts 1986). Many wader species nest in open habitats with little or no vegetation cover and rely on cryptically coloured eggs. In this study, clutch predation was lower on unimproved pastures than on any other grassland type. On unimproved pastures, the diverse vegetation forms and irregular broken surface combined to create a disruptive background of mosaics. Within this habitat, clutches and incubating birds tended to be less obvious to predators. Conversely, improved pastures were more uniform and lacked the structural diversity found in unimproved pastures. The vegetation did not have a disruptive effect on nest detection, and eggs were more conspicuous to aerial predators, hence predation was greater. This has been clearly supported by the experimental study on predation of clutches put out in the field, with approximately twice as many clutches on improved pastures being taken by predators as on adjacent unimproved fields. Predation of the eggs was the principal factor limiting lapwing productivity. On improved fields, the excessive predation resulted in insufficient fledglings to maintain the population at the correct density. Similarly, Skeel (1983) found that whimbrel *Numenius phaeopus* nesting in a hummock-bog habitat, 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. Schranck (1974) found that waterfowl nesting within denser vegetation had higher hatching success. Jones & Hungerford (1972) and Dwernychuk & 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.

Higher densities of lapwing were found in unimproved pastures, 54 pairs per 100 ha, than on improved pastures, 14 pairs per 100 ha (Baines 1988). Higher densities may give more effective protection from predators through joint efforts in detecting and harassing 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. My experimental study

suggested the importance of other lapwings in the same field as a factor reducing egg predation. After 1 day, approximately six times more clutches were taken by predators in fields without breeding lapwing than in fields where breeding lapwing were present.

Myrberget (1972) suggested that corvid predation on eggs may lead to reduced numbers of willow ptarmigan. In this study, it is proposed that a high level of predation of lapwing clutches on improved pastures caused reduced productivity and significant reductions in breeding densities on improved grassland. A line of evidence frequently used to support the role of predation in determining breeding success is that prey often increase when their predators are removed. Reductions in mammalian predators resulted in increases in hatching success of ducks (Balser, Dill & Nelson 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 (Potts 1986). Experimental removal of predators is required to evaluate more fully the role of predation in determining breeding success and population dynamics of the lapwing.

#### *Food availability*

Differences in food abundance were found between unimproved and improved fields. Despite fewer surface-active invertebrates on improved fields, particularly carabid beetles on which foraging chicks often fed, invertebrate food was plentiful on both field types and there was no evidence of chicks starving in 1986 or 1987. Growth rates were high and similar in 2 out of 3 years considered. Only in the dry spring of 1985 was there a difference between the growth rates of chicks in the two types of field, with those on unimproved fields growing faster than those on improved fields. Jackson & Jackson (1980) have already found that dry conditions provide less suitable feeding conditions for lapwing chicks by reducing the activity of surface invertebrates (Potts 1986), forcing earthworms deeper into the soil (Gerard 1967; Nordstrom 1975; Rundgren 1975) and by making the ground too hard for subsurface probing. Improved fields, being better draining, are more susceptible to drying out.

There were small but significant differences between the growth rates of lapwing chicks in each year of the study, which probably reflect differences in the abundance or availability of invertebrates. The spring of 1986 was cold and the growth rates of lapwing chicks were significantly reduced relative to 1985 and 1987. Low temperatures render invertebrates less active and therefore less available (Avery & Krebs 1984), and result in the chicks being brooded for longer periods, thus reducing foraging time (Green 1984).

No significant difference was found in the growth rate of lapwing chicks reared in fields of differing beetle or other invertebrate abundance. This is in contrast to increased survival of partridge *Perdix perdix* and pheasant *Phasianus colchicus* chicks with increasing density of prey arthropods. This evidence suggests that adequate levels of food were available in all fields used in the study. Certainly, there was no evidence that food shortage resulted in appreciable chick mortality. However, in drier areas, particularly in the east of the country where rainfall is considerably less, chick mortality through reduced foraging success may be more important.

#### *Agricultural practice*

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 and destroyed all clutches. The period during which

improved meadows are suitable for nesting has been reduced by rapid grass growth making them unsuitable for lapwing and so curtailing the breeding season (Lister 1964). Hence, lowered productivity on improved meadows is attributable to more intensive management resulting in higher clutch loss to agricultural activities and the production of a faster growing grass sward that leaves insufficient time for replacement clutches.

Wader nest losses through trampling by stock has been studied in the meadows of The Netherlands (Beintema *et al.* 1982; Beintema & Muskens 1987). About 40% of lapwing nests, 60% of snipe nests and 72% of redshank nests were trampled at a stocking density of one cow ha<sup>-1</sup>. 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 (Baines 1988).

The key factor determining the breeding success of lapwings on improved areas was predation of clutches. The effect of predation was increased by clutch loss due to agricultural activities. These factors resulted in a reduced fledgling production insufficient to maintain the population at existing levels and have probably been largely responsible for the 69% reduction in lapwing densities on improved grassland. Whilst differences in food availability did occur, this had only minor effects on breeding success in this study.

#### ACKNOWLEDGMENTS

I especially thank J. C. Coulson for his supervision and advice during this study. J. Butterfield, P. R. Evans, G. R. Potts and anonymous referees commented on earlier drafts of this manuscript. I am grateful to A. J. Martin for her help in sorting invertebrates and drawing the figures. I also thank G. Longrigg for his assistance in the field and J. Mather for typing the manuscript. The black-headed gull eggs were taken under licence from the Nature Conservancy Council. The work was financed by a NERC studentship.

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(Received 21 July 1988)