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AGRICULTURAL PRACTICES
AND THEIR EFFECTS
ON LAPWINGS

by

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INTRODUCTION

Recent decades have seen a substantial decline in the breeding population of the lapwing (Vanellus vanellus) on farmland in Britain (Marchant et al 1990). It is widely held that the causes lie in changes in agricultural practices. The aims of the research reported here were twofold. First, to draw together the very substantial literature pertaining to the species so that the evidence of effects of agriculture on lapwings could be assessed and critical areas for future research identified. Second, to analyse the long-term trends in breeding populations that have occurred on the farmland plots monitored in the BTO's Common Birds Census project, in relation to changes in cropping and weather. These two pieces of work are presented here as parts I and II respectively.

The literature review reveals that there is a very substantial body of scientific evidence indicating that lapwing populations have been affected by agricultural practices on both local and regional scales. However, a major gap in knowledge at the present time is the absence of any detailed study of the population dynamics of the species to assess the critical factors limiting lapwing populations.

The analysis of breeding population trends on CBC plots produced three particularly important findings. First, there is good evidence, on a local scale, that the temporal shift towards autumn sowing of crops was associated with large declines in lapwing populations on the farms concerned. Second, lapwings strongly prefer to nest on spring-sown crops. Third, an index of lapwing abundance in lowland England was found to be strongly related to weather, particularly the severity of the preceding autumn and winter. This last result is important in that it suggests lapwing populations are subject to an interaction between agricultural changes and weather. It is suggested that in recent years lapwing populations may have lost some their capacity to recover from effects of adverse weather; this may have come about as a result of agricultural changes. Research is needed on the population dynamics of lapwings to assess the relative effects of weather and agricultural changes; this should ideally incorporate an experimental approach as well as further analyses of existing data.
EUROPEAN LAPWING (*Vanellus vanellus*) POPULATIONS IN RELATION TO AGRICULTURAL CHANGES: A REVIEW

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1. INTRODUCTION

Within the temperate zone of western and central Europe, where man has been modifying the landscape for centuries, the lapwing Vanellus vanellus has become increasingly associated with farmland throughout its annual cycle. In recent decades, however, this terrestrial plover has experienced bigger difficulties as agriculture has become more intensive, through changes in grassland management and arable cropping practices, more regional specialisations in farming, and through extensions of active husbandry to marginal land. Lapwings have declined within or disappeared from many lowland areas, and this trend has stimulated considerable research into the species’ ecological requirements. However, the results of these studies are widely scattered in the literature, in several languages, and the time is right to produce a synthesis.

The present review of current knowledge of lapwing ecology will be limited to discussions of those factors which may influence the population levels of the species. In particular, those factors resulting from man’s activities will be examined in detail. Since much of the recent research has been conducted in western Europe (including Britain), the review will concentrate on lapwing populations there and, in particular, on those breeding on farmland.

The objectives of the review are:

1) to examine the long-term spatial and temporal trends in lapwing populations in western Europe;

2) to identify those farming practices which affect lapwing breeding success and/or adult survival;

3) to identify those factors which may control lapwing population levels, and which may have caused the observed changes in distribution and densities;

4) to identify aspects which require further research; and

5) to suggest practical means of conserving lapwings.

2 LONG-TERM TRENDS IN LAPWING BREEDING POPULATIONS

2.1 Britain: the period before 1950

For a long time now, pastoral man has been encroaching upon the lapwing’s natural habitats (rough grasslands, wetland fringes, saltmarshes) though concurrently creating suitable substitutes in the form of farmland. This trend has been especially pronounced since the mid-19th century, as human populations of western Europe have increased sharply, leading to the growth of towns and cities whose inhabitants demanded cheap foods from the countryside.
During the first half of the present century, European lapwings were influenced by several opposing trends. This was a period of temporary climatic warming (amelioration) in northern Europe, which enabled lapwings to colonise northern Scotland and the Faeroes and to spread northwards within Fennoscandia and the USSR (e.g. Kalela 1949). Yet there were also declines then in many areas of temperate Europe; these were attributed to habitat loss and excessive egg-colllecting, though cause and effect were not then investigated in the rigorous manner expected nowadays. In West Germany, for example, lapwings were said to have reached a low ebb in the 1920s and 1930s, but to have increased again after 1940 as more of them took to breeding on cultivated land (Glutz et al 1975).

In Britain, where adaptation to breeding on farmland is of long standing, there were numerous subjective reports of lapwing declines from the mid-19th century onwards. Excessive egg-colllecting (for human consumption) was often offered as a major cause, and considerable recovery was reported after implementation of a protective measure, the 1926 Lapwing Act (Alexander and Lack 1944). However, this later period also coincided with the nadir of English agricultural recession, in which arable gave way to stock rearing and neglected fields reverted to rough grazing, so that conditions became more favourable for breeding lapwings. Yet, since recession had been severe since the 1890s (except during the First World War years), the 1926 restrictions on egg-gathering almost certainly did play a part in the lapwing increase during the 1930s (Morton 1971).

The first large-scale lapwing survey conducted in Britain, in 1937-38, was directed towards habitat selection (Nicholson 1938-39), and no attempt was made to review numbers or status changes. Fisher (1941) assessed the lapwing breeding population of England and Wales at that period at 175,000 pairs. No revised figure was offered in the lapwing monograph by Spencer (1953), though this author noted that widespread decline in England and Wales had resumed during the agricultural revival which was generated by the Second World War emergency. Presumably decline then (the scale of which was not documented) involved some adjustment to the abrupt farming changes, though four severe winters during the 1940s were also implicated, especially that of 1946/47 (Spencer 1953).

2.2 Britain: the period 1950-1980

The 1940s and 1950s marked the first phase of the modern agricultural revolution, involving mechanisation, land drainage, a major introduction of chemicals (for fertilisers and pest control), and much increased areas given over to arable (especially cereal) production. Arable land in England and Wales increased by 1.94 million ha between 1938 and 1960, equivalent to 20% of improved farmland; this was mainly at the expense of lowland permanent grass. The rather meagre information available for this period suggests that, after initial adjustment, the national lapwing population was more or less stable until the early 1960s. By the time a second BTO Lapwing Habitat Enquiry was held, in 1960-61, local reports of lapwing gains and losses were
fairly evenly balanced and did not indicate that any marked general change in status was occurring (Lister 1964). Nevertheless, recent re-analysis of the 1960-61 data (Shrubb and Lack, 1991a) suggests that there may have been some regional changes then, with more reports of decline than of increase in northern and south-western counties but more of stability or increase in the arable counties of central, eastern and south-eastern England. All regional samples were small, however.

Shortly afterwards, lapwings were affected adversely by the severe winters of 1961/62 and 1962/63. Recovery from these coincided with the onset of the second phase of modern agricultural changes, which lasted until well into the 1980s. This phase was essentially one of increasing intensification and specialisation in farming: greater reliance upon agrochemicals, abandonment of rotations, enhanced regional concentrations on farming types (livestock versus arable), higher stocking rates on improved grass, switches from hay to silage and from spring to autumn sowing of cereals (greatly reducing spring tillage), plus the introduction of new crops such as oil-seed rape (also autumn sown).

These changes affected especially the English and Welsh lowlands; and after about 1970 a divergence was claimed between the lapwing population trends of northern and southern counties, as indicated by the BTO Common Birds Census (Sharrock 1976). According to those population indices, there was progressive decline in the south, though in the north there was compensatory increase. However, CBC indices have recently been recalculated, after a plot-reselection exercise and a change of datum year (Marchant et al 1990). The revised indices for lapwing are plotted in Figure 1, and these indicate a more confused picture. The suggestion there is that lapwings in central and southern England fluctuated between fairly narrow limits for much of the period (with a temporary increase around 1968-70), whilst in northern counties there was a more consistent pattern of increase which was reversed after 1981. According to these indices, the general decline became very marked from the mid-1980s onwards.

Such apparent regional differences must, however, be treated with some caution. Whilst it has been shown that CBC plots are representative of farming practices in central and southern England, this may not be true of the north (Fuller et al 1985). Moreover, with fewer plots in the northern samples, the figures derived from these are open to bias from censuses conducted on atypical farms. The data in Figure 1 are based on annual plot samples of 22-38 (mean 30) for the south, but only 8-17 (mean 14) for the north.

During the BTO Breeding Atlas survey period of 1968-1972 (see Sharrock 1976), lapwings were found to be still widely distributed, with breeding season presence in 91.8% of 10-km squares in Britain (compared to 65.5% of squares in Ireland). Then, the main distributional gaps in Britain were in the Scottish west highlands, south-western Wales, Devon and Cornwall. Sharrock offered an estimate of "over 200,000 pairs" for Britain and
Ireland combined. Since this was based on an (untested) assumption of 0.70 pairs/10km², and 78.3% of all occupied squares were in Britain, one may attribute some 160,000 pairs as the British portion. But this figure was clearly too low (see below).

2.3 Britain: the period since 1980

During the 1970s and early 1980s, the national CBC index for lapwing fluctuated between relatively narrow limits (Marchant et al. 1990). There was no indication from the CBC that lapwing numbers were affected seriously by the severe winters of 1978/79 and 1981/82; but after 1984 the national index fell sharply, and by 1988 it was only half that for ten years earlier. This suggested strongly that the decline was affecting northern counties also, with agricultural change as the most probable explanation (Marchant et al. 1990). Baines (1988) showed that lapwing densities were lower on improved than on unimproved grasslands in north-east England, a region where much agricultural improvement of upland grass had taken place.

In contrast, the EIO Waterways Bird Survey indices show little overall change between 1979 and 1988 (Marchant et al. 1990), possibly because riverside fields are more likely to include good lapwing habitat, which the birds may occupy preferentially when establishing their territories in spring. Shrubbs and Lack (1991b) are of the opinion that the lapwing decline in the 1980s has been exaggerated by the series of cold winters which marked this decade. There is no clear evidence for this in the CBC or WBS indices which, however, need to be interpreted cautiously in the light of the caveats given above. Additional analysis, still in progress, indicates that there probably was a cold winters effect in the 1980s, which worked together with agricultural changes to tip the balance firmly against lapwings (Tucker and Hudson, in prep.).

Within England and Wales, the damp lowland grasslands now hold only a small proportion of the total population of breeding lapwings. Less than 7,000 pairs in 1982-1983 (Smith 1983) probably represented only 5-6% of the total. This has fallen further since then; on a monitored sample of lowland grassland sites, lapwing numbers dropped by 37% between 1984 and 1989 (O'Brien 1990).

The numbers and distribution of lapwings in England and Wales were assessed by a further EIO enquiry held in April 1987 (Shrubbs and Lack 1991a). This was a sample survey of one randomly chosen tetrads (2km x 2km) within each 10-km square of the National Grid which contained any land. For each tetrads, a complete count was made of the number of nesting lapwings present plus details of the habitats they were using. From the data obtained, it was estimated that the lapwing breeding population of England and Wales was then 123,000 ± 14,000 pairs. No less than 96% of pairs located were on farmland. Lapwings were absent from 61% of the sampled tetrads, these being especially those in central and southern England and in Wales, where lapwings are now very thinly
distributed; there were particularly few in south-western England and in the western half of Wales. Just over 40% of occupied tetrads and just over 60% of estimated total numbers of pairs were in regions north of a line from the Humber to Cheshire, which comprised about 24% of the total area under survey. The major concentration was confirmed as being in north-western England on the west side of the Pennine ridge, where 75% of visited tetrads were occupied.

For 27 sites it was possible to compare lapwing numbers in 1987 with those counted in years around 1960, mainly from the BTO Enquiry of that time (Lister 1964). The samples were small and biased towards tilled farmland, but showed a consistent pattern of decline. This averaged 61% overall, and was least (-23%) in the north-west (Shrubb and Lack 1991g). Of course, it was possible that there had been some redistribution by lapwings during these 25 years, so that overall decline was less than this. In comparison, the estimate of 123,000 pairs in England and Wales in 1987 was 30% lower than Fisher's (1941) estimate of 175,000 pairs in the 1930s. Yet the latter figure may have been too low for that period; Fisher left no indication of the extent of sampling from which his estimate was derived.

The 1987 survey did not cover Scotland. There, Galbraith et al (1984) estimated from 1982-83 density sampling that there were approximately 64,000 pairs on Scottish agricultural land, including the Outer Hebridean machair. Densities average lower in other Scottish habitats, such as moorland and shingle, and Thom (1986) thought it reasonable to place the Scottish total at between 75,000 - 100,000 pairs. Population change there is believed to have been less than in England and Wales, for agricultural intensification has so far been less pronounced, but local decreases associated with grassland drainage and altered arable regimes have been noted (Thom 1986, Marchant et al 1990).

2.4 Recent trends in continental Europe

The latest available assessments of lapwing breeding numbers in European countries are listed in Table 1. Britain, the Netherlands and Finland are believed to hold the most, followed closely by Sweden, but in no other country is the population total believed to reach six figures. There is a general trend for the highest numbers to be in the northern and middle latitudes of the continent, but simple comparisons are invalid since countries vary greatly in size. Lapwing numbers become lower towards the south, though they have increased there (see below). These countries include mountainous areas that are less suited to this species.

The most recent overviews of population trends (Sharrock and Hilden 1983, Cramp 1983, Hilden and Sharrock 1985) indicate that lapwings are stable or increasing in most European countries (see Table 2). The reported trends are for increase in 11 countries, overall stability in 11, and decrease in five (excluding the British Isles). In particular, a modern southward spread is apparent. Until recently this applied to a wide longitudinal zone from Spain to the Balkans. But of late the expansion has halted in Spain, whilst in France there has been a considerable decline
which seems to be linked to reduced breeding success on agricultural land (Dubois 1990). Declines have also been reported from Finland and Sweden (Hilden 1989), parts of the Soviet Baltic States (Sharrock and Hilden 1983) and from Denmark (DOFP 1989). In Denmark at least, the decrease is attributed to land-use changes rather than any climatic factor (Ettrup and Bak 1985).
Surprisingly, perhaps, the literature does not provide any indication of major population changes in the agricultural zone of temperate Europe in any way comparable to those which have occurred in southern Britain, though various local ones are known.
It has, however, been noted that breeding success on intensive farmland in middle Europe is below the level required to maintain the numbers of lapwings, which are assumed to be dependent upon immigration by surplus birds reared in more favourable habitats (e.g. Imboden 1970, Matter 1982). More will be said on this subject later in this review (see 7.2).

3 FACTORS AFFECTING BREEDING SUCCESS:
HABITAT SUITABILITY

3.1 Some general points

Lapwing chicks, like those of other waders, are precocial: that is, they leave the nest soon after hatching and are led by their parents to suitable foraging sites. Hence, in areas of mixed farming, lapwings can exploit the range of field types which are available. In such mosaics, this often means that the birds lay their eggs on bare soil or newly-emerging crops and then, after hatching, lead their chicks to adjacent pasture where livestock grazing keeps the sward low throughout the breeding season, and where the grassland fauna provides a reliable food source for the young birds (Redfern 1982; Galbraith 1987, 1988a). In other faunistically-poor habitats also, such as blanket bog, lapwing chicks are led away to pasture soon after hatching (Redfern 1982). Even within rough grazing areas, chicks will be led from unimproved sections to lusher and greener improved grass (Galbraith 1988a,g). Thus there are different optimum conditions for nesting and chick rearing.

The 1987 BTO survey found that 96% of breeding lapwings in England and Wales were on agricultural land, varying from 90% in the south-east to 98% in East Anglia and northern England (Shrubb and Lack 1991a). On the basis of the figures given by Thom (1986), this applies to up to 85% of Scottish lapwings also. Hence farmland is much the most important habitat type for this species in Britain. In upland regions, lapwings are more likely to be found in valleys than on hills. High moorland is avoided in Scotland, as also are the exposed uplands of the English Lake District, Wales, Devon and Cornwall. This, however, is probably related to land-use regimes, since lapwings are well-represented in the Pennines where farming is more mixed (Shrubb and Lack 1991a).

In Britain there have been three major changes in farming practices which affect lapwings since the 1960-61 habitat enquiry by Lister (1964). First, there has been a major switch to autumn-sowing of cereals and of oil seed rape. Hence autumn tillage has
increased but spring tillage has declined. Autumn-sown crops are usually unsuitable for nesting lapwings by April since growth is too far advanced. Furthermore, on many farms the autumn sown cereals have been planted after minimal cultivation following burning of the straw and stubble of the previous crop, so that there has been no conventional ploughing at all. Second, pastures have often been drained, reseeded and high levels of nitrogenous fertiliser used to promote grass growth, which either produces too dense a sward for lapwing chicks to move about in, too dry a substrate, or is grazed at a higher stocking rate so that the trampling and desertion risks to lapwing nests are increased. Such grassland improvements can also affect plant diversity and vegetation structure, abundance and diversity of soil invertebrates, and soil pH values (Baines 1988). Moreover, the use of modern leys for silage rather than for hay cropping means more and earlier cuts per season, which may jeopardise chicks. Lastly, there has been a phasing out of rotational farming, accompanied by increased regional specialisation (livestock or arable), so that there is now much less of a farming mosaic in the lowlands which reduces lapwings' habitat choice. As a consequence of these changes, lapwings have become more dependent for nesting upon the much reduced acreages of spring tillage and rough (= unimproved) grassland, which have declined more rapidly in southern Britain than in northern counties (Shrubb 1990; Shrubb and Lack 1991a).

3.2 Nest site suitability on tillage

The strong preference by lapwings for nesting on bare tilled land or on bare patches within sprouting arable crops (Spencer 1953, Shrubb 1990) is believed due to three advantages that are conferred by such situations: good feeding conditions for egg formation by females, camouflaged concealment of unattended eggs, and clearer views of any approaching predators. Klomp (1954) considered that lapwings could judge the grey-brown or grey-green tints to fields in spring in order to discriminate in favour of those on which plant growth would not become too tall during the nesting phase. Inboden (1970, 1971) noted, in his Swiss study, that dark and as-yet unvegetated arable ground was preferred, though agricultural practices there compelled up to 30% of pairs to nest on meadows which were sub-optimal due to rapid grass growth.

The 1987 BTO survey of England and Wales found that lapwings strongly favoured spring tillage whilst autumn tillage was strongly avoided. The 1937 and 1960 BTO enquiries had also reported a preference by lowland lapwings for nesting on bare ploughed land, which was then almost entirely spring ploughing. Moreover, in 1987 the spring-tilled fields that abutted grass fields were occupied by lapwings more often than would be expected by chance alone, whilst fewer lapwings than expected were breeding on spring-tilled fields that were separated from grass. This is related to the advantage of having adjacent pasture for chick rearing (see 3.1).

Only 310 pairs were found breeding on autumn tillage in April 1987 sample surveys, of which 90% were on winter cereals and 10% were on oil-seed rape. In these cases, more pairs than expected by
chance were on fields with bare patches (often less intensively farmed), and fewer than expected on fields with tramlines (often the most intensively farmed). In contrast to these small numbers, the 1987 sampling located 1,312 pairs on spring tillage. For these, the crop type was not always determined since sown fields were often still bare of vegetation in April: 16% of pairs were reported on bare plough, 31% on bare tilled, 36% on spring-sown cereals, 10% on vegetable crops (potatoes, peas, beans), 2% on sugar-beet and 4% on as-yet unploughed stubble (Shrubb and Lack 1991g).

On autumn tilled and sown land, the crop will generally be too tall by April for such fields to be used for nesting (see above). The extensive switch to autumn tillage in England and Wales has served to emphasise the importance to lapwings of remaining spring plough acreages. Lapwings have declined less in Scotland where a trend towards autumn ploughing did not begin until the 1980s so that a much higher proportion of spring tillage is retained (Marchant et al 1990; Shrubb and Lack 1991a). Hatching success can be higher on tillage than on grass, because lower levels of predation and absence of trampling and disturbance by livestock outweigh the cultivation risks to clutches, but fledging success depends heavily upon the availability of alternative grassland feeding sites for chicks (Shrubb 1990).

3.3 Nest site suitability on grassland

In northern Britain the major breeding habitat has been the marginal upland grasslands, and (as mentioned in 2.3) lapwings have declined there where such grasslands have been improved through drainage, reseeding or the application of inorganic chemical fertilisers. Where fields are grazed, such improvements lead to higher stocking rates of cattle and sheep, resulting in increased nest losses through trampling and livestock-caused desertions (Shrubb 1990). Baines (1988) sought to quantify this deterioration in a northern England study. He found that a mean density of 53.9 nesting pairs/100 ha on unimproved pasture fell by 74% to 14.1 pairs/100 ha on improved pasture; on meadows, the corresponding densities were 59.5 and 26.2 pairs/100 ha, a decrease of 56%. The overall density of 35.3 pairs/100 ha on marginal grass in northern England (Baines 1988) corresponds to densities of 31-39 pairs/100 ha on the machair and blacklands of the Outer Hebrides, derived from figures given by Fuller et al (1986). All of these figures, however, are well above the mean of only 2.7 pairs/100 ha found forlowland grass sites surveyed in England and Wales in 1982 (Smith 1983).

In the 1987 BTO survey, lapwing densities on grassland showed marked regional variations, none related to stocking parameters. However, there was a general trend for grazed grass to be preferred to ungrazed, and for leys to be the least preferred of grassland types. Nearly 60% of pairs on grassland were on grazed grass, with the strongest association being with sheep on rough grazing - much of which is unenclosed.

Lister (1964) noted that lapwings leave a site when grass reaches 6 inches (15 cm) in height or cereal is 12 inches (30 cm) tall.
These figures were slightly higher than those estimated by Klomp (1954). Lister predicted that lapwings would avoid silage grass because the sward would be too dense and tall for them, and this has been confirmed by Shrubb and Lack (1991a). The implications of this are serious because silage acreages have increased at the expense of hay-making; in 1985, silage accounted for 26% of all ley and permanent grass in England and Wales (Chalmers and Leech 1986). Lowland hayfields, on the other hand, generally receive lower levels of nitrogen fertiliser, and these are still usable in spring by nesting lapwings. Lowered lapwing nesting densities on improved upland grass in northern England may be due ultimately to the more uniform structure of the sward which is created; much of this improved grassland is used for silage (Baines 1988). Such structural changes are believed to result in increased levels of nest predation (Baines 1990). Moreover, reduced breeding success on grazing, due to higher stocking rates, is also implicated (Shrubb 1990). Nevertheless, Galbraith (1988a, b) noted a preference for using improved grass for chick rearing, by pairs which had nested on unimproved rough grazing.

The modern practices of promoting grass growth through the use of artificial fertilisers, coupled with land drainage (one effect of which is to raise soil temperature), are believed to be responsible for a shift in the timing of the lapwing breeding season. In the Netherlands, this now begins up to two weeks earlier than was the case at the beginning of this century (Beintema et al. 1985). BTO nest record cards do not indicate any change in the timing of nesting on grassland during the period 1962-1985, but the onset does seem to be earlier than in the period 1940-1961 (Shrubb 1990). Moreover, the timing of fertiliser applications on cereals now encourage more rapid early growth as well as producing a denser crop (O'Connor and Shrubb 1986). With the lapwing's requirements for short (or no) ground vegetation while nesting, early promotion of plant growth as a consequence of changed agricultural techniques will almost inevitably affect the species, particularly in regard to chick rearing.

3.4 Other factors

Superimposed onto these broad trends associated with land-use changes, there are also local factors which can limit suitability of a site for nesting. For example, significantly lower breeding densities of lapwings have been reported from upland grasslands bordering coniferous afforestation (Stroud and Reed 1986), though it has been challenged that this result may have been a chance effect rather than an edge effect (Avery 1989). However, Elliot (1982) had earlier noted that lapwings nested significantly further than expected from all trees, and furthest from those which held crow nests. Local nesting numbers are also decreased by disturbance from roads, which follows a logarithmic disturbance profile, and there seem to be similar effects for farmsteads and clusters of other buildings (Van der Zande et al 1980). It appears that the choice of nesting field is not influenced by food density therein but, rather, by avoidance of nest predation and the proximity of alternative feeding fields for adults and chicks (Galbraith 1989b, Baines 1990).
4 FACTORS AFFECTING BREEDING SUCCESS: FOOD AVAILABILITY

4.1 Adult and chick diets

The breeding season foods of adult lapwings comprise a wide range of ground and soil invertebrates, including earthworms, beetles and earwigs, plus adult and larval stages of flies (especially Tipulidae - leatherjackets), moths, grasshoppers and caddisflies (e.g. Lange 1968, Hogstedt 1974, Glutz et al 1975, Cramp 1983).

During the pre-laying period, the birds feed mainly in habitats having high densities of leatherjackets and earthworms and where feeding success is highest (Galbraith 1989b, Baines 1990). Earthworms are a major food source in spring in Sweden, where the length of the pre-laying period is inversely proportional to Lumbricid abundance (Hogstedt 1974). Both earthworms and leatherjackets become less accessible during dry weather, and in those conditions the birds become dependent upon surface invertebrates, especially beetles, earwigs, spiders and moth larvae (Voous 1962). Baines (1990) noted a dietary change by adult lapwings during the breeding season, with concentration on soil invertebrates (earthworms and insect larvae) in April, but on surface-active adult invertebrates (especially beetles) thereafter.

The diet of chicks is varied and opportunistic, including surface arthropods, tipulids and earthworms (Galbraith 1989a). Continental studies have also found that chicks take a wide spectrum of foods, including earthworms and dipteran larvae (especially tipulids) (e.g. Matter 1982). The latter author noted that lapwing chicks are especially likely to be found feeding on field perimeters where spiders and larger beetles are most abundant; small beetles are common but require too much effort to capture in relation to foraging efficiency. Dutch studies have reported a clearer dichotomy between the diets of adults and chicks: the latter hunt for surface insects on the ground and vegetation, whilst adults probe for soil fauna (Beintema and Visser 1990b). This, however, is partly at variance with the findings of Baines (1990), quoted above.

4.2 Habitat type and food resources

Cultivated soils (stubble as well as plough) are known to contain lower densities of earthworms than grassland (Edwards and Lofty 1977), as a result of the combined effects of mechanical damage during ploughing (Zicsi 1958), the loss of insulating material (Evans and Guild 1948), and the low amount of organic matter present (Edwards 1984). Furthermore, soil invertebrates within grass fields increase with the length of time since it was last ploughed, and are therefore highest in permanent grassland as opposed to temporary grass leys and recently improved grass (Edwards and Lofty 1977, Barnard and Thompson 1985). There is an exception, however: peat soils are always faunistically poor, and contain few earthworms (Satchell 1955, Edwards and Lofty 1977).
Within permanent grasslands, the abundance of earthworms is lower on rough grazing than in pasture or other improved grazing (Galbraith 1987, 1988).

It is not necessary for lapwing nesting fields to be good feeding sites also, provided that productive foraging areas are available in the near vicinity. Pastures are important for feeding, for the reasons given above. They are especially important nowadays for chick-rearing by pairs which nested on arable fields. Arable soils soon become unsuitable, for crop growth makes movement difficult within it, and reduces visibility for predator detection and avoidance (Galbraith 1987, 1988a). Hence lapwing chicks hatched on arable are preferentially led to pastures, and chicks hatched on rough grazing and peat habitats are often led to improved grazing nearby. It is for these reasons that a mosaic of crop types presents the best potential conditions for lapwings breeding on lowland farmland.

4.3 Effects of farming practices of food resources

As indicated above, soil invertebrates tend to be fewer in plough (tillage) than in grassland and, in the latter, increase with the age of the grass. However, there can be variations with husbandry practices.

Deep ploughing can decrease soil invertebrate populations by 50%, whereas shallow cultivation techniques are less harmful. Invertebrate numbers in direct drilled soils were between 17 and 37 times greater than in ploughed soils after eight years (Edwards and Lofty 1975; Lofty 1975, 1982b). The densities of earthworms and other soil invertebrates are inversely proportional to the period of continuous cultivation (Edwards and Lofty 1975, 1982b; Tucker, in prep.). Furthermore, fertiliser applications have marked effects where levels of organic matter are low, as in arable soils. In such soil conditions, applications of organic farmyard manures increase the invertebrate populations; although artificial nitrogenous fertilisers have similar effects, these are more limited (Edwards and Lofty 1982a; Tucker, in prep.). In general, therefore, the decreased usage of farmyard manures (resulting from the decline in mixed farming enterprises) in favour of fast-acting artificial fertilisers has resulted in a decrease in both diversity and size of most soil invertebrate populations in arable land (Edwards 1984).

The foregoing does not apply to grass, where higher invertebrate densities already occur as a result of higher levels of organic matter being present naturally in the soil. Applications of farmyard manure to pastures do not increase invertebrate population levels further. However, they do lead to increased surface activity by earthworms (Scullion and Ramshaw 1987), and therefore may make them more readily available to foraging lapwings.

Against this, the greatly increased use of pesticides (Potts 1977, Sly 1986) is harmful to invertebrate populations, and not only to the agricultural pests that are being targeted. In particular,
carbamate fungicides and the molluscicide methiocarb are toxic to earthworms (Edwards 1984; Bieri et al 1989a). However, it is the surface dwelling invertebrates which are most exposed to the effects of pesticide applications, and a number of chemicals have been shown to have deleterious effects upon non-target arthropods. These include the herbicide 2,4-D (Sotherton 1982), methiocarb (Bieri et al 1989b, Buchs et al 1989), and numerous insecticides including the organophosphate dimethoate (Sunderland and Wickerman 1977), the pyrethroids deltamethrin and cypermethrin (Batesow 1985, Pullen 1987), and some synthetic pyrethroids (Smith and Stratton 1986). Clearly, pesticides may have important effects upon food availability for lapwings, particularly in relation to the requirements of chicks when on arable land.

5 FACTORS AFFECTING BREEDING SUCCESS: EGG AND CHICK MORTALITY

5.1 Some general points

The lapwing is a determinate layer in respect of clutch size (normally four eggs) and broods reared per year (one only), but frequently lays replacement clutches for those which have been predated or destroyed. A Dutch study, which incorporated an egg-removal experiment, found that individual pairs could lay up to five clutches per season if necessary and might even replace lost chicks (Klomp 1951). But chick replacement is probably exceptional, based on British experience (Jackson and Jackson 1975). Hence farmland lapwings have an ability to minimise losses caused by predation, cultivation and livestock trampling.

Not all pairs do replace first-clutch losses, however. Baines (1989) found that, on his grassland habitats, 73% of pairs replaced first clutch losses on rough grazing whilst only 26% of pairs did so on the suboptimal improved pastures. There may, of course, be territorial shifts by some pairs between nesting attempts. Yet Shrub (1990) noted a lower incidence of relaying on grassland than on tillage in Britain, which he attributed to disturbance caused by higher densities (nowadays) of grazing livestock. The replacement rate also varies temporally. In Dutch meadows, approaching 100% of pairs will relay after losses during the first weeks of the breeding season, though the probability of relaying decreases with the advancement of the season (Klomp 1951, Beintena and Muskens 1987).

There is a temperature-influenced onset to the breeding season, to ensure subsequent synchronisation with peak food availability for chicks (Imboden 1974, Ettarp and Bak 1985). This restricts the length of the potential egg-laying season in northern and eastern Europe, through later starting there (Cramp 1983).

Now that large-scale egg-collecting for human consumption is a thing of the past, the principal causes of nest failure are predation and agricultural activity, together with desertion for unascertained reasons. Of 1,803 eggs of known outcome that were laid in Switzerland, 23.5% were predated, 11.5% were deserted, and 6.7% were destroyed by farming operations (Glutz et al 1975). In Dutch studies of meadow birds, 44.0% of lapwing clutches were lost
to predation, 22.7% were trampled by livestock, 7.1% were destroyed by farm machinery, and 7.4% were deserted (Beintema and Muskens 1987). On marshland in Schleswig-Holstein (65% arable, 35% grassland), 26% of clutches were predated, 14% were lost through active cultivation, and 9% were trampled by cattle (Matter 1982). A Scottish study, made on pasture, rough grazing and blanket bog, found that the survival probability for individual eggs was 0.9967 per day, or 0.918 over an incubation period of 26 days (Redfern 1983a).

5.2 Predation and disturbance

Figures given above reveal that as many or more nests are lost to predators as through farming operations. Baines (1990) showed that nest predation in northern England was significantly higher on improved grass (76% of clutches) than on unimproved grass (47%). Fieldwork in Scotland (Galbraith 1988a) confirmed that predation was much more frequent on rough grazing (89.4% of egg failures) than on arable (59.3%), though overall breeding success was lower on arable in that study, as a consequence of additional egg losses through cultivation and (especially) poorer chick survival due to crop growth. In view of the ability of lapwings to relay after egg losses in March and April (in most habitats), and evidence that birds hatched from late (i.e. repeat) clutches survive at least as well as those from early clutches (Klopp and Speek 1971), it is likely that chick survival chiefly determines the productivity of lapwing populations. Only when clutches are lost in May are these generally less likely to be replaced, as the breeding season advances, and so influence overall breeding success (Matter 1982). Nevertheless, Baines (1988, 1990) found that on improved upland grass there was not only a higher nest predation rate (than on unimproved fields) but also a reduced frequency of laying replacement clutches; and this author considered that hatching success was the most important factor influencing productivity in that habitat.

As would be expected, there are regional variations in the importance of predation species. However, the commonest ones are gulls (Laridae), crows (Corvidae) and certain mammals (especially Mustelidae). Mink Mustela vison and polecat Mustela putorius figured high amongst predators in a Danish study (Iversen 1986), while in Switzerland the carrion crow Corvus corone and black kite Milvus migrans were named as the principal species (Heim 1978). The latter author noted that there was much annual variation in the extent of predation; while Beintema and Muskens (1987) reported the interesting finding of a link between predation levels and vole (Microtus) densities. When vole numbers collapse suddenly after peaks, then predators (especially mustelids) turn more to ground nesting birds as an alternative food source; the link seems to be more with the abruptness of vole population changes than with a simple relationship to vole densities. Experimental work in Wiltshire, involving predator removal, showed that predator control to protect gamebirds (Phasianidae) could also benefit other ground-nesting species; lapwing nest survival increased by 61% in that study (Pearson and Stoate 1991).
The effects of disturbance are less readily assessed, but nest
desertions from unknown causes will doubtless include many cases
in this category. Shrub (1990) has shown that nesting failures
on grazed grassland are due as much to disturbance from livestock
as to direct trampling. Even livestock damage to a single egg in
a clutch can lead to the birds deserting the nest (Beintema and
Muskens 1987).

Human disturbance can be harmful, but probably only locally so.
On Danish saltmarshes, human intrusions comprised 80% of all
disturbances, with lapwings reacting at intruder distances of 70–
80 m; the latter compared to 80–100 m for approaching birds of
prey, 30–60 m for crows and 15–20 m for gulls (Iversen 1986).
The well-known mobbing behaviour of lapwings is effective in
reducing natural predation risks. However, there does not seem to
be any enhanced value from nesting semi-colonially; lapwing
nearest-neighbour distances are related more to quality of the
nesting habitat (Galbraith 1988a, b). In Polish riverine marshes,
waders that are bold in nest defence, notably the black-tailed
godwit Limosa limosa and the lapwing, have been found to form a
‘protective umbrella’ for more timid waders such as snipe
Gallinago gallinago and ruff Philomachus pugnax (Dyrcz et al
1981). It has even been suggested that passerine field species
choose to nest in lapwing territories to take advantage of the
lapwings’ anti-predator defences (Eriksson and Gotmark 1982).

Human disturbance to lapwings is more harmful in non-agricultural
sites, especially those used for recreation. A disused airfield
colony in the New Forest (Hampshire) declined almost to
disappearance, when recreational intrusion increased nest losses
and chick mortality (Jackson and Jackson 1980).

5.3 Effects of weather

This section considers the impact of weather conditions on lapwing
chicks. The points which merit consideration fall into two
groupings: the effects on chick foraging time, and the effects on
food availability.

Beintema and Visser (1990 a, b) have shown that chicks grow faster
in captivity than under natural field conditions. In nature,
they do not start to gain weight until at least three days old,
and may by then have fallen below their hatching weight. Chicks
 hatch at the season when the number of dry daylight hours of above
15°C have begun to rise sharply. Small chicks require at least
25% of daytime hours with temperatures above 15°C as minimum
conditions in which to survive and start growing. Time budgets
of chicks comprise alternating spells of foraging and parental
brooding, the length of each spell depending upon air temperature
(with rain having an extra cooling effect) and age of the chick.
During adverse weather, small chicks need so much brooding (to
prevent chilling) that too little daytime is left for feeding and
their growth is retarded, this leading eventually to death if the
weather does not improve. Parental brooding ceases above a
threshold ambient temperature, this threshold falling as the chick
grows older and its own thermoregulation improves.
The foregoing summary was based on Dutch studies, which used modelling to refine the position more closely than had been done previously. Of course, many previous authors had noted a link between chick mortality and inclement weather conditions. Beintema and Visser (1990a) noted that their Dutch growth curves for chicks showed a much slower rate of growth than was indicated in a Scottish study by Redfern (1983b). Weight gains certainly vary between sites, according to their quality as chick-rearing habitats (Ettrup and Bak 1985).

Whilst wet weather interferes with foraging by small and unfeathered chicks, as described above, paradoxically the availability of prey is increased in conditions of moist soil. Conversely, in very dry weather - when lapwing chicks can forage freely - prey becomes scarcer. In such conditions, the surface invertebrates taken preferentially by lapwing chicks (notably beetles and insect larvae) become fewer and harder to find so that foraging efficiency is reduced (Matter 1982). Moreover, earthworms burrow deeper and aestivate as the top layers of soil dry out (Edwards and Lofty 1977).

5.4 Influence of farming activities

On grasslands, trampling by livestock constitutes an important cause of nest loss. Moreover, the problem is increased as drainage and fertiliser applications promote grass growth, and so encourage higher stocking rates as well as earlier turning-out of cattle that were housed indoors during the winter (Beintema et al. 1985; Beintema 1988; Shrub 1990). It has been shown that the probability of nest survival from trampling on Dutch agricultural grasslands is a function of stock density and exposure time. Yearling cattle are the worst trampers in terms of grazing pressure per animal, though the higher stocking density of sheep make these equally hazardous to lapwing nests (Beintema and Muskens 1987). On English hill farms, trampling may not always be the sole problem. Whilst cattle grazing produces an uneven sward, leaving patches in which lapwings can nest, sheep create a more even one on which incubating lapwings are more conspicuous to predators (E. Ward, in litt.). Nevertheless, lapwings appear to tolerate sheep more than they do cattle in nesting fields, a tolerance that may be misplaced (Shrub 1990).

Nesting on arable farmland also poses risks, and clutch losses are particularly high in the early part of the season due to farming activities then (Galbraith 1988a). Successive ploughing, harrowing, seeding, rolling and spraying all destroy eggs laid between these different operations; consequently, repeat layings are frequent (Imboden 1970, Shrub 1990). Also, modern cereals grow faster and produce denser crops, due to increased use of fertilisers and to modern sowing methods (O’Connor and Shrub 1986). Hence they soon become inhospitable to lapwing broods. Where no suitable chick-rearing pastures are available nearby, this results in reduced overall lapwing productivity on arable land, though success can be higher in years when weather is poor in spring and cereal growth is less advanced (Galbraith 1988a).
Adult female lapwings on arable or mixed farmland often have access to good quality pre-nesting feeding sites, whereby they can produce larger eggs which in turn result in larger chicks, but this initial advantage is now often lost through anthropogenic factors on tillage farmland having decreased the survival prospects for chicks (Galbraith 1988b).

The movement of chicks from their natal field to a nearby feeding area itself imposes risks. Most chick mortality occurs in the first few days after hatching: on arable fields, these losses are more severe but are concentrated within a shorter period than on unimproved grass (Galbraith 1988g). For their survival, chicks need to be led quickly to suitable feeding areas. Deaths at this time are associated with weight loss and deterioration of body condition which (presumably) results in chilling (see 5.3). A Scottish study found that chicks which had easy access to pasture survived better after a shorter and less hazardous movement than did chicks which had to be led further from their natal field. But chick survival was best in the one year of that study when poor spring weather retarded crop growth, so that the lapwing chicks were able to remain within their natal cereal fields (Galbraith 1988g).

Analysis of BTO nest record cards for the years 1962-1985 has confirmed how agricultural changes have affected the fortunes of British lapwings (Shrubb 1990). Many more nests are now lost for agricultural reasons, compared to the period 1940-1961. Though nest robbing by humans has declined sharply, the incidence of nest desertion has doubled on grassland due to the disturbance (in addition to trampling losses) caused by the higher densities of grazing livestock. With the additional impact of predation (see 5.2), overall nesting performance on upland grass is now poor (especially on improved grass), with stocking densities inhibiting the rate of replacement of lost clutches. Thus Baines (1989) found that, in northern England, only 17% of eggs laid on improved pasture survived to hatching, compared to 40% of eggs on unimproved pasture. Clutch sizes now average larger on tillage, where there are fewer partial losses, and mean brood size is larger at hatching. Cultivation is destroying more nests on arable, in part due to higher March rainfalls in recent years delaying farming work until lapwings have begun nesting (Shrubb 1990), but replacement rates for lost clutches are higher on tillage than on grass. Hence tillage farming may be the better potential nesting habitat, although the big change to autumn sowing of cereals has limited the amount of spring ploughing, and denied to lapwings the good rate of hatching success needed to offset the more difficult chick-rearing conditions on tilled farmland (Shrubb 1990). Again, one sees the advantage of mixed farming types, which are so much less in evidence since the reduced use of rotational farm cropping.

These trends have led to a recent tendency for English lapwings to depend upon minority habitats within regions of farming specialisation. Thus where there is only a small area of grass in a relatively large area of spring tillage, as in East Anglian arable areas, lapwings increasingly prefer grass for nesting; but where there is only a moderate amount of spring tillage in a
predominantly grassland area, there is an overriding preference for
the tillage (Shrubh and Lack 1991a). Clearly, the presence of
both types (spring tillage and grass) is especially important in
areas of improved and intensive farmland.

6 FACTORS AFFECTING POST-BREEDING AND POST-FLEDGING SURVIVAL

The lapwing breeding season draws to a close towards the end of
June though a small proportion of young, from late (= replacement)
clutches, do not fledge until July. The birds gather into flocks
from mid-May onwards (initially non-breeders and failed breeders),
when non-juveniles begin their protracted annual moult (Appleton
and Minton 1978). Hence the post-breeding and post-fledging
periods for lapwings encompass the summer months as well as the
autumn and winter seasons. No longer tied to breeding sites, the
birds can be more mobile in seeking optimum conditions. Outside
the breeding season, lapwings congregate into discrete flocks
ranges each encompassing several feeding and roosting sites, with
such ranges having core areas several kilometres apart (eg. Milsom
1991, Kirby and Fuller 1991). Yet even then they are still
influenced by the consequences of modern farming for habitat
availability and quality.

6.1 The effects of farming practices

Inevitably, pasture is a key farmland feeding habitat in summer,
before mature arable crops are harvested. It has already been
stressed (see under 4.2) that the highest densities of soil
invertebrates occur in permanent grass, the lowest in long-term
tillage, with intermediate densities related to the interval since
last ploughing. Hence it is not surprising that a range of
studies has found permanent grass to be a preferred feeding
habitat in autumn and winter, whether airfield or farmland pasture
(Puller and Youngman 1979; Balanca 1984; Milsom et al 1985;
Tucker 1991). Balanca (1984) noted that grass fields are used
especially in cold weather, and this is consistent with findings
in the Vale of Aylesbury (Puller and Youngman 1979, Kirby and
Fuller 1991). There has not yet been any close study of the
reason for this temperature-related preference, but it does seem
feasible that the more dense sward of pasture (compared to winter
cereals or even young leys) creates a top-soil microclimate in
which invertebrates remain more accessible to feeding lapwings
(Shrubh 1988). On Nottinghamshire pastures, young leys were used
mainly in mild weather, but older pastures with denser swarids in
cold conditions (Barnard and Thompson 1985).

However, a preference for winter cereals has been found in other
studies (Gregory 1987, Shrubh 1988), particularly in the early
winter when surface activity of invertebrates is greater. This
could, of course, include a temperature effect, with mild early
winter conditions causing more invertebrates to be close to the
surfaces of arable fields and so more readily available to
lapwings. Autumn plough is used also, though usually for a very
short period only, as though the lapwings confined themselves to
searching for prey items turned upwards by the ploughing activity
(R.J. Fuller, pers. comm.).
On mixed farmland in Sussex, feeding lapwings selected winter cereal crops that followed leys or (to a lesser extent) other grass fields, and there was a weaker selection for winter cereals which followed an oil-seed rape break-crop; but the birds largely avoided fields which had been used for cereals for three years or more (Shrubb 1988). Presumably, this was related to prey densities available (at this season, surface invertebrates rather than earthworms), with fields cultivated continuously over long periods having the lowest invertebrate densities (see above). A preference for winter cereals, despite the availability of grassland, was noted in North Yorkshire also; with a range of crop heights available, the birds made most use of fields in which the young crop was 8–10 cm tall (Gregory 1987). The latter measurement was based on small samples, however, and may also have been confounded by changes in regional numbers of wintering birds.

In a Hampshire study (Milsom et al 1985, Milsom 1991), lapwing flocks fed on non-arable sites in June and July (when near-mature crops were too tall for use), but occupied a range of habitats in August and September, including much use of arable after harvesting when stubbles had been burnt off or ploughing begun. From October to January there was a strong preference for mown semi-permanent grass, especially for areas which had been kept short by mowing throughout the growing season. The grassland preference held in February and March also, though there was then more use of pastures and meadows, especially after grass had been flattened by snow or frost. However, this study did not always distinguish between feeding and roosting flocks.

Other studies (Kirby and Fuller 1991, Village and Westwood 1991) found an avoidance of pasture in early autumn, when earthworms were likely to have burrowed deeper into the drying soil. Plough and recently sown cereals were used then and into the early part of the winter, for they provided an easily exploited food source which (however) declined or became less readily located by the birds as the crop grew. Village and Westwood (1991) reported a crop height of 75 mm to be the critical one above which cereal fields were rarely used. From December onwards, these studies found pastures to be the preferred feeding habitat, even in mild winters, possibly because increasing moisture levels in the ground forced earthworms upwards within the soil profile. Often, individual fields within a flock range will be used over periods of years, and become traditional feeding sites (Fuller 1986).

The much expanded extent of autumn-sown cereals nowadays seems likely to have increased the availability of early winter feeding sites for this species (O’Connor and Shrubb 1986). Yet this advantage may well have been offset by increased trends for fields to have long periods under continuous arable/cereal cultivation (i.e. less rotation), high pesticide inputs (including molluscicides), and more frequent applications of nitrogen fertilisers than of farmyard manure. These practices are likely to have depleted considerably the soil invertebrate densities over much of England’s arable farmland (see 4.3).
6.2 Roosting

This aspect has been less studied than has feeding ecology. Certain roost-site preferences have been noted, though evidence is lacking that availability influences survival prospects for lapwings. It has been noted that fields used for roosting are of above average size for the farm or area. In a Sussex study, 79% of birds used fields larger than 16 ha, and this was taken to be for better detection of predators (Shrubb 1988). In autumn and winter, such mammals as fox *Vulpes vulpes* and stoat *Mustela erminea* may be the principal natural predators, in Britain at least. The vigilance of individual lapwings is reported to be lower in larger fields, so the birds may benefit from increased warning of predators when they are in mixed flocks with gulls (Thompson and Barnard 1983).

Shrubb (1988) noted that in his Sussex study area the lapwings preferred pastures for roosting, especially old and tussocky ones with pools for bathing and drinking. Nevertheless, up to 40% of birds roosted on tillage, both plough and winter wheat, so that the majority used different field types for roosting than were used for most feeding activities. In contrast, a North Yorkshire study found that the same cropping type, winter cereals, was used preferentially for both feeding and roosting (Gregory 1987). In the Vale of Aylesbury, tilled land (especially ploughed or recently sown) was strongly preferred for nocturnal roosting, there being a camouflage effect, and grassland was used more towards the end of the winter when cereals were growing vigorously; diurnal roosts, on the other hand, were nearly always on large cereal fields (Fuller 1986, Kirby and Fuller 1991).

6.3 Competition

In winter, lapwings often occur in mixed flocks with golden plovers Pluvialis apricaria, and they exploit similar species and sizes of invertebrate prey. This suggests that competition may occur between the two plovers. Thompson (1983) confirmed this prey spectrum overlap, and speculated that golden plovers may peck or probe for prey at shallower depths than lapwings, so reducing interspecific competition. Gregory (1987), as well, found near-total overlap in field use between these two species.

Lapwings are also the regular victims of food piracy by golden plovers, common gulls *Larus canus* and (especially) black-headed gulls *L. ridibundus*. This applies particularly at seasons when earthworms are readily available; and especially in autumn and early spring, black-headed gulls are able, at least at times, to subsist by kleptoparasitism alone (Kallander 1977). Such kleptoparasitism reduces lapwings' feeding efficiency, since they are pressured into taking smaller and suboptimal prey items instead of the larger items which are more likely to be stolen from them (Thompson 1983, Thompson and Barnard 1984, Barnard and Thompson 1985). Possibly the regular nocturnal feeding by lapwings on moonlit nights (Milsom 1984) is one way by which the species avoids such kleptoparasitism (Fuller 1986).
6.4 Adverse weather conditions

Whilst wet weather is often harmful in the breeding season, causing chick mortality, this is not necessarily so at other times of the year. Rainfall induces earthworm movement to the surface (Edwards and Lofty 1977) and therefore makes feeding conditions easier for lapwings (and their kleptoparasites!). Conversely, drought conditions in high summer pose problems through reducing the availability of prey. In such conditions, earthworms burrow deeper and become unavailable; the lapwings turn to less profitable and unusual foods (caterpillars, earwigs, spiders), they lose body condition, the incidence of internal parasites rises, and lapwing mortality increases (Vougas 1962). Starvation also follows late, heavy snowfall in spring in northern Europe (Vepsäläinen 1968).

Cold weather in winter has long been known as a problem which lapwings must face. Earthworms move deeper in cold temperatures (Rundgren 1975, Nordström 1979), but lapwings seem able to cope with nocturnal frosts which thaw by day. Their response to prolonged frost and snow cover is to move away for the duration, or even emigrate (see below: 6.5). Particularly severe winters can cause heavy mortality, judged from the numbers which return to breeding areas the following spring (Spencer 1953). This happened in Britain after 1946/47 and 1962/63, but it is unclear how much of the decline of lapwings in the 1980s is attributable to cold winters then (see under 2.3). It is likely that lapwings are most at risk of cold weather mortality when severe cold extends as far as the Mediterranean, and therefore affects the whole of the European wintering range. Few winters are severe over so wide a spread of latitudes. However, any southwards migration from the British Isles almost inevitably takes the birds into countries where hunting pressure is far higher (see below: 6.6).

6.5 Movements and migrations

Lapwings are mainly migratory in northern and eastern Europe, where winters are normally severe; but many birds are resident in western maritime countries except under duress of hard weather. The species' winter distribution reflects a preference for maritime climates at that season, and a general avoidance of continental-type weather (Cramp 1983). The overall winter range extends southwards as far as the coastal plains of North Africa and the wetter parts of the Middle East.

The movements of this species were studied in depth by Imboden (1974), through ringing recoveries, and this was the main source used for the migration account given by Cramp (1983). Major westward movements through Europe begin in early summer, comprising adults only, and these seem to be especially central European birds. It is likely that the migration urge arises as gonads regress at the conclusion of breeding, as in other waders; but Schüz (1971) suggested that adult departures then from the drying continental interior helped to reduce food competition for the inexperienced juveniles, which do not move out until the conventional autumn migration season (September - October).
Autumn migrations of all continental populations are mainly W-SW across Europe, on broad fronts, whereby many Scandinavian birds enter Britain then; but south-westerly movements from south and east Baltic countries largely bypass the British Isles. France, Italy and Iberia are important for wintering. Winter numbers in France are correlated to temperature, and are reduced only in periods of extreme cold (Balancia 1984). Numbers reaching or crossing the Mediterranean vary from year to year, according to weather conditions further north.

British lapwings tend to remain local to their breeding area until late autumn, not moving away until cold weather restricts feeding opportunities (e.g. Evans 1966). Subsequent movements may be southwards within Britain, or westwards into Ireland, or further afield into France and Iberia. In European lapwing ringing recoveries, the proportions recovered September to March within 60 km of ringing site were highest for Britain (22.5%) and Denmark (21.3%), and lowest (under 3%) for central European countries (Imboden 1974, Cramp 1983). Recoveries suggest that when there are major redistribution movements in severe winters, many of the birds involved do not return northwards until the normal spring migration period, even if the cold spell ameliorates. In Britain, however, areas vacated by lapwings during short spells of severe weather are often reoccupied after completion of a thaw. Such birds had not necessarily travelled far afield in the interim period (Fuller 1986).

6.6 Hunting pressure

Lapwings now have all-year-round legal protection in Britain. This, however, is not the case elsewhere, especially in south European countries. Nevertheless, the recent increase of the Italian breeding population has been attributed to restrictions imposed upon hunting during the spring (Boano and Brichetti 1986). Estimated winter shooting figures vary from 2,000 per season in Belgium to 1,357,000 in France (Bertelsen and Simonsen 1989), and shooting is also practised on a large scale in Spain, Italy and Greece. Hence British lapwings moving south in cold winters are at risk from hunters in the countries they reach as well as from the direct effects of hard weather. Moreover, such birds remain at risk for the rest of that winter when they do not return north until the spring migration season.

7 LAPWING POPULATION DYNAMICS

7.1 Mortality rates and productivity requirements

Post-fledging mortality estimates have been calculated from ringing recoveries, separately for the first-year and older ("adult") age-classes. The latest available figures are given in Table 3.

Assuming that first-year mortality is in the order of 37% and annual adult mortality is around 33%, then lapwing pairs would need to raise on average one young per year to balance post-fledging losses and maintain the population level (Baines 1989).
However, mortality tends to be overestimated by ringing recovery data, in part due to ring loss which affects the older cohorts especially (Evans and Pienkowski 1984). Galbraith (1988a) suggested that lapwing body size comparison with other waders was indicative of a first-year mortality of 35-40% and an annual adult mortality of 25-30%. These estimates, somewhat lower than those in Table 3, would require a mean production of 0.8 young per pair per annum in order to maintain numbers. Matter (1982) calculated that an annual adult mortality of 29.4% in central Europe (Glutz et al. 1975; Table 3) would require a mean annual productivity of 0.84 young per pair. Yet such figures are but a rough guide, since mortality rates may vary annually and regionally in accordance with variable pressures, such as weather conditions and hunting levels, in different parts of the species’ wintering range. It has been suggested that adult mortality is low during the breeding season (Baines 1989), but no detailed study of seasonal trends in survival has yet been made.

(pp. 00-00 tables)

Breeding productivity figures, from individual studies, are given in Table 4. It is not clear how much significance attaches to the different mean clutch size values; some workers may have been more careful than others to exclude clutches which had experienced partial losses. In 1970 nest record cards (Shrubb 1990) the mean clutch size values are 3.63 on grass (n = 2,269) and 3.78 on tillage (n = 844), the difference being attributed to fewer partial losses on tillage in the absence of livestock. There are also conflicting views on whether replacement clutches average smaller than first clutches. No differences were found by Ettrup and Bak (1985) or Galbraith (1988a), while Jackson and Jackson (1975, 1980) found replacements to average smaller, and Baines (1989) reported different trends between improved and unimproved grasslands.

The hatching success figures in Table 4 show a wide variation. Other than the reserve, marshland and airfield sites which are little influenced by agricultural activities, there is a tendency for higher hatching success on arable than grass. Baines (1989) found highest hatching success on arable, followed by unimproved grass, and especially low hatching success on improved grass. Particularly relevant here is the nest record card analysis by Shrubb (1990), based on much larger samples of nests than possible in individual field studies. He found a higher brood size at hatching on tillage than on grassland, but with the mean figures declining over time in both habitat types. During the period 1962-1966 the mean brood sizes at hatching were 2.78 on tillage and 2.32 on grass, but by 1982-85 they had fallen to 2.27 and 1.89 respectively.

The pre-fledging mortality of chicks is high, exceeding 75% in some assessments (Table 4). In relation to this, the figures in Table 4 show a clear difference between grass (especially rough grazing) and arable. As stated earlier, a mean annual figure of 0.8 young per pair needs to be fledged in order to maintain population levels (Matter 1982, Galbraith 1988a). This figure is reached or exceeded in most of the rough grazing/unimproved
pasture studies in Table 4, but not in any of the arable or improved grass assessments there. However, Van Impe (1988) reported a mean productivity of 1.45 - 1.58 young per pair on Belgian arable farmland. This seems remarkably high, in comparison with studies in Table 4, but Belgium is a country where lapwings have increased considerably in recent years. The disused airfield study (Jackson and Jackson 1975, 1980) is interesting. During the first part of the study the output of young was satisfactory and the population level was stable, but during the second phase there was much increased human recreational disturbance of the site, lapwing productivity was halved, and the population level fell.

7.2 Natal philopatry and sink populations

It is known that young lapwings often return to the vicinity of their birthplace to breed (Spencer 1953, Evans 1966) although the incidence of this has never been adequately quantified, and it is one of the major areas needing future research. Heim (1978) recaptured, at his study site, lapwings which had been ringed there up to 14 years previously; but his recaptured samples were small in relation to the numbers ringed there during his long-term study. Nevertheless, the proportion of breeding adults returning to an area in the following year is higher than the return rate for one-year-old birds, even after taking differential survival rates into account (Onnen 1989). European ringing recoveries indicate that 9.70% of lapwings which survive the winter return in spring to within 20 km of their natal areas (Cramp 1983).

In contrast, lapwings ringed as chicks have also been recovered in subsequent summers far from their natal areas, for examples Dutch and British-bred birds found in the USSR, perhaps through having joined migrating flocks in spring. It has been suggested that such gene-flow is regular and has been responsible for inhibiting subspecific variation across the huge Palearctic breeding range of the species (Evans 1966, Mead et al 1968). In spring recoveries (1 May - 14 June) of post-juvenile lapwings (i.e. ringed in an earlier year), 88% of those ringed in the British Isles were found within 50 km of their ringing site, with an overall mean displacement of 133 km. In the temperate zone of continental Europe 78% were found 0-50 km from where ringed and the mean overall distance was 245 km, whilst the corresponding figures for Scandinavia were 77% and 115 km (Imboden 1974). Hence by no means all lapwings are faithful to their natal area, so that local population levels are influenced by immigration and emigration, as well as by local breeding productivity.

Given this evidence that lapwings can settle, in a subsequent spring, a few or many kilometres from their natal area, one can see how lapwings may persist over a period of years in suboptimal breeding habitats such as tillage and improved grassland. Various recent studies have noted how productivity has become too low on arable farmland to balance adult losses; examples are Galbraith (1988a) in Scotland, Shrub (1990) in England and Wales, Ettrup and Bak (1985) in Denmark, and Matter (1982) in West Germany and Switzerland (see also Table 4). Such unfavourable habitats become effectively "sink areas", absorbing surplus territory-seekers from
elsewhere which are unlikely to be able to breed successfully enough to replace themselves.

7.3 Factors influencing population levels

This review has identified a number of factors that have the potential to influence lapwing population levels. These are summarised diagrammatically in Figure 2, although their individual importance differs markedly between areas of grass and arable dominated farmland. Such factors may influence population levels either through limiting the size of the breeding population (through a restriction of suitable habitat) or by affecting productivity or survival.

Although individual studies have been able to establish various measures of lapwing breeding productivity, there has been no overall assessment of the population dynamics of the species. Thus the relative contribution of each stage of the life cycle to the eventual population level is unknown. Furthermore, it is unclear how or to what extent the population levels of lapwings are influenced by density-dependent regulation. Galbraith (1988c) found no evidence for density-dependent effects upon hatching or fledging success; but his data on the temporal and spatial patterns of lapwing territories suggested strongly that territorial behaviour exerted a density-dependent effect through excluding other lapwings from good-quality nesting habitats. It is difficult to see how lapwing populations could behave as they do without quite strong density-dependence somewhere in the system. The very idea of "sink populations" (see 7.2) implies that competition occurs.

Additionally, survival may prove to be density-dependent, in which case the estimates from regional combinations of ringing recovery data may be misleading with respect to the levels of productivity required to balance them. However, given the extremely low productivity in improved grass and arable areas and the fact that lapwing populations are declining in those areas, then it is clear that even if there is a density-dependent effect, this cannot be fully compensatory. Furthermore, the low productivity suggests strongly that there is little potential density-dependent compensation for fluctuations in overwinter survival rate. Hence a full population biology study of lapwings, using a K-factor analysis approach (Varley and Gradwell 1960), is required to establish which stages of the life cycle are most important in determining population levels. Such information would be invaluable for targeting conservation measures, and maximising their effects on population levels.

Despite the gaps in our knowledge concerning the factors influencing lapwing populations, it is likely that the observed population decline in many areas is due at least in part to two factors. These are, first, a reduction in suitable nesting habitat and, second, a reduction in productivity of nesting pairs. Suitable nesting habitat has decreased most on lowland farms where spring cereals have been replaced by autumn sown crops which are too tall and dense in spring for nesting lapwings. Similarly, much lowland grass has been reseeded and heavily fertilised for
silage production, and this is also avoided by the lapwings. Productivity is now very low for nesting lapwings on improved grassland and arable farmland and in both cases is probably normally too low to maintain population levels (Table 4). Clearly, this must either be a recent phenomenon or lapwing populations breeding in these habitats have long been maintained by immigration from other populations having higher productivity (i.e. source populations). Alternatively, adult survival may have decreased and thus created a need for higher productivity. No information is currently available to examine these possibilities. However, Shrubbs (1990) has shown that hatching success has decreased over time in both grassland and arable farmland, thus suggesting that this may have contributed to a general decline in lapwing productivity.

Low productivity by lapwings on improved grass is at least partly attributable to the current high stocking rates of cattle and sheep, permitted by the drainage, reseeding and fertilisation of what was previously rough grazing, plus government subsidies which encourage increased stocking rates independently of grassland management. Although lapwings on grass prefer to use grazed fields for nesting (because ungrazed grass is often too tall and dense), the most agriculturally efficient stocking rates are devastating, due to the high trampling risk and related levels of nest desertion (Beintema and Muskens 1987, Shrubbs 1990).

Predation is also a potentially important factor affecting lapwing productivity on farmland. Low productivity on improved grass was found in one study to be most consistently attributable to variation in hatching success between improved and unimproved grass as a result of differing nest predation rates between the two types (Baines 1989, 1990). However, other studies found that although lapwing nests were subjected to high predation levels, the birds compensated by their readiness to lay repeat clutches. Furthermore, these seem not to be significantly smaller, only two studies having reported the contrary (Jackson and Jackson 1975, Baines 1989). Nor is there any reduction in juvenile survival from that achieved from first clutches (Klop and Speek 1971). Clearly, the degree of compensation for nest losses requires further investigation.

The low productivity on arable is mostly attributable to chick losses through predation. Thus, one possible cause of the lapwing decline on both grass and arable habitats is an increase in predator populations. However, although magpies Pica pica and crows Corvus corone have increased substantially on farmland since the 1960s (Marchant et al 1990) there is no evidence that this has led directly to increased predation rates on chicks over the period. Indeed, egg predation rates have remained unchanged (Shrubbs 1990). Instead, it seems likely that the high predation rates on arable farmland are attributable to the increasing need for chicks to be moved large distances from arable to grass fields for rearing. Chicks hatched in fields alongside grassland showed substantially higher survival rates than those that were led across several fields to find grass (Galbraith 1988a). Thus it appears that chick survival is closely related to the extent of necessary movement, which is itself related to the proximity to
grass. Galbraith's study also suggests that the requirement for
movement is not necessarily to find better feeding conditions, but
to avoid fields with tall vegetation. However, further
clarification of this is clearly needed. Cereal: grass rotations
have decreased substantially over the last 10-20 years as a result
of increased reliance upon artificial fertilisers and the greater
tendency for regional specialisations. The former mosaic of
arable and grass would have provided many opportunities for
nesting in cereals alongside grass. Consequently, chick movement
and predation risk would probably both have been less, and overall
productivity might then have been sufficient to sustain the
population level. Hence it appears that the provision of
suitable nesting fields (eg. spring cereals) would not alone be
sufficient to maintain lapwing populations on arable farmland,
unless coupled with the provision of adjacent grass fields for
chick rearing in order to improve breeding success. It is also
important that such grass fields should contain wet or damp areas,
for the young will not survive in dry pasture; grassland drainage
during agricultural improvements has certainly been harmful to
lapwing productivity (P.S. Thompson, pers. comm.).

8. REQUIREMENTS FOR FUTURE RESEARCH

This review has highlighted many gaps in our knowledge of lapwing
ecology relevant to the conservation of the species. Furthermore,
where information is available, the data are often derived from
a small geographical area, few seasons, and a restricted range of
environmental conditions. Therefore there is a need to repeat
several of the studies in other areas, particularly the
estimation of breeding performance and survival. Such new work
should include studies of both stable and decreasing populations.
We also list below current priority areas for research that
could be aimed specifically at providing new information to help
target conservation measures. The list follows a suggested order
of priority.

1) A full population biology study by K-Factor analysis (Varley
and Gradwell 1960) to establish:

   a) the stages in the life cycle that are most important in
      limiting populations size and

   b) how density-dependent regulation occurs.

2) An assessment of site fidelity and natal philopatry to
   establish the role of immigration in the maintenance of sink
   populations.

3) A detailed study of overwinter survival using ringing
   recoveries, to establish whether survival rates have changed and
   whether such changes are related to trends in agricultural
   practices or weather.

4) Investigate the potential role of 'nesting habitat islands' in
   providing suitable nesting sites in otherwise unsuitable farmland.
For example, tilled or rough grass strips might be placed through the centre of winter cereals or (particularly) across improved grass fields, as part of the current MAFF set-aside scheme.

5) Experimental studies on the effects of predator control on lapwing breeding productivity in grassland and arable.

6) An assessment, using ringing recovery data, of geographical and temporal variation in the hunting pressure on lapwings outside the breeding season. If sufficient ringing data are available, this should be combined with an assessment of the effects of hunting on average survival rates.

7) Examine further the effects that farming practices, particularly pesticide applications, have on food availability for lapwing chicks and adults and the resulting risk of starvation. This should include the use of molluscsides and aphicides in autumn and winter (on autumn-sown cereals), and the impact of the straw burning ban which comes into force in 1993.

9. POTENTIAL STRATEGIES FOR LAPWING CONSERVATION

It is clear from the information currently available that any strategy for lapwing conservation must include two major actions to achieve success. Firstly, prime nesting habitat needs to be protected and ultimately increased in extent. Secondly, assuming that adult survival rates cannot easily be influenced, measures must be taken to increase breeding productivity in ‘sink’ populations. Probably the most practical and efficient means of achieving these goals will include the following actions (not in any particular order of priority).

1) Protect existing areas of rough grazing possessing sizeable numbers of breeding lapwings. Probably this could best be achieved by educating landowners, combined with a campaign for some form of compensation scheme to maintain rough grazing. Such compensation could be administered within the framework of the current Environmentally Sensitive Areas (ESA) scheme, but would require the latter’s extension to wider geographical units. Except in cases involving extremely high densities of nesting lapwings, protection of rough grazing sites by land purchase would be inefficient and probably would not contribute greatly overall to lapwing conservation.

2) Encourage the spring sowing of cereals as opposed to autumn sowing, where such fields can be placed alongside areas of non-silage grass. This would re-create a mixed farmland mosaic of spring cereal and grass to provide suitable nesting and high quality feeding habitats. The success of this would be dependent upon the two components being alongside. The encouragement of spring cereals for suitable nesting habitat will not alone increase population levels – adjacent chick rearing sites must be present also. Again, this goal might best be achieved by education and a campaign for a compensation scheme within the current ESA framework, but it would have little effect if comparatively small areas were involved. There would be more
potential if spring cereal and non-silage grass production were encouraged through a wider ‘agricultural extensification’ scheme.

3) Many farmers are sympathetic towards lapwings, and would be amenable to conserving them if steps were economically viable. Inform farmers of the effects of livestock trampling and farming operations on lapwing breeding success, and encourage them to take avoiding action when practical. Thus, where possible, cattle and sheep should first be turned out onto fields other than those known to have breeding lapwings, with the latter fields being used at a later date. Some agricultural operations could be delayed until the second week in June - after the main nesting period according to laying data from Shurb (1990) and incubation data from Jackson and Jackson (1975) – with little cost to the farmer. Rolling is best avoided on lapwing nesting fields, unless strictly necessary, and then it would be preferable to roll straight after drilling. Alternatively, nests could be located and marked (carefully and inconspicuously to avoid increasing predation) so that tractor drivers could avoid them. Such practices are already carried out successfully on some farms, sometimes with the help of local birdwatchers who take on the task of nest location and marking. This practice should be encouraged through a co-ordinated campaign of articles in birdwatching and farming magazines, and combined with a scheme where farmers with lapwings are put in touch with interested local birdwatching groups. Individual advice will be necessary in many cases, because different soils and crops lead to different management practices.

4) Traditional lapwing wintering sites should be protected where possible, by education and, where necessary, by objections at planning enquiries. This should apply especially where wintering numbers regularly exceed nationally (10,000) and internationally (20,000) important levels (Prater 1981, Scott 1982). Such sites are normally large, open grazed areas of long-established grassland which often receive large inputs of organic farmland manure. These attributes should be maintained on such sites.

5) A general public awareness campaign should be carried out covering the decline of the lapwing and its likely causes. The main benefit of this would be to create public pressure and backing for agricultural policies that take into account the environmental implications of farming practices. Moreover, information reaching landowners would provide further encouragement for carrying out conservation measures relative to the awareness campaigns outlined above. Commercial sponsorship of further research would also be more likely if the issue were widely publicised.
The present review was prepared following a one-day workshop on lapwing conservation (held on 12 January 1990) which was hosted by DP Oil UK Ltd. One of the present authors (GT) was financed by a grant from The Environmental Research Fund (TERF), as part of a larger programme of research on lapwings, and the other of us (RH) under a contract from the Nature Conservancy Council to the British Trust for Ornithology. The work was supervised by Dr R.J. Fuller. We thank all of these, as well as Dr J.D. Goss-Custard, Dr P.C. Lack, Michael Shrubb and Dr P.S. Thompson whose constructive criticisms of an earlier draft did much to improve the final version.
Table 1. National breeding population estimates (in pairs) for lapwings in Europe

<table>
<thead>
<tr>
<th>Country</th>
<th>Population estimate</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iceland</td>
<td>0-5</td>
<td>Piersma (1986)</td>
</tr>
<tr>
<td>Faeroes</td>
<td>&gt;10</td>
<td>ibid</td>
</tr>
<tr>
<td>Britain</td>
<td>185-225,000</td>
<td>this review</td>
</tr>
<tr>
<td>Ireland</td>
<td>33,500</td>
<td>Piersma (1986)</td>
</tr>
<tr>
<td>Norway</td>
<td>58,000</td>
<td>ibid</td>
</tr>
<tr>
<td>Sweden</td>
<td>120,000</td>
<td>ibid</td>
</tr>
<tr>
<td>Finland</td>
<td>100-200,000</td>
<td>Koskimies (1989)</td>
</tr>
<tr>
<td>Denmark</td>
<td>30-40,000</td>
<td>Piersma (1986)</td>
</tr>
<tr>
<td>Netherlands</td>
<td>160-175,000</td>
<td>ibid</td>
</tr>
<tr>
<td>Belgium</td>
<td>15-17,000</td>
<td>Devillers et al (1988)</td>
</tr>
<tr>
<td>West Germany</td>
<td>50-60,000</td>
<td>Piersma (1986)</td>
</tr>
<tr>
<td>East Germany</td>
<td>15-20,000</td>
<td>ibid</td>
</tr>
<tr>
<td>Poland</td>
<td>&gt;5,000</td>
<td>Gromadzka et al (1985)</td>
</tr>
<tr>
<td>Czechoslovakia</td>
<td>&gt;2,000</td>
<td>Piersma (1986)</td>
</tr>
<tr>
<td>Hungary</td>
<td>10,000</td>
<td>ibid</td>
</tr>
<tr>
<td>Austria</td>
<td>1,500-2,000</td>
<td>ibid</td>
</tr>
<tr>
<td>Switzerland</td>
<td>730</td>
<td>ibid</td>
</tr>
<tr>
<td>France</td>
<td>17-20,000</td>
<td>ibid</td>
</tr>
<tr>
<td>Spain</td>
<td>40-70</td>
<td>Dominguez et al (1987)</td>
</tr>
<tr>
<td>Italy</td>
<td>600-900</td>
<td>Tinarelli &amp; Baccetti (1989)</td>
</tr>
<tr>
<td>Yugoslavia</td>
<td>275</td>
<td>Bartovsky et al (1987)</td>
</tr>
<tr>
<td>Bulgaria</td>
<td>600-800</td>
<td>Nanknov (1989)</td>
</tr>
</tbody>
</table>

NOTE. Countries not listed above are those for which no estimate is available.
Table 2. Breeding population trends of lapwings in European countries in the 1980s

<table>
<thead>
<tr>
<th>Decreased</th>
<th>Apparently stable</th>
<th>Increased</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finland</td>
<td>Iceland</td>
<td>Faeroes</td>
</tr>
<tr>
<td>Sweden</td>
<td>Estonia</td>
<td>Norway</td>
</tr>
<tr>
<td>Lithuania</td>
<td>Latvia</td>
<td>European USSR</td>
</tr>
<tr>
<td>Denmark</td>
<td>Poland</td>
<td>West Germany *</td>
</tr>
<tr>
<td>Britain</td>
<td>East Germany</td>
<td>Belgium</td>
</tr>
<tr>
<td>Ireland</td>
<td>Netherlands</td>
<td>Luxembourg</td>
</tr>
<tr>
<td>France</td>
<td>Czechoslovakia</td>
<td>Austria</td>
</tr>
<tr>
<td></td>
<td>Hungary</td>
<td>Switzerland</td>
</tr>
<tr>
<td></td>
<td>Bulgaria</td>
<td>Italy</td>
</tr>
<tr>
<td></td>
<td>Greece</td>
<td>Yugoslavia</td>
</tr>
<tr>
<td></td>
<td>Spain</td>
<td>Romania</td>
</tr>
</tbody>
</table>

* Some regions only

<table>
<thead>
<tr>
<th>Region of sample</th>
<th>First year Mortality (%)</th>
<th>Annual adult mortality (%)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Britain &amp; Ireland</td>
<td>37.5</td>
<td>33.9</td>
<td>Glutz et al (1975)</td>
</tr>
<tr>
<td>Central Europe</td>
<td>40.1</td>
<td>29.4</td>
<td>ibid</td>
</tr>
<tr>
<td>Scandinavia</td>
<td>40.4</td>
<td>33.1</td>
<td>ibid</td>
</tr>
<tr>
<td>Denmark</td>
<td>44.0</td>
<td>33.0</td>
<td>Bak &amp; Ettrup (1982)</td>
</tr>
<tr>
<td>Habitat</td>
<td>Mean clutch size</td>
<td>Hatching success (%)</td>
<td>Fledging success (%)</td>
</tr>
<tr>
<td>---------------------------------------------</td>
<td>------------------</td>
<td>----------------------</td>
<td>----------------------</td>
</tr>
<tr>
<td>Grassland (part reserve)</td>
<td>3.83</td>
<td>58.4</td>
<td>?</td>
</tr>
<tr>
<td>Unimproved pasture</td>
<td>3.73</td>
<td>39.9</td>
<td>35.5</td>
</tr>
<tr>
<td>Unimproved meadow</td>
<td>3.73</td>
<td>32.3</td>
<td>35.5</td>
</tr>
<tr>
<td>Rough grazing</td>
<td>3.74</td>
<td>34.3</td>
<td>24.4</td>
</tr>
<tr>
<td>Marsh (some arable)</td>
<td>3.70</td>
<td>40.0</td>
<td>33.2</td>
</tr>
<tr>
<td>Rough grazing*</td>
<td>3.75</td>
<td>77.9</td>
<td>23.9</td>
</tr>
<tr>
<td>(a) 1971-74 (stable popln.)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) 1975-78 (popln. decline)</td>
<td>3.72</td>
<td>65.8</td>
<td>15.0</td>
</tr>
<tr>
<td>Improved pasture</td>
<td>3.61</td>
<td>16.7</td>
<td>21.5</td>
</tr>
<tr>
<td>Improved meadow</td>
<td></td>
<td>22.3</td>
<td></td>
</tr>
<tr>
<td>Grass (1962-85)</td>
<td>3.63</td>
<td>62/66</td>
<td>63.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>82/85</td>
<td>51.9</td>
</tr>
<tr>
<td>Mixed farmland (70% grass)</td>
<td>?</td>
<td>63.5</td>
<td>?</td>
</tr>
<tr>
<td>Mixed farmland (44% grass)</td>
<td>3.79</td>
<td>58.8</td>
<td>14.7</td>
</tr>
<tr>
<td>Arable</td>
<td>3.74</td>
<td>45.6</td>
<td>23.5</td>
</tr>
<tr>
<td>Arable</td>
<td>3.75</td>
<td>28.2</td>
<td>14.7</td>
</tr>
<tr>
<td>Intensive arable</td>
<td>3.80</td>
<td>39.1</td>
<td>13.9</td>
</tr>
<tr>
<td>Tillage (1962-85)</td>
<td>3.78</td>
<td>62/66</td>
<td>75.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>82/85</td>
<td>60.0</td>
</tr>
</tbody>
</table>

* Disused airfield
Lapwing CBC Index

Figure 1 Common Birds Census indices for Lapwings in northern and southern Britain, 1962-1988.
Figure 2  Potential factors influencing Lapwing populations.
THE INFLUENCE OF CROPS AND WEATHER ON LAIWING V. VANELLIUS

POPULATIONS BREEDING ON LOWLAND FARMLAND IN SOUTHERN BRITAIN.

G.M. TUCKER, R.W. HUDSON & R.J. FULLER

British Trust for Ornithology, Beech Grove, Tring, Herts. UK.
1. SUMMARY

The numbers of breeding lapwings have undergone a serious decline in southern Britain during the 1980s, and this has been widely regarded as a consequence of agricultural intensification. Against this background, the present study examined BTO Common Birds Census data on the breeding densities and habitat use by lapwings on lowland farmland between 1962 and 1987.

Data from CBC plots which had been surveyed annually for 15 years or longer confirmed a decline in lapwing densities on farmland as the extent of autumn-sowing of cereals increased, and showed a preference by remaining pairs for nesting on spring-sown fields which were adjacent to pasture (grass is needed for chick rearing). In contrast, adjacent grass fields did not increase the use by nesting lapwings of autumn-sown crops. Multiple regression indicated that 45.9% of variation in lapwing densities could be explained by the increase in mean extent of autumn-sown fields. Grassland used for silage production was generally avoided, yet lapwings showed a marked preference for pastures which were grazed in spring and then used for a late silage crop. However, no clear habitat preferences could be found in a different set of CBC census plots which were sampled at 4-year intervals. These plots were chosen at random, irrespective of whether they held lapwings, whereas the long-term plots had all been selected for having held lapwings at some time during the study period.

A multiple regression of CBC annual indices against various weather parameters found that 3 weather variables together explained 66% of variation in lapwing population changes for the years since 1962. Deterministic models were constructed, using the 1962 index and weather variables for the subsequent years. These models predicted the observed population changes quite well up to 1985, though differences between models suggested that there was not a consistent relationship with weather. In particular, a predicted increase from 1987 has not happened. We suggest that adverse agricultural changes have depressed lapwing productivity and made it more difficult for the species to recover from weather-induced reductions.
2. INTRODUCTION

Lapwing populations in Britain have declined substantially since the 1960s (Shrubb & Lack 1991a), with a particularly rapid decline in the last ten years (Marchant et al. 1990, Hudson & Tucker 1991). In general, agricultural intensification has been suggested as the major cause of this decline, acting through changes in arable cropping practices and grassland management, greater regional specialisation and increased use of marginal land (O'Connor & Shrubb 1986). Specifically, it is likely that these changes have caused the lapwing population decline through two effects. Firstly, there has been a reduction in suitable nesting habitat, particularly on lowland farms, as a result of the replacement of spring-sown with autumn-sown crops (Shrubb & Lack 1991a).

Autumn-sown crops are too tall and dense in spring for nesting lapwings. Similarly, improvement of grassland by drainage, re-seeding and fertilization creates a uniform and dense grass sward unsuitable for nesting in (Beintema et al. 1985, Baines 1988). Secondly, productivity of nesting pairs on improved grassland and arable farmland is now so low that these populations cannot maintain their present levels (Hudson & Tucker 1991).

Although lapwings prefer grazed grass for nesting, the low productivity there is at least partially attributable to currently high stocking rates of cattle and sheep and the resulting high risk of clutch loss by trampling (Beintema & Muskens 1987, Shrubb 1990). High predation rates on improved grassland, resulting from the conspicuousness of nests in these habitats, may also be partly responsible for currently low productivity levels (Baines 1989, 1991); nevertheless, an ability to relay and rear late broods successfully may compensate to some degree (Klomp & Speek 1971). Low productivity on arable land is mostly attributable to chick losses, with predation levels being one factor (Hudson & Tucker 1991). This may be a consequence of an increase in Magpie Pica pica and Crow Corvus corone populations on farmland (Marchant et al. 1990). However, there is no evidence of a corresponding increase in predation rates; indeed, egg predation rates have remained unchanged (Shrubb 1990). Rather, it seems likely that the currently high chick mortality on arable farmland is at least partly attributable to the increased need for chicks to move large distances to reach grass fields suitable for rearing (Galbraith 1988). Mixed farming and the use of grass in cereal rotations has decreased substantially, such that the former farmland mosaic of arable and grass has been widely replaced by monocultures. Consequently, the opportunities for nesting in cereals alongside grass have decreased.

Using the British Trust for Ornithology’s Common Birds Census (CBC) population index and habitat data, this study attempts to test the generality of some of the suggested effects of agricultural practices and to establish whether temporal changes in these match the temporal changes in lapwing populations.
Studies of the effects of weather on lapwings have shown that chick mortality is highly dependent on weather conditions (Matter 1982, Beintema & V.isser 1990b). Furthermore, adults are susceptible to summer drought (Vosos 1962) and their winter distributions are affected by winter weather conditions (Evans 1966, Lack 1986) probably as a result of reduced prey availability in cold weather (Rundgren 1975, Nordstrom 1979). Despite these studies, and the clear effects of the severe 1962/63 winter on lapwing populations, there have been few suggestions that annual population levels are normally influenced by weather conditions. Shrubb & Lack (1991a) have, however, suggested that the lapwing decline in the 1980s has been exaggerated by a series of cold winters during that decade. The present study also attempts to establish if annual fluctuations in seasonal weather conditions could have been partly responsible for the observed lapwing population trends since 1962.

Only lowland lapwing populations were considered in this study. This was because the processes causing declines in upland populations are probably different from those on lowland farmland (Hudson & Tucker 1991), whilst the comparatively low number of CBC plots in upland habitats precluded a separate analysis.

3. METHODS

3.1 Population indices

The population indices used in this study are based on the British Trust for Ornithology’s Common Birds Census (CBC) data, in which bird numbers, crop types and other habitat features are recorded on 1:2500 maps for defined farmland plots, each of at least 50 ha (Marchant et al 1990). Such plots vary considerably in the period of years over which they are censused by (mainly amateur) observers; hence the data have been utilised in three ways.

Firstly, data were extracted on an annual basis for the 20 farmland plots censused over a continuous period of 15 years or more (since 1966) and which held lapwings in one or more seasons during this period of continuous coverage. For these plots, the size of each field was measured (ha) and where lapwings were present, their territories were allocated to individual fields in proportion to their use of those fields over that breeding season (to the nearest 0.2 of a territory) as shown by the position of individual visit registrations. Most plots were located in lowland English farmland (Figure 1). This was termed the ‘continuous study’.

Secondly, data were extracted from 50 farmland plots sampled at four-year intervals (1966-1986) from the entire set of CBC plots, regardless of whether these held lapwings at any time. The only selection was against plots which were wholly unsuitable for lapwings, in practice those farms where hops and orchard fruits were principal crops. For each plot the total area and number of lapwing territories was established and the territory density calculated. Different CBC plots were used from the continuous plot study, although these were also drawn mainly from lowland farmland.
south of a Mersey-Humber line and east of the River Severn. This was termed the ‘four year study’.

Thirdly, for an analysis of the effects of weather on lapwing populations, CBC data were used from all plots within the south and east area (indicated in Figure 1) to generate annual population indices for the period 1963-1988 inclusive. On average, 30 plots were available in each year to calculate this index.

3.2 Cropping information and crop preferences

Crop information was extracted from the CBC habitat maps supplied by each observer for each plot. The size of each field was measured (ha) using an overlay grid of 1 hectare squares on the 1:2500 plot map.

For the continuous plot study (20 plots over 15 or more years) the crop type was categorised for each individual field and, when available, the following additional information was taken where relevant: (a) whether cereals were spring or autumn-sown, (b) whether grass was grazed, kept for hay, silage or a combination of these, (c) the timing of grazing and silage cutting, (d) the presence or absence of sheep, horses and cattle on grass fields, and (e) whether arable fields were adjacent to grass.

For the four year study, crop information was only used in the form of the percentage of the entire crop comprised by each crop type. Where detailed information was available then cereals were categorised as either spring or autumn-sown and grass as grazed or mown. The area of the entire plot was also measured.

Crop preferences for territory location were calculated for each main crop type using Jacob's (1974) preference index (D):

$$D = \frac{(r-p)}{(r+p-2rp)}$$

where

- $r$ = the proportion of the plot’s territories in a particular crop
- $p$ = the proportion of the plot of the particular crop type

Thus the index ranges from -1 to 1, with negative indices indicating avoidance and positive indicating a preference for a particular crop type.

3.3 Meteorological information

Weather data supplied by the Meteorological Office for the period 1962-1987 were used from ten weather stations situated within the area used for the calculation of the southern lapwing CBC index (see Figure 1). From each station, monthly means of seven weather variables (Table 1) were used to produce mean values for the entire study area over five periods corresponding to phases of the birds’ annual cycle for each indexed year.
4. RESULTS

4.1 Crop preferences and the effects of changes in cropping on the continuous study plots

Inspection for trends in plots of the index against year for each main crop type only revealed a significant increase in preference for spring sown vegetables over the analysis period (\(y = -2.54 + 0.0361x, t=3.50, P < 0.01\)). No other trends were apparent or significant. Therefore a mean preference index was calculated for each crop type across all years (Figure 2). These mean preference indices differed significantly amongst crop types (\(F8,179 = 15.4, P < 0.001\)), with spring cereals and spring vegetables preferred significantly more than ley, permanent grass, autumn cereal and oil-seed rape.

Further investigation of the use of grass by lapwings showed that the use to which grassland was put, significantly affected the density of territories, whilst the type of grass had no consistent effect (Table 2). Grass used for early silage supported lower densities of lapwings, whilst pasture consistently had high lapwing territory densities (Figure 3). However, grass used for late silage, and therefore grazed in early spring, supported the highest densities, but only on permanent grass. In this case there was a significant difference between grassland types (\(t24 = 2.48, P < 0.05\)).

Analysis of the effect of stock type (ie. sheep, cattle or horses) indicated that there was no significant difference in lapwing territory density between grassland grazed by these different stock (\(F = 1.46; df = 2,598\); NS).

To test whether cereal fields that were alongside grassland supported higher densities of lapwings, the densities on spring and autumn-sown cereals known to be adjacent to grass were compared with those not adjacent to grass. Both cereal type and proximity of grass had significant effects on territory density (Table 3). However, there was also a significant interaction between these effects. Thus, although spring cereals consistently had higher lapwing densities than autumn cereals, the presence of adjacent grass only significantly increased lapwing densities on spring cereals (Figure 4).

Lapwing populations on the 20 continuous study plots have shown large changes over the study period (Figure 5). Mean territory density was initially low in 1964, presumably as a result of the cold and prolonged winter of 1962/63. Territory density then increased to a peak in 1968, thereafter decreasing through the remaining study period. However, these density figures are not representative of farmland in general because they are inflated as a result of only selecting continuous study plots which held lapwings at some point. To establish whether these changes in lapwing density could be attributable to changes in crop-use, a stepwise multiple regression was carried out of yearly territory density against yearly mean area of each main crop type. Only data after 1967 were used, to avoid effects of cropping changes being obscured by effects from the 1962/63 winter. This analysis
indicated that 45.9% of the variation in mean lapwing territory density could be explained by the increase in the mean area of autumn-sown cereals (Figure 6). No other variable significantly affected territory density.

4.2 National effects of overall changes in crop use on farmland

To test the generality of the effects of changes in the use of different crops on lapwing populations, data were used from 50 CBC plots from a large geographical area sampled every 4 years. These plots showed an increase in lapwing density from the first 1966 sample to 1970, by which time mean lapwing density had doubled to 0.04 birds per hectare (Figure 7). However, by 1986 the density had fallen back to its original 1966 level. The proportion of farms with lapwings reflected the density trend but with changes of lower magnitude. Thus, the overall density changes appeared to be caused mainly by changes within individual farms.

During this period there were also substantial changes in the areas of different crops on CBC plots, with marked increases in winter cereals and rape but a 73% drop in the area of spring-sown cereals (Figure 8). However, regression analysis could find no relationship between these changes, expressed as either the area grown or the percentage of plots with particular crops, and either mean lapwing density or the percentage of farms with lapwings. Thus although the continuous plot study indicated that reduced lapwing densities were related to the increased area of autumn cereal (Figure 6), this wider scale study did not support this finding, nor that lapwing populations were affected nationally by any other broad scale agricultural change.

4.3 The effects of weather on southern Lapwing populations

The relationship between lapwing population change and weather was investigated using the southern CBC lapwing index values (from the area indicated in Figure 1). A stepwise multiple regression was carried out in which the dependent variable was the population change expressed as a rate of change, i.e. log10 (Index in year t/Index in year t-1). The weather variables listed in Table 1 were used as the independent variables, together with the logarithm of the index of the previous year. The latter value allowed density dependent effects to be included in the model, although it is not itself a rigorous test of density dependence (Pollard et al. 1987). Initially, the analysis was carried out for the entire period for which complete census and weather data were available, i.e. 1962 to 1987.

The analysis indicated that 66% of the variation in the lapwing population changes in southern England could be explained by three weather variables (Table 4). These variables were the number of days with frost in the March of the index year, the mean winter temperature and the mean autumn temperature. No other individual variables significantly improved the regression.

A simple deterministic model was then constructed (cf Baillie 1990) to predict the resulting population changes, using the multiple regression terms and the initial population value for
1962 (Figure 9). The simulation showed a close match to the observed population changes throughout the period, successfully predicting the population crash in 1963, and the recent period of decline from 1985 to 1987. Thus, these results suggest that much of the recent lapwing population decline in southern Britain can be accounted for by cold spring, winter and autumn periods in the 1980s.

To test whether the recent decline was a result of a consistent relationship between weather and population, this period was excluded and the analysis was repeated using only the CBC data up to 1985. The resulting multiple regression explained 93% of the variation in population change through the combined effects of four weather variables and the previous population level (Table 4). In this model the density dependent effect was clearly most important and alone explained 65% of the variation in population change. However, examination of correlations between the independent variables showed that the previous population index was itself negatively correlated with winter temperature and soil temperature and positively correlated with snow days. This may, therefore, explain the absence of the effects of winter weather from the second model. It is clear that the relationship between population change, previous population size and weather is not consistent across the period. The model based upon the data up to 1985 does not predict the recent decline (Figure 10). Instead, it predicts a rapid increase in population in 1987. This, therefore, suggests that a density dependent potential for recovery may have been lost in recent years. Hence the recent decline may be due to the combined effect of a reduced ability to recover from declines and recent weather patterns.

5. DISCUSSION

This study supports some of the previous findings that agricultural practices affect the choice of nesting site. Furthermore it strengthens previous evidence that the decline in lapwing populations in lowland farmland is at least partly caused by the reduced availability of suitable nesting habitats (O’Connor & Shrubb 1986, Shrubb 1990, Shrubb & Lack 1991a).

As previously found by Shrubb & Lack (1991a), nesting lapwings had a distinct preference for spring-sown crops, probably because these had bare earth patches on which to lay but sufficient cover to conceal the sitting birds. In contrast, autumn-sown cereals were avoided because they were probably too tall and dense for successful nesting.

Grassland was a less preferred nesting habitat (though other work has established their importance for chick rearing), and in general there was no difference between ley and permanent grassland in territory densities. Instead differences were due to the effects of different grassland use. Grazed grass supported the highest densities, and grass for silage was generally avoided. Similar results were found by Shrubb and Lack (1991a). However, this study revealed that grass for late silage supported the highest lapwing densities. This type of silage is often initially grazed in the spring before being allowed to grow for a summer.
silage cut. Presumably, this was preferred because the early grazing prevents the sward becoming too tall whilst later, the absence of stock avoided the risk of desertion due to trampling. However, this only applied to permanent grass. Ley grass for late silage was still generally avoided. This was presumably a result of the normally denser, more uniform and taller grass swards which develop on ley grass through drainage, re-seeding and heavy fertilizer use (Lister 1964, Baines 1988). Thus, although the recent increase in silage use, at the expense of hay and grazing land, had been regarded as a serious threat to lapwings, this can be mitigated if early spring grazing is practised on permanent grassland used for silage. This should be possible in many areas of lowland farmland with little cost to the farmer. Clearly, though, the replacement of grazed permanent grassland with silage leys is a serious threat.

This study also supported the finding of Shrubb & Lack (1991a) that cereal fields are preferred if positioned alongside grazed grass. Presumably this is because ready access is provided to the preferred feeding areas for rearing chicks (Galbraith 1988). However, the present study also found that this applied only to spring cereal fields. Autumn-sown cereals had similar low densities of nesting lapwings, whilst the lapwing density in spring cereals alongside grass was nearly four times greater. This result is difficult to explain, unless the birds nesting in autumn cereals do not need to move their young to grass for rearing (unlike in spring cereals) or there were sufficient spring cereals in the study sites to support most of the lapwing population. The former is unlikely given the necessity for lapwings to avoid tall crops (Galbraith 1988). The latter is also unlikely to apply now, given the large decrease in the use of spring-sown cereals in modern agriculture.

The marked avoidance of autumn-sown cereals by lapwings and the large increase in acreage of these crops in the last 20 years at the expense of spring-sown cereals was reflected in the declining lapwing population on the long-term study plots. This study found that 45.9% of the variation in lapwing territory density on these plots could be explained by the area of autumn-sown cereals alone. Yet analysis over a wider geographical area using 50 randomly sampled plots failed to support this relationship. This may be because these plots represented a diverse range of farmland types, some of which may have been unsuitable for lapwings for reasons other than the types of crops present. Consequently, the effects of broad changes in the availability of different crops may have been obscured by other unmeasured effects.

Weather has been shown previously to affect chick and adult lapwing mortality (Voous 1962, Matter 1982, Beintema & Visser 1990b), yet it had not been suggested that this could substantially control yearly population levels. Nevertheless, the present study has shown that most of the year to year variation in lapwing populations up to 1985 can be explained by variation in weather conditions combined with density dependent regulation. Based on population data from 1962 to 1985, a deterministic model incorporating fluctuations in spring and autumn weather accounted for the major population crash after the 1962/63 winter and the
smaller scale fluctuations in population up to 1985. However, extrapolation of the model beyond 1985 predicted a sudden population increase in contrast to the observed sudden decline. A further model based on the entire data set from 1962 to 1987 predicted the 1986 decline, although it described less of the variation and did not include a density dependent component. This, therefore, suggests that the recent decline was not the result of a consistent relationship with the effects of weather. Instead, it is more likely that the population's ability to recover has been lowered, probably as a result of agricultural changes. Given the currently low breeding success of lapwings in lowland intensive farmland (Hudson & Tucker 1991), it is possible that this has arisen through a decrease in productivity. Clearly, further studies are required to quantify the relative impacts of weather and farming changes.

6. ACKNOWLEDGEMENTS

Our thanks go to all those BTO members who have contributed many hours of fieldwork to the Common Bird Census. This paper is based entirely on their efforts. The Common Bird Census is conducted by the BTO under contract from the Nature Conservancy Council, the study reported here was funded by The Environmental Research Fund. Carolyne Ray helped prepare data for analysis and Liz Murray drew the figures. We also thank Dr Stephen Baillie for helpful discussions.
Table 1. Weather variables and periods used in the analysis of the effects of weather on southern lapwing populations.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Temp</td>
<td>Mean monthly mean daily temperature</td>
</tr>
<tr>
<td>2. Soil temp</td>
<td>Mean monthly mean daily temperature at 30 cm depth</td>
</tr>
<tr>
<td>3. Frost</td>
<td>Number of days with grass minimum below 0°C (frost)</td>
</tr>
<tr>
<td>4. Rainfall</td>
<td>Total rainfall</td>
</tr>
<tr>
<td>5. Rain days</td>
<td>Number of days with more than 0.2mm rain</td>
</tr>
<tr>
<td>6. Wet days</td>
<td>Number of days with more than 1.0mm rain</td>
</tr>
<tr>
<td>7. Snow</td>
<td>Number of days with snow lying at 09.00 hrs</td>
</tr>
</tbody>
</table>

**Period**

<table>
<thead>
<tr>
<th>Period</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Pre-breeding</td>
<td>March of index year</td>
</tr>
<tr>
<td>2. Winter</td>
<td>Previous November - February inclusive</td>
</tr>
<tr>
<td>3. Autumn</td>
<td>Previous July - October inclusive</td>
</tr>
<tr>
<td>4. Breeding season</td>
<td>Previous April - June inclusive</td>
</tr>
<tr>
<td>5. Previous March</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Two-way analysis of variance of the effects of grassland type and its use on territory density.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
<th>F</th>
<th>df</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland type*</td>
<td>0.042</td>
<td>2.64</td>
<td>1</td>
<td>NS</td>
</tr>
<tr>
<td>Use</td>
<td>0.448</td>
<td>6.96</td>
<td>4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>0.065</td>
<td>1.01</td>
<td>4</td>
<td>NS</td>
</tr>
</tbody>
</table>

* Ley or permanent grass. Rough grass was not included because it was only used as pasture.

Table 3. Two-way analysis of variance of the effects of the timing of sowing and the presence of adjacent grass on lapwing territory density in cereals.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of squares</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cereal type</td>
<td>1.251</td>
<td>61.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Adjacent grass</td>
<td>0.381</td>
<td>18.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interaction</td>
<td>0.415</td>
<td>20.6</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

All tests had 1 degree of freedom
Table 4. Multiple regression analysis of the effects of weather on the rate of change of southern lapwing populations.

1962-1987 data

<table>
<thead>
<tr>
<th>Variable</th>
<th>Slope</th>
<th>SE</th>
<th>R²</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-0.6665</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pre-breeding frost</td>
<td>-0.0146</td>
<td>0.0033</td>
<td>40.1</td>
<td>15.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Winter temp</td>
<td>0.0402</td>
<td>0.0123</td>
<td>18.3</td>
<td>10.6</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Autumn temp</td>
<td>0.0470</td>
<td>0.0033</td>
<td>7.8</td>
<td>4.8</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Complete model</td>
<td>-</td>
<td>-</td>
<td>66.2</td>
<td>13.7</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

1962 - 1985 data

<table>
<thead>
<tr>
<th>Variable</th>
<th>Slope</th>
<th>SE</th>
<th>R²</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.3268</td>
<td>0.2020</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Log popn indx</td>
<td>-0.8870</td>
<td>0.0718</td>
<td>65.5</td>
<td>152.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Prev march frost</td>
<td>0.0110</td>
<td>0.0017</td>
<td>14.9</td>
<td>41.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Pre-breeding rain days</td>
<td>-0.0049</td>
<td>0.0014</td>
<td>7.1</td>
<td>11.2</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Autumn rainfall</td>
<td>0.0013</td>
<td>0.0004</td>
<td>3.6</td>
<td>10.5</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Autumn temp</td>
<td>0.0209</td>
<td>0.0083</td>
<td>2.4</td>
<td>6.3</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Complete model</td>
<td>-</td>
<td>-</td>
<td>93.4</td>
<td>48.5</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Figure 1  The location of the Common Birds Census plots used in the continuous plot study, the area from within which CBC plots were selected for the analysis of the effects of weather, and the location of the weather stations.
Figure 2  Jacob's preference indices for Lapwing territory location on continuous study plots. Crop types are: BL Bare Land; FL Fallow; LY Ley; PG Permanent Grass; RG Rough Grass; OR Oil-seed Rape; SC Spring Cereal; AC Autumn Cereal; SV Spring Vegetables. Crop types which share the same letter do not have significantly different preference index values. Standard errors are indicated by vertical bars.
Figure 3  Mean Lapwing territory density in continuous study plots on ley, permanent grass and rough grass according to its use. Vertical bars indicate standard errors of the density estimate.
Figure 4  Mean Lapwing territory density in continuous study plots on spring and autumn cereals with and without adjacent grass. Standard errors are indicated by the vertical bars.
Figure 5  Mean territory density on continuous study plots
Figure 6  The relationship between mean Lapwing territory density and the mean area of autumn cereals on continuous study plots.

Regression equation: Density = 0.077 - 0.089 (area of autumn cereal), F1 = 17.0, P < 0.001.
Figure 7  Changes in the percentage of farms with Lapwings and Lapwing density in each 4-year period.
Figure 8  Changes in the mean percentage of the total plot area comprised of spring cereal, winter cereal, grazed grass, mown grass, oil-seed rape and bare fallow, and the percentage of farms with each crop.
Figure 9  Observed Lapwing Common Birds Census indices in southern Britain and those predicted from the simulation model derived from data from 1962 to 1987.
Figure 10  Observed Lapwing common Birds Census indices in southern Britain and those predicted from the simulation model derived from data from 1962 to 1985.
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