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EFFECTS OF AGRICULTURE ON THE BREEDING ECOLOGY OF LAPWINGS *VANELLUS VANELLUS*

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SUMMARY

(1) The breeding ecology of lapwings (*Vanellus vanellus* L.) in relation to predation and agricultural land-use was compared in rough grazing and arable study areas in the Midland Valley of Scotland in 1984–86.

(2) The laying season extended from late March until late May but was truncated on the arable site by crop growth in the spring cereal fields (the preferred nesting habitat).

(3) In both study areas, the modal clutch size was four eggs (78% of clutches) and was not affected by laying date or whether or not previous clutches had been laid that year.

(4) Hatching success was not affected by breeding density and the main cause of clutch failure was predation (most severe on the rough grazing study area); but early season losses due to cultivation were also heavy on the arable site. Disturbance by cultivation during laying was responsible for a greater frequency of smaller clutches early in the season than later on the arable site.

(5) Chick movements, hatching and fledging success were heavily influenced by a combination of predation, weather, crop type and growth rate and timing of cultivation.

(6) Productivity on the arable site was not normally sufficient to maintain the population. The main causes were egg losses during cultivation and poor chick survival due to crop growth.

INTRODUCTION

The effects that recent agricultural intensification might have on British animal populations are conjectural. Drastic effects, such as those due to the overuse of pesticides, have been well documented but the more subtle consequences of habitat modification are less easy to detect. There have been reports of reductions in local breeding populations of waders following changes in agricultural land-use (Green 1980; O'Connor & Shrubbs 1986). Such consequences, however, are likely to vary between species according to the extent of their adaptation to their particular agricultural habitat; timing of breeding, feeding and nest-site specialization in relation to cultivation régime, crop type and growth, and whether the young feed themselves or are fed by the adults may all be important.

Throughout their European breeding range, lapwings (*Vanellus vanellus* L.) are primarily farmland waders. The success of their adaptation to agriculture is evident in their abundance throughout the once afforested areas of the northern Palearctic, where they are now probably commoner and more widespread than before agricultural development. There is a danger, however, that the rate of change of contemporary agricultural patterns and processes will prove detrimental to lapwing populations. In Britain, the scale of agricultural change has been greatest and most rapid on arable land, a

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favoured lapwing breeding habitat (Galbraith & Furness 1983; Galbraith, Furness & Fuller 1984). Studies elsewhere on European arable land have detected low breeding success and population declines (Beser & Helden-Sarnowski 1982; Matter 1982; Kooiker 1984).

In this paper, lapwing breeding success and productivity in their two main Scottish agricultural habitats are compared. The factors responsible for inter- and intra-habitat differences were investigated, and the consequences of land-use changes for population stability are discussed.

STUDY AREAS

The two study areas, in the Midland Valley of Scotland, differed widely in topography and land-use.

Arable site

This was at sea level on the Carse of Stirling (NN7395) and comprised 9 km² of flat, well drained and intensively cultivated farmland on which the main crops were cereals (45% of the total land area), grass for hay and silage (30% land area) and permanent pasture (19% land area). Root crops, oilseed rape, peas, roads and farm-buildings made up the remainder. The arable site was surrounded by similar habitat on most sides, except where some local afforestation had taken place.

Rough grazing site

This was in c. 8 km² of largely unimproved, poorly drained hill farmland at 150 m above sea level (NN6192). Most of the area was only partly enclosed and provided grazing for a few beef cattle and sheep. The vegetation was dominated by coarse grasses (mainly *Deschampsia flexuosa* L., *Nardus stricta* L. and *Molinia caerulea* L.), moor rush *Juncus squarrosus* L. and stunted heather *Calluna vulgaris* L. In the wetter areas, *Juncus* spp., cotton grass *Eriophorum vaginatum* L. deer sedge *Scirpus caespitosus* L. and sphagnum mosses predominated. In places, an attempt had been made to improve the quality of the land by the application of lime and these areas contrasted with the surrounding unimproved land because of the dominance of greener, lusher grasses, and a greater abundance of herbs and legumes. More or less widely spaced *Juncus* clumps were dotted about these improved areas. Grazing kept the vegetation short, particularly in the improved areas where cattle and sheep concentrated and where the mean grass height was c. 5 cm in June–July, compared with 10–15 cm on the unimproved areas. Like the arable site, the rough grazing study area was largely surrounded by similar habitat.

METHODS

Estimation of first egg dates

The date on which the first egg of a clutch was laid and expected hatching dates were estimated by one of two methods. (a) If the clutch was found prior to the last egg being laid, the first egg and clutch completion dates were calculated on the assumption that the laying interval between successive eggs was 2 days. Published laying intervals range from 1 (Klomp 1951) to 2.8 days (Heim 1974), and any errors incurred by assuming an interval of 2 days are likely to be small. The expected **hatching** date of each clutch was estimated as

25 days after clutch completion, since that was the mean of fifteen accurately measured incubation periods (Galbraith 1986). (b) Most nests were found after the last egg had been laid, and the first egg and expected hatching dates were estimated from the mean egg density (mean egg weight/mean egg volume (obtained from $\text{length} \times \text{breadth}^2 \times 0.457$; Galbraith 1988a)). The density of avian eggs decreases during incubation mainly because of water loss (Drent 1970; Rahn & Ar 1974; Furness & Furness 1981). The eggs in sixty clutches of known hatching date lost, on average, 16.8% of their fresh weight. Density measurements from these clutches gave a predictive equation of: days till hatching = $150.84 \text{ density} - 140.68$ ($r = 0.905$, $P < 0.001$), with a mean error (the mean deviation from the regression line) of 2.3 days (S.D. = 1.876).

Once the hatch date of each clutch of unknown age had been estimated, the first egg date was calculated by assuming that (i) there was a laying interval of 2 days between each egg; and (ii) incubation began when the last egg was laid and lasted 25 days. Egg density was only used to estimate stage of incubation if neither laying dates nor hatching dates were known.

Hatching success

Each nest position was marked with a short length of garden cane stuck upright in the ground 20–30 m from the actual nest site. Nests were checked at intervals of 3–4 days and more often near to hatching. Marking and visiting nests did not affect their survival (Galbraith 1987).

Daily nest survival rates and hatching success were estimated by Mayfield's (1961 and 1975) method and confidence limits were calculated by the method of Johnson (1979) and Hensler & Nicholls (1981).

Most nests were visited on the day of hatching to ring the chicks. However, in a few cases, the nest was empty when visited and then the presence or absence of eggshell fragments in the nest lining was taken as evidence of successful hatching. The lining of nests that successfully hatched chicks invariably contained small eggshell fragments, a feature previously noted in other wader studies (e.g. Nethersole-Thompson & Nethersole-Thompson 1942; Higgins & Kirsch 1975). Unsuccessful nests did not show this feature.

Predation of clutches was identified either by the presence of partially eaten eggs in or close to the nest, or the complete disappearance of the clutch. Clutch destruction by cultivation was the other important cause of nest failure and signs of this were obvious, i.e. the complete disappearance or flattening of nest and contents as the ground was ploughed or rolled.

Marking breeding adults

Some adult lapwings were individually recognizable by soft-part or plumage characteristics. These were too few to constitute adequate sample sizes for investigating breeding success and it was necessary to mark birds. Various marking methods were used: (a) chicks were given unique combinations of colour rings and a few of these birds returned as breeding adults in subsequent years; (b) nest-trapping and marking of breeding adults; clap-netting was effective in catching adults on their nests but resulted in desertion at four out of twenty nests and was discontinued as a catching method; (c) the least intrusive method was marking using nest 'sponges'; wads of cotton wool soaked in an aqueous solution of picric acid were placed in plastic culture dishes in shallow depressions on the rim of the nest cup. When the adults sat on the nest, the sponge dyed

their white breast feathers yellow. Some adults refused to sit on sponges that were too obvious; however, they returned to the nest and quickly resumed incubation if the sponge was camouflaged by a thin layer of dried sphagnum moss. The moss soaked up the dye and transferred it to the feathers.

Using a combination of these techniques (with most emphasis during the last 2 years of the study on nest sponging), sufficient numbers of adults were individually marked to allow the nesting success of individual pairs to be investigated. Totals of 21, 43 and 50 birds were marked in the 3 consecutive years of the study, respectively (1984–86), and these comprised *c.* 25%, 45% and 60%, respectively, of the study populations.

Fledging success, chick mortality and productivity

The survival of study broods was checked from a vehicle or hide at 2–3-day intervals. Once located, a brood was watched, without disturbing it, until I was confident that my brood-size estimate was accurate. This was easy when the chicks were small, since they generally stayed close to the parents and were brooded periodically. Older chicks wandered further from the adults and estimation was more difficult. In spite of this difficulty, the method worked well, since I seldom had to increase my estimate of brood size after subsequent checks.

Only broods in which the chicks or females were individually marked were used in the investigation of nestling mortality and fledging success. Wader chicks are able to move considerable distances after hatching and it was possible that broods thought to have died had merely left the study areas. This is unlikely, however, since (a) the longest brood movement recorded was only 1.5 km and the study areas were large by comparison; (b) frequent searches carried out on all suitable land peripheral to the study areas failed to reveal any missing study broods; and (c) most adults apparently left the study areas soon after failing but similar proportions of failures were confirmed in both study areas by finding colour-marked adults without their chicks (rough grazing: 10 out of 42 failed broods, arable: 11 out of 33, $\chi^2 = 1.71$, 1 d.f., N.S.). This indicates that there were no serious biases due to differences in brood detectability between study areas. Nonetheless, the possibility of broods escaping detection means that my chick survival and productivity estimates were minima.

Fledging was taken to occur when the chicks were able to fly. Although a more suitable criterion might have been when they became independent of their parents, this was impossible to ascertain since many flying juveniles apparently left the study areas still in the company of their parents.

Brood habitat use

After hatching, chicks in arable areas usually moved to pasture fields. Not all pasture fields were equally attractive, since some were used regularly and by many broods whereas others were not used at all. These apparent preferences were tested by regularly censusing the broods in all eighteen of the pasture fields and converting the maximum count to maximum brood density (MBD) by dividing by field area. The grass height in each field was measured by randomly throwing a 0.25 m² quadrat ten times, measuring the height at each corner and calculating the mean height (MGH). The grazing intensity was assessed by counting the number of cowpats within a circular quadrat 5 m in radius from the centre of each randomly thrown quadrat and calculating the mean cowpat density (MCD). Stock was regularly moved between fields and MCD is thought to be a better indicator of grazing intensity than counts of grazing animals. MCD was negatively correlated with

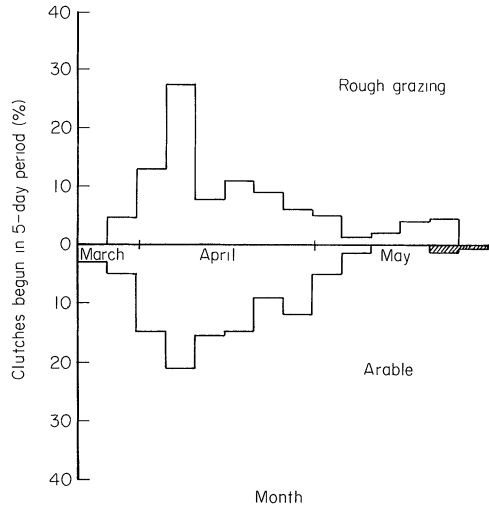


FIG. 1. Distribution of first-egg dates in 154 rough grazing and 135 arable clutches in 1984 and 1985. The hatched area denotes clutches in arable fields cultivated abnormally late in the spring.

MGH ($r = -0.58$, $P < 0.02$) indicating that intensive grazing resulted in a shorter sward. Multiple regression was then used to identify the variables important in determining whether broods used particular pasture fields.

RESULTS

Factors affecting the timing and duration of the laying period

Habitat

Laying began at the same time on the two study sites, although a smaller proportion of the clutches on the arable site was laid in May (Fig. 1). The preferred nesting habitat on the arable site was spring cereals (this comprised only 35% of the available habitat yet held 68% of all nests; Galbraith 1988b). Lapwings are open-country nesting birds and require uninterrupted views from the nest. In early April when crop growth was in its initial stages, spring cereals was a suitable nesting habitat, but by May the crops were about knee-high and were no longer suitable. The few clutches begun on the arable site in mid-late May (shown hatched in Fig. 1) are further evidence that crop growth may shorten the laying season. These were all laid in fields that had been cultivated about 6 weeks later than normal, when the crops in all other fields were *c.* 20–30 cm high. Furthermore, at least two of these three clutches were laid by females that had failed 3–4 weeks earlier on more typical cereal fields and had joined flocks of other failed breeders. These birds had apparently suspended breeding but left the flocks and quickly colonized the new bare-ground nesting habitat as it became available. Thus, by cultivating these fields in late May, suitable breeding habitat was once more made available in an area that had become unsuitable because of vegetation height.

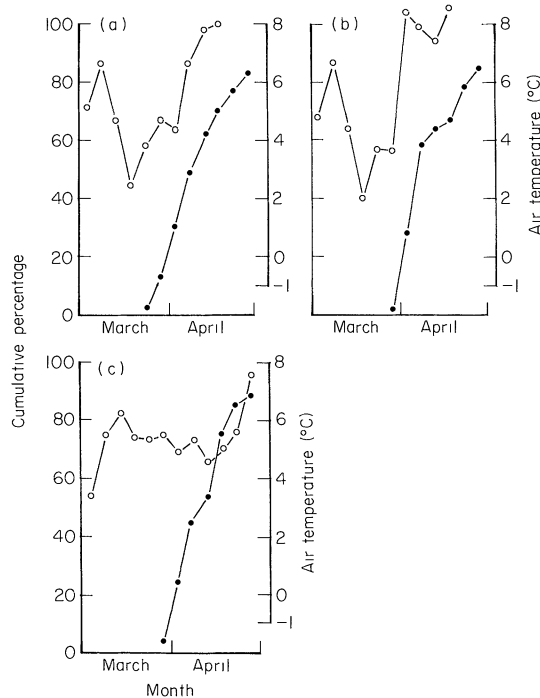


FIG. 2. Mean daily air temperatures (recorded at 09.00 h GMT and 1 m above ground level) and the cumulative percentage of clutches begun in both study areas in each 5-day period between March and April. (●) cumulative percentage, (○) air temperature; (a) 1984, (b) 1985, (c) 1986.

Weather

April and May 1986 were much wetter than in the two previous years but the timing of egg laying was the same (Fig. 2). In 1984 and 1985, the start of laying coincided with a consistent rise in air temperature. In 1986, this was delayed by about 20 days, yet laying began as normal. There was, therefore, little evidence of any relationship between weather conditions and the start of laying.

Factors affecting clutch size

Clutch sizes in the two study areas are shown in Table 1. These frequencies may have differed from those at the time of clutch completion because of partial predation of nests. However, the frequencies in nests checked within 5 days of clutch completion, and less

TABLE 1. Clutch size distribution (percentage frequency in parentheses)

	Clutch size				
	1	2	3	4	5
Rough grazing	0	4 (3.3)	23 (19.0)	94 (77.7)	0
Arable*	0	4 (4.7)	14 (16.5)	66 (77.6)	1 (1.2)
Both sites	0	8 (3.9)	37 (18.0)	160 (77.7)	1 (0.4)

* Nests begun on spring cereal fields prior to 10 April are excluded since their clutch sizes were probably affected by disturbance during cultivation.

likely to have been robbed (assuming that the likelihood of predation increases with the time the nest is available to predators), and in clutches checked later in incubation were not significantly different ($\chi^2 = 1.40$, $P > 0.50$).

The occurrence of the three main clutch size frequencies (3, 4, 2 and 5 lumped) did not differ significantly between study areas ($\chi^2 = 0.57$, 2 d.f., $P > 0.8$). However, significantly fewer than expected clutches of four eggs, and more than expected smaller clutches, were found in arable-site nests begun before 10 April in cereal fields (compared with nests begun after that date). Since this difference was not found in uncultivated fields (i.e. hay or pasture), it was likely to have been caused by egg losses due to cultivation interrupting laying (Table 2).

There were no significant differences between first and replacement clutches (i.e. relayings after the loss of the preceding clutch) laid by individual females in the same year ($\chi^2 = 0.62$, 1 d.f., $P > 0.40$). Moreover, dividing the clutch size data into two periods, clutches begun before or after 30 April, failed to reveal any significant seasonal trends ($\chi^2_{\text{arable}} = 0.38$; $\chi^2_{\text{rough grazing}} = 0.27$; $P > 0.40$, 1 d.f., $P > 0.95$).

TABLE 2. Clutch size frequencies in cereals and hay + pasture on the arable site for clutches begun before, on or after, 10 April

	Clutch size			
	Before 10 April		On or after 10 April	
	4	Other	4	Other
Cereals	10 (14.0)	12 (8.0)	29 (29.4)	12 (11.6)
Hay + pasture	32 (28.0)	12 (16.0)	32 (31.6)	12 (12.4)
	$\chi^2 = 4.710$, 1 d.f., $P < 0.05$		$\chi^2 = 1.257$, 1 d.f., $P > 0.80$	

Numbers in parentheses are those expected if the clutch size frequencies in each crop type and period conformed to the common frequency distribution for that period (the null hypothesis of the χ^2 test).

Factors affecting hatching success

Most egg losses were due to predation or destruction during cultivation (Table 3). The incidence of these factors varied seasonally and between study sites. Few eggs that survived the incubation period failed to hatch.

TABLE 3. Causes of egg failure on the arable and rough grazing study areas (all years combined)

	Eggs failed	Percentage of failures due to:			
		Predation	Cultivation	Infertility or embryo death	Other*
Arable	273	59.3	29.7	7.6	3.4
Rough grazing	293	89.4	0.0	5.4	5.2

* Includes trampling by stock and damage during handling.

Field use and laying date

There were no significant overall differences between study sites in hatching success (Table 4), but observations suggested that hatching success among early clutches on the arable site may have been reduced by egg losses during the cultivation of spring cereal

TABLE 4. Nest survival in the two main study areas

Year	Study area	Nests	Nest days	Clutches lost	P	S.E.	Hatch success (%)
1984	Rough grazing	68	1165	28	0.976	4.5×10^{-3}	45.9
1984	Arable	75	1252	42	0.966	5.1×10^{-3}	33.5 ^t =1.47, N.S.
1985	Rough grazing	54	747	31	0.958	7.3×10^{-3}	25.8
1985	Arable	27	348	20	0.942	1.2×10^{-2}	15.0 ^t =1.09, N.S.
1986	Rough grazing	30	400	17	0.957	1.0×10^{-2}	24.9
1986	Arable	33	412	16	0.961	9.5×10^{-3}	28.1 ^t =0.28, N.S.
All	Rough grazing	152	2312	76	0.967	3.7×10^{-3}	34.3
	Arable	135	2012	78	0.961	4.3×10^{-3}	28.2 ^t =1.04, N.S.

P is the daily survival probability, S.E. its standard error, and *t* was calculated from $P_1 - P_2 / \sqrt{v_1^2 + v_2^2}$ (Hensler & Nicholls 1981). Hatch success is the percentage of nests that hatched at least one egg ($P^{32} \times 100$).

fields (the preferred nesting habitat). This was investigated, initially, by separating the arable clutches into those on spring cereals or hay and comparing their daily survival probabilities. Clutches in spring cereal fields had a significantly lower survival probability, *P*, than hayfield clutches ($P_{\text{spring cereal}} = 0.956$; $P_{\text{hay}} = 0.983$; $t = 3.18$, $P < 0.01$). Cultivation on the arable site was normally completed by mid-April and, when the spring cereal and rough grazing clutches were subdivided by first egg date into two periods, clutches begun (i) on and before, or (ii) after 15 April, the earlier spring cereal clutches had a significantly reduced survival probability (Table 5; *t*-test comparing early and late spring cereal clutches: $t = 4.95$, $P < 0.01$). When this operation was repeated, but excluding all arable clutches known to have been lost because of cultivation, the difference in nest survival in clutches begun before or on 15 April was reduced and was no longer significant ($t = 1.50$, N.S.). Thus, the cultivation régime on the arable site apparently resulted in a significant reduction in hatching success among the birds nesting early in the preferred habitat, i.e. spring cereal fields. Hayfield clutches were too few to be included in this analysis.

TABLE 5. Effect of timing of laying on nest survival among spring cereal and rough grazing clutches

Habitat		Nests	Nest days	Clutches lost	P	S.E.	Hatch success (%)
Spring cereals	(a)*	66	755	54	0.928	9.4×10^{-3}	9.3
	(b)*	49	885	17	0.980	4.7×10^{-3}	53.7
Rough grazing	(a)	83	1221	39	0.968	5.0×10^{-3}	35.3
	(b)	71	1121	37	0.967	5.3×10^{-3}	34.1

P is the daily survival probability and S.E. its standard error. Hatch success is calculated from P^{32} .

* Clutches separated into two periods by first-egg dates: (a) before and on, or (b) after 15 April. 1984–86 combined.

Predation

When losses due to cultivation were excluded, there were no significant seasonal trends in predation intensity on either study area (Table 6). However, significantly fewer spring cereal than rough grazing clutches were robbed ($t = 2.11$, $P < 0.05$, both periods

TABLE 6. Predation intensity in relation to season among spring cereal and arable clutches

Habitat		Nests	Nest days	Robbed nests	Daily predation rate (1-p)	
Spring cereals	(a)*	44	634	21	0.033	} $t = 1.15$, N.S.
	(b)*	49	885	20	0.023	
Rough grazing	(a)	83	1221	45	0.037	} $t = 0.04$, N.S.
	(b)	71	1121	44	0.040	

* Samples separated into two periods according to first-egg date: (a) before and on, or (b) after 15 April. 1984-86 combined and losses due to cultivation excluded (see text), 1-p and t calculated according to method of Hensler & Nicholls (1981). Robbed nests lost at least one egg to predators.

combined). Most predation was thought to have been caused by crows (the eggs either removed entirely or with holes pecked in them) or unknown mammalian predators (eggs eaten in nest). There was no evidence that predation was anything other than the primary cause of failure, i.e. predation after desertion of the nest due to some other factor was not found.

Breeding density

Breeding lapwing groups communally defend their nests against predators and it might be expected that the denser the group the more efficient this defence might be. This was investigated by comparing nest survival in different breeding densities. After measuring the nearest-neighbour distances between nests on the rough grazing site, the total sample was subdivided into four categories (< 26, 26-50, 51-100 and > 100 m) and nest survival was compared. There were no significant differences in daily survival probability between any combinations of distance categories ($t < 0.78$). An alternative approach was made by comparing the density of nests within a 100-m radius of each nest that either hatched one or more eggs, or was entirely robbed. Although there was a tendency for a higher proportion of nests that were robbed to have no neighbours within a 100-m radius, the difference was not significant ($\chi^2 = 2.5$, 1 d.f., $P > 0.1$). There was, therefore, no convincing evidence for density dependence in hatching success.

Factors affecting chick survival and movements

Egg size and hatchling body condition are intrinsic factors that have already been shown to influence chick survival (Galbraith 1988a). In this section, putative extrinsic factors are considered.

Habitat

Fledging success was significantly poorer on the arable site than on the rough grazing site (Table 7; $\chi^2_{\text{all years}} = 6.06$, 1 d.f., $P < 0.05$). The difference was most marked in 1984 ($\chi^2 = 11.3$, 1 d.f., $P < 0.001$), less so in 1985 ($\chi^2 = 1.43$, 1 d.f., $P < 0.20$), and fledging success was similar on both sites in 1986.

In 1984 and 1985, the chicks on arable land left their natal cereal fields shortly after hatching and moved to permanent pasture fields (Fig. 3). In those 2 years, arable chick survival was poor (Table 7) and was influenced by the proximity of pasture to the nest field. Of twenty-eight chicks that hatched in spring cereal fields from which there was

TABLE 7. Fates of chicks on both study sites in 1984–86 (percentage fledging success in parentheses)

Habitat	Year	Chicks died	Chicks fledged
Arable	1984	94	7 (6.9)
	1985	35	6 (14.6)
	1986	33	15 (31.2)
	All	162	28 (14.7)
Rough grazing	1984	95	27 (22.1)
	1985	64	20 (23.8)
	1986	36	16 (30.8)
	All	195	63 (24.4)

direct access to pasture, 21.4% fledged, compared with 8.7% of eighty-one chicks that had to cross intervening hay or cereal fields, or the River Forth ($\chi^2=3.34$, 1 d.f., $P<0.07$). In 1986, crop growth was retarded by adverse weather, and arable chicks stayed in their natal spring cereal fields (Fig. 4). Fledging success, in that year, was high and similar to that on the rough grazing site (Table 7).

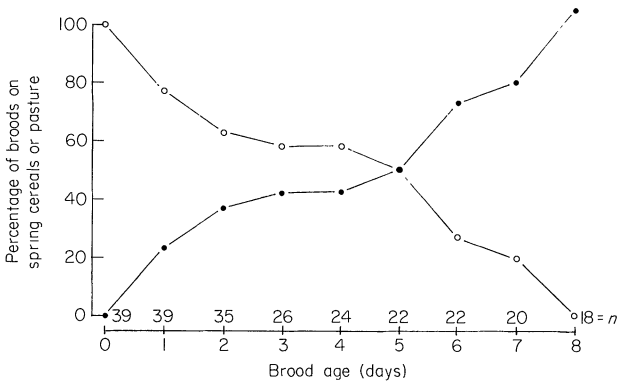


FIG. 3. Habitat use by recently hatched broods of lapwings on the arable study area in 1984 and 1985. (O) spring cereal, (●) permanent pasture fields.

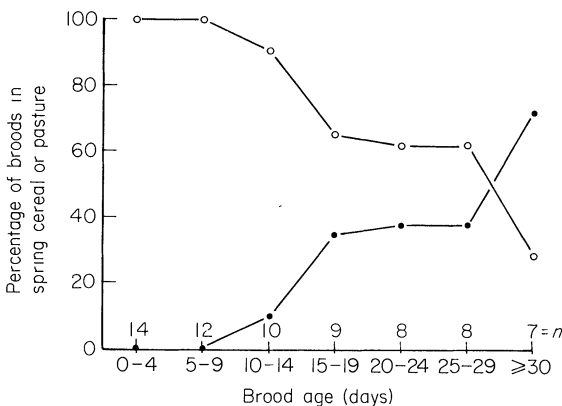


FIG. 4. Habitat use by lapwing broods on the arable site in 1986. (O) spring cereal, (●) permanent pasture fields.

The above results indicate that vegetation height in both the natal and chick-rearing fields was an important influence on brood movements and survival. However, food availability might also have been involved (Tables 8 and 9). Surface and subsurface invertebrates were more abundant in the habitats to which the rough grazing chicks moved (see below) as were subsurface invertebrates in the habitats to which arable chicks moved (subsurface invertebrates were sampled by soil coring and hand sorting, while surface invertebrates were sampled by pitfall trapping. For more detail of the sampling techniques, see Galbraith 1988b).

As arable fields dry out in summer, earthworms burrow deeper and aestivate (Edwards & Lofty 1972). During summer 1986, however, when the fields were permanently damp, earthworms may have remained closer to the soil surface and accessible to lapwing chicks. This too may have been a factor encouraging chicks to remain in their natal fields (although the fact that chicks that did remain in cereal fields moved to areas where the ground was entirely bare, because of failure of the seed to germinate, or largely bare because of stunted plant growth, indicated that crop growth is of overriding importance.)

The factors contributing to the 'attractiveness' of particular pasture fields were investigated using a stepwise multiple regression analysis in which MBD was the dependent variable and field area, MCD and MGH were the independent variables. Only MGH contributed significantly to the variation in MBD between fields (42.2% of the

TABLE 8. Mean numbers and dry weights of soil invertebrates in 0.04 m² and 10 cm deep soil samples from nesting (spring cereals, unimproved rough grazing) and chick-rearing habitats

Habitat	Number of samples	Lumbricidae		Tipulid larvae	
		Mean number per sample	Mean dry wt per sample (mg)	Mean number per sample	Mean dry wt per sample (mg)
Arable					
Spring cereals	15	5.1	128	0.8	5
Pasture	15	20.3***	881***	15.5***	182***
Rough grazing					
Unimproved	18	0.9	18	1.3	11
Improved	20	2.3**	102***	4.0**	32**

* Asterisks indicate significance levels when Mann-Whitney tests were carried out: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 9. Mean numbers and dry weights of surface invertebrates caught in pitfall traps on nesting (spring cereals, unimproved rough grazing) and chick-rearing habitats

Habitat	Number of trap-days	Mean numbers per trap-day	Mean dry wt per
			trap-day (mg)
Arable			
Spring cereals	143	0.2	4.9
Pasture	123	0.4	2.1
Rough grazing			
Unimproved	250	1.8	0.8
Improved	115	4.0***	1.4**

* Asterisks indicate significance levels when Mann-Whitney tests were carried out: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. One trap-day = 1 pitfall trap in place for 24 h.

variation explained), giving a regression equation of $\text{MBD} = -5.13 \text{ MGH} + 56.7$. Thus, chicks on the arable site moved to pasture fields soon after hatching but preferred those in which intensive grazing kept the grass short.

Rough grazing chicks also moved after hatching: the preferred nesting habitat on the rough grazing site was unimproved land (Galbraith 1988b), but most chicks left that habitat soon after hatching and moved to improved rough grazing where the sward was shorter. The unimproved rough grazing nesting areas were immediately adjacent to the improved areas and these movements were accomplished quickly with no high mortality.

Laying date

Rough grazing chicks were separated into four categories according to the first-egg dates of the clutches from which they hatched and their fates were compared (Table 10). Arable chicks were excluded from this part of the analysis because of the strong habitat influence on their survival.

Survival among the earliest three cohorts was similar but was lower in chicks from eggs laid late in the season. In addition to poorer survival, the late-hatched chicks grew more slowly (irrespective of their weight and size at hatching) than the earlier chicks (Galbraith 1986). This suggests that the higher mortality among the late-hatched chicks could be due to a deterioration in feeding conditions.

TABLE 10. Fates of rough grazing chicks according to the first-egg dates of the clutches from which they hatched

	First egg-date		(days after 1 March)	
	<46	47-61	62-76	>76
Chicks fledged (%)	37 (26.6)	15 (31.9)	11 (25.0)	0 (0.0)
Chicks died (%)	102 (73.4)	32 (68.1)	33 (75.0)	21 (100)

$\chi^2 = 8.42, 3 \text{ d.f.}, P < 0.05^*$

* 1984-86 combined. χ^2 value calculated by assuming that the proportions of chicks dying or fledging were unaffected by laying date.

Weather

The first few days after hatching is the most vulnerable period of a chick's life (see below). The possible effects of weather during this period were investigated by calculating the chill factor during the 5 days after hatching and comparing percentage survival among broods. The chill factor was given by $(20 - T) + R$, where T is the mean temperature at 09.00 h (GMT), and R is the mean daily rainfall during the period (after Makepeace & Patterson 1980; Thompson, Thompson & Nethersole-Thompson 1986).

A regression of the arcsine transformations of the percentages of broods that survived the 5 days after hatching against the chill factors during that period failed to reveal any significant trends ($n = 25, r = 0.05$). This result must, however, be treated with caution since it was difficult to ascertain the exact date of chick death. Furthermore, chick survival may depend more on micro-climatic features, e.g. the amount of shelter afforded by the surrounding vegetation, than the gross measurements used in the calculation of the chill factors.

Timing of chick mortality

The mortality patterns of chicks were investigated in 1984 and 1985. The patterns were similar on both study sites in that most deaths occurred during the first 10 days after

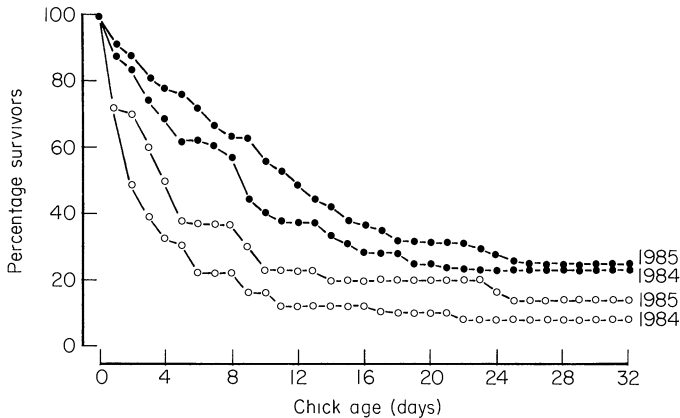


FIG. 5. Chick survival curves on the rough grazing (●) and arable (○) study areas. Initial sample sizes are, in rough grazing, $n=74$ (1984), 59 (1985); in arable, $n=49$ (1984), 30 (1985).

hatching (Fig. 5). Post-hatching mortality was, however, more severe on the arable site, where *c.* 80% of chicks died before they were 10 days old, compared with only 50% on the rough grazing site. On the arable site, the mortality rate was greatest during the first 5–6 days after hatching (when they were transferring from spring cereals to pasture) but levelled out after 10 days. On the rough grazing site, the initial mortality rate was less severe but did not begin to level out until *c.* 16 days after hatching.

Productivity

During the first 2 years of the study, productivity was higher on the rough grazing than on the arable study area (Table 11). The difference was most marked in 1984 (Mann–Whitney test; $z = -2.61$, $P < 0.01$), and less so in 1985 ($z = -1.18$, $P < 0.10$). Productivity was similar on the two sites in 1986 ($z = -0.34$, $P > 0.30$).

TABLE 11. Reproductive effort and productivity of female lapwings on the rough grazing and arable study areas (number of females in parentheses)

		Mean number of			
		Attempts per female	Eggs per female	Hatchlings per female	Fledglings per female
Rough grazing	1984 (30)	1.43	4.8	2.7	0.9
	1985 (25)	1.52	5.6	2.6	0.8
	1986 (19)	1.52	5.4	2.2	0.7
	All years (74)	1.48	5.2	2.5	0.8
Arable	1984 (24)	1.37	4.7	2.0	0.2
	1985 (16)	1.62	6.0	2.1	0.4
	1986 (22)	1.60	5.4	2.2	0.7
	All years (62)	1.52	5.3	2.1	0.4

DISCUSSION

Both predators and local land-use patterns exert important influences on the breeding ecology of lapwings on farmland. Egg and chick survival is affected by the intensity of predation, while crop type and growth rate and the pattern and timing of cultivation influence clutch size, the length of the laying season, hatching and fledging success.

Hatching success

Egg predation was the most important cause of failure to hatch on both study sites, accounting for *c.* 75% of all losses. Predation was unaffected by breeding density and was more severe on the rough grazing site where, because of the refuges offered by the numerous copses, isolated trees, rank areas of vegetation and dry stone walls, predators were commoner. Stoats and foxes were seen far more frequently on the rough grazing site and carrion crows were certainly commoner (as shown by the numerous old and extant nests).

Hatching success on the arable site was reduced further by egg losses during cultivation. Since most birds nested in spring cereal fields and the start of laying coincided with that of cultivation, these losses were seasonally heavy. Furthermore, arable clutches laid immediately after cultivation were abnormally small, probably because of the disruption to laying caused by cultivation. Thus, egg losses during cultivation helped reduce the final productivity of lapwings on the arable site, since birds ended up with smaller clutches than the usual four eggs. If a female is laying a clutch of four eggs and her nest is destroyed by cultivation when the clutch is incomplete, she may lay the remaining eggs in a new scrape and incubate this partial clutch (Klomp 1951). Moreover, rapid crop growth on the arable study area shortened the laying season and reduced the time available to make up for losses due to cultivation or predation.

Chick survival and brood movements

Most chick mortality occurred during the first few days after hatching and may have been due to the poor feeding efficiency of young chicks and their inability to regulate their body temperature (Chappel 1980).

On the arable site, the early mortality was more severe but of shorter duration than on the rough grazing site. This suggests that additional, habitat-specific, mortality factors were operating: during the first 2 years of the study, when the adults and broods moved from the natal spring cereal fields to pasture, a high chick mortality occurred (associated with a loss of weight and deterioration of body condition among chicks that failed to reach suitable pasture early (Galbraith 1986)). Chicks with access to suitable pasture undertook shorter, less hazardous journeys and survived better than chicks that hatched without easy access to pasture. In 1986, crop growth was delayed by severe weather early in the spring, chicks were able to remain in their natal cereal fields after hatching and survived better than in the 2 previous years.

Why should broods undertake such apparently hazardous movements? Food availability is one possible answer: in both chick rearing habitats (pasture and improved rough grazing) the prey biomass was significantly higher than in the natal areas. However, in the last year of the study, crop growth on the arable site was retarded and chicks remained in their natal cereal fields (although only in areas where the ground was bare because of poor germination or the vegetation was stunted). Thus, on the arable site at least, vegetation height may also be an important constraint on habitat suitability. Presumably, either adults are unable to watch over their broods efficiently in tall vegetation, or the mobility and feeding efficiency of the adults and chicks is reduced. Moreover, arable adults preferred to nest in spring cereal fields close to pasture fields (Galbraith 1988b), resulting in enhanced chick survival. Thus, the habitat mix (in particular the accessibility of short-grass pasture) and the timing of agricultural operations and crop growth in relation to that of breeding, were major determinants of breeding success on the arable land.

The earlier levelling out of the initial chick mortality on the arable site was probably due to a lower intensity of predation. After the initial mortality, there may have been few further losses because of scarcity of predators. On the rough grazing site, predators were commoner and chicks may have been exposed to a predation risk until later in development, when they may have been better at evading detection or capture.

On the rough grazing site, fledging success was low among later-hatched chicks. This was associated with slower growth and poorer body condition (Galbraith 1986), and may have been caused by a reduction in food availability. Earthworms burrow deeper during the summer months, and leatherjackets metamorphose into adults. These organisms are an important food source for lapwing chicks and their decreasing availability may explain the reduced chick survival. Thus, seasonal patterns of prey abundance might, ultimately, be an important influence on the timing of breeding in lapwings.

Productivity

Ring recovery studies suggested that the annual adult mortality of lapwings is *c.* 33% and the first-year mortality is 44% (Bak & Ettrup 1982). Ring recoveries consistently overestimate the mortality of waders, however (Evans & Pienkowski 1984). If the true adult and first-year mortalities of lapwings are similar to those of other waders of similar body size, *i.e.* 25–30% and 35–40%, respectively, each female in a hypothetical population would have to fledge, on average, 0.8 young year⁻¹ if the population was to remain stable. Whereas the rough grazing females produced approximately enough fledglings to maintain their population in all 3 years of the study, the arable females only did so in 1986. Clutch destruction during cultivation and poor chick survival mainly accounted for inadequate overall productivity on the arable site. Between the first and final year of the study, the arable lapwing population fell from 162 pairs to 98 pairs and local farmers thought that the population was previously much larger. Similarly low productivities and population declines were found during recent studies of lapwings breeding on intensively farmed European arable land by Matter (1982), Beser & Helden-Sarnowski (1982) and Kooiker (1984).

These results raise the obvious question: Why do lapwings nest in arable farmland when their breeding success is low there? Feeding conditions for the adults are better on the arable site, resulting in better maternal body condition, larger eggs and bigger and heavier chicks (Galbraith 1988a). However, given the reduction in productivity due to the land-use policy, these benefits are only short-term and are unlikely to explain entirely the prevalence of arable nesting. It is more likely that changes in the management of arable farmland may have only recently resulted in it becoming a less suitable nesting habitat than it once was.

The habitat mixture on the arable site has changed greatly over the last 10–15 years. These local changes match those that have characterized British arable farmland as a whole, with a reduction in the amount of livestock and pasture and more emphasis on cereal production. Whereas, during the 3 years of the study, pasture comprised *c.* 19% of the total land under crops, 15 years previously it comprised *c.* 50%; hay and cereals made up the remainder. As pasture fields were replaced with cereals, the amount of suitable nesting habitat increased, but easy access from those fields to pasture became more restricted.

The nature of the cereal crop itself has also changed: traditional crop varieties have been replaced with strains that are more tolerant of crowding, more resistant to diseases and pests, and faster growing. This has resulted in an earlier and denser crop with fewer

bare patches. Modern cereal fields are, therefore, more impenetrable and less hospitable habitats than they once were. In 1986, when harsh weather in the early spring simulated the more 'primitive' conditions by slowing down crop growth and creating bare patches in the fields, the chicks were able to remain in their natal cereal fields and survived as well as rough grazing chicks.

The attraction of short-term benefits derived from comparative security from predators and better feeding conditions, together with the nature of recent habitat changes, may explain the continued existence of lapwings on the arable site. If so, the situation is unstable and further population reductions might be expected if the recent trend towards the elimination of permanent pasture continues.

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