The Effects of Intensive Agriculture on the Breeding Ecology of the Lapwing (*Vanellus vanellus* L.).

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Abstract

Changes in modern agriculture have been shown to have detrimental affects on those bird species whose populations mainly inhabit the wider countryside. Recently extensive changes to the farmed landscape have occurred through implementation of European agricultural policy much of which has been concerned with decreasing agricultural production. Lapwing (*Vanellus vanellus*), with almost the entire British population breeding on farmland, is a species that is thought to have been particularly affected by agricultural change.

A study attempting to assess the impact that modern, intensive arable farming had on a breeding population of lapwing was undertaken from 1995 to 1997 in south-west Lancashire. The study site had an open character and was predominantly winter farmed (cultivation occurring September-February), although more than a third of the area was spring cultivated. Permanent pasture and rotational set-aside (RSA) accounted for about 2% and 5% of the cropped area respectively.

Lapwings preferred to nest in spring farmed fields and RSA. The overall nest survival was 55.5% and did not differ significantly between years. Hatching success was highest in RSA (88%), lowest in spring farmed fields (48.4%) and intermediate in winter farmed fields (57.2%). Hatching success was significantly higher in spring farmed fields than in other habitats but did not differ significantly between winter and spring farmed fields. The hatching success of winter farmed fields was elevated by the success of nests of fields cultivated late in the winter. The main cause of nest losses was farming operations which caused 77.4% of all nests lost. Predation accounted for 14.4% of nest losses and desertion for 8.2%. There were annual differences in nest destruction in winter farmed crops caused by differences in the timing of agricultural operations. Nest destruction was highest in unsown fields but was compensated for by a high rate of replacement and high hatching success in replacement clutches. Two types of crop were spring farmed, combinable (mainly cereals) and vegetable (mainly potatoes) crops. Higher hatching success in spring cereals than in vegetables was related to the differing intensities of management between the two crop categories.

Lapwing preferred to nest in dense aggregations and far from ditches both of which reduced the risk of predation. Low densities of nest predators were maintained in the study area by predator control.

Chicks from larger eggs survived better than chicks from smaller eggs. Chicks undertaking movements from natal to rearing fields suffered high levels of mortality. Chick mortality was caused by poor body condition, entrapment in field boundary ditches or predation or from the interaction of these factors. Brood movements were influenced by the distribution of crop types. Spring farmed fields and pasture were used for rearing broods. Predation was the main proximate cause of mortality for radio-marked chicks and accounted for 52% of all losses. Predation was a significant mortality factor until chicks were at least 20 days old, whereas poor body condition (31% of all radio-marked chick losses) and ditch entrapment (17% of all losses) only killed very young chicks. Fledging success, not hatching success, was thought to be the main limit on productivity.

Dietary studies revealed chicks ate mainly beetles but their diet varied depending upon rearing location. Surface living chick prey was abundant throughout the season in arable fields and late-hatched chicks suffered higher mortality than those hatched earlier mainly due to an increase in predation late in the season.

Recommendations to maintain or improve the conditions for breeding lapwing within the study site are discussed. They include proposals which could operate under the agri-environment regulations of the CAP, such as an increase in the area spring farmed with the cultivation of both cereal and vegetables and changes to the management of rotational set-aside to make such fields more suitable for brood rearing.

1.0 Introduction

1.1 The lapwing

The northern lapwing[1] (*Vanellus vanellus* L.) is a widespread and well known bird of the British countryside. Within the British Isles it is the only representative of the Vanellinae, a sub-family of the Charadriidae family of waders, which holds 24 species world-wide. These are mainly terrestrial waders found predominately in Africa with only 6 vanelid plover species occurring within the Western Palearctic (Cramp and Simmons 1983). The lapwing is a particularly successful member of the group with a breeding range stretching from Iberia and the Atlantic coasts of France and Ireland across the Eurasian landmass to the Russian Pacific coast. Within this geographical area lapwings inhabit the upper and middle latitudes from the boreal and temperate to the steppe and Mediterranean zones generally choosing low-lying, flat or undulating habitats in unenclosed terrain (Cramp and Simmons 1983). Apart from the lapwing only one other member of the Vanellinae, the spur-winged plover (*Vanellus spinosa*), breeds in Europe, this being confined to just a few locations in Greece and Turkey (Hagemeijer and Blair 1997). In contrast, the lapwing is ubiquitous breeding in every European country and within the Western Palearctic is absent as a nesting species only in much of North Africa (although small numbers breed in Morocco) and the Middle East (Cramp and Simmons 1983, Hagemeijer and Blair 1997). The main wintering areas in the south and west of the Western Palearctic (including Britain, Ireland, the low countries, France, Iberia and the Mediterranean basin) reflect its reliance on ground dwelling arthropods for food (Cramp and Simmons 1983). Within the U.K., the lapwing is the most numerous and widespread breeding wader, being absent only from the extreme south-west, much of Wales and parts of west Scotland (Gibbons *et al.* 1993). Wintering lapwings avoid the higher ground of north and west Britain being most abundant in southern and central Britain and Ireland (Lack 1986).

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[1] Hereafter referred to as just 'lapwing'.

1.2 The U.K. lapwing population

1.2.1 Size and distribution

There have been four surveys of breeding lapwings covering England and Wales this century. The first took place in 1937 (Nicholson 1938 & 1939) with a second in 1960-61 (Lister 1964). There was concern about the British lapwing population even earlier in the century when subjective reports of decline were linked to the excessive collecting of eggs for human consumption (Hudson *et al.* 1994). This concern resulted in implementation of a statutory protective measure, the 1926 Lapwing Act, after which considerable recovery was reported (Alexander and Lack 1944). At the time of the first two surveys, though, it was considered impossible to attempt to accurately estimate the population of such a widespread and common species and so surveys were confined to the investigation of habitat selection for nesting (Shrubb and Lack 1991). Fisher (quoted in Spencer 1953), however, provided an estimate (although with no documentation of the extent of sampling) for the 1930's of 175,000 pairs for England and Wales which Spencer (1953) did not revise in his monograph on the lapwing in Britain. Spencer did note, however, that sudden farming changes caused by the Second World War and severe winters in the 1940's appeared to have resulted in widespread decline. Conversely, a period of temporary climatic warming during the first half of this century had enabled lapwings to move into and colonise northern Scotland (Hudson *et al.* 1994). Lister (1964) believed that no marked general change in status had occurred as reports of local losses were balanced by those of gains. Surveys during 1968-72 for the British Trust for Ornithology (BTO) Breeding Atlas survey (Sharrock 1976) showed that lapwings were very widespread. Lapwing breeding season presence was recorded in 91.8% and 65.5% of all 10 km by 10 km squares in Britain and Ireland respectively. Sharrock gave a lapwing population estimate of about 160,000 pairs for Britain or over 200,000 pairs for Britain and Ireland. He based these figures on (the untested) assumption of 68 pairs/10 km by 10km square, a density obtained from the 1972 farmland CBC (Common Bird Census of the BTO) plots. Later surveys and CBC results showed Sharrock's figure to be a considerable underestimate (see below).

It was not until the third survey in April 1987 that the first attempt was made to determine the size as well as the geographical distribution and habitat preferences of lapwings nesting in England and Wales (Shrubb and Lack 1991). Survey procedure was a complete count of nesting lapwing in one randomly selected tetrad (2km x 2km) in every 10 km square in England and Wales which contained any land. A total of 123,134 pairs in England and Wales was estimated from the survey with 95% confidence limits of about 110,000 and 138,000. The figure was considered to be somewhat depressed, however, as it was thought the population had not fully recovered from mortality induced by severe winters in the mid 1980's (Shrubb and Lack 1991). Recent analysis of CBC data has indicated a cold winters effect on lapwings in the 1980's (Hudson *et al.* 1994), albeit not as serious as after the severe winters of 1978/79 and 1981/82 (Marchant *et al.* 1990). The 1987 survey showed that most nesting lapwing were found in northern England with just over 60% of the total estimated numbers of pairs north of a line from Cheshire to the Humber. This area represented only 24% of the total survey area. Within the north lapwings were concentrated west of the Pennine ridge. Elsewhere they were sparsely distributed with particularly few nesting pairs in south-west England and west Wales.

To assess the status of the lapwing population, comparison was made between counts made in 1987 at 27 sites which were also surveyed between 1956-65 (Shrubb and Lack 1991). This showed that over period there had been a decline of 61% in the number of pairs breeding in England and Wales. This decline is equivalent to the loss of *c.*192,000 pairs or over 7000 pairs each year. Despite the decline, lapwings were still widespread. The 1988-91 breeding atlas showed 83% of British and 48% of Irish 10 km squares occupied. This represented a decline in distribution of 9% and 28.8% respectively. The decline affected lapwings most in Eire, West Wales, North-west Scotland, Devon and Cornwall.

Additional information obtained from a survey of lowland wet grasslands in England and Wales showed a 38% decline in lapwing numbers between 1982 and 1989. This meant that such habitats held less than 4% of the total breeding population (O'Brien and Smith 1992). This survey showed that even in areas protected as reserves significant declines had occurred.

The 1987 lapwing breeding survey only covered England and Wales. Thom (1986) estimated a total Scottish population of between 75,000 and 100,000 pairs using results of density sampling undertaken in 1982-83 (Galbraith *et al.* 1984). Shrubb and Lack (in Gibbons *et al.* 1993) estimated 21,500 pairs for Eire (based on the 1988-91 Breeding Atlas data) and gave a total population for Britain and Ireland for 1986-87 of 205,000 to 260,000 pairs. In 1997 the APEP (Avian Population Estimates Panel), using the same data, gave a breeding population for Great Britain (excluding Ireland) in 1986-87 of 190,000 to 240,000 pairs (Stone *et al.* 1997).

The fourth BTO/Royal Society for the Protection of Birds (RSPB) survey in 1998 repeated that of 1987 and has been reported by Wilson, Vickery and Browne (in press) and Mead (1999). This gave a total of 62,923 pairs (95% confidence intervals of 55,268 to 74,499) in England and Wales. The total indicates a decrease of 49% (or 60,211 pairs) since 1987 (Table 1.2.1a).

The 1998 survey showed that, over the preceding 11 years, each region had recorded a population decline, all of which were close to or exceeded 50%. The most severe declines were recorded for Wales and South-west England. In these regions population levels are low enough to envisage modern extirpation of the species. The North was still the lapwing stronghold with 68% of the population in 24% of the land area. The decline recorded in the North was of similar magnitude to the South-east indicating the factor or factors responsible for the population decline have been operating throughout the entire English and Welsh range. An associated decline in distribution was also noted with only 29% of tetrads (of a total 1,312) found to hold breeding lapwings compared to 39% (of a total of 1,470) in 1987.

Table 1.2.1a Results of two lapwing surveys carried out in 1987 and 1998 in England and Wales showing regional (percentage) decline. Figures in parenthesis represent regional proportions (%). Figures for 1987 from Shrubb and Lack (1991) and for 1998 from Mead (1999) and Wilson *et al.* (in press). The North includes the North-west, Yorkshire/Humberside and the North.

Region	Number of breeding pairs		Percentage decline
	1987	1998	
Wales	7448 (6.0)	1700 (2.7)	77
South-west	5718 (4.6)	2057 (3.3)	64
East Anglia	6495 (5.3)	2977 (4.7)	54
Midlands	19388 (15.7)	8912 (14.2)	54
South-east	9522 (7.7)	5147 (8.2)	46
North	74565 (60.6)	42610 (67.7)	43
England and Wales	123134	62923	49

1.2.2 Status

In 'Birds of Conservation Concern' (RSPB/BTO 1996) new priorities for bird conservation and listing red data birds in the U.K. were established using the objective criteria of national threat, international importance and international threat (Avery *et al.* 1995). Under the rationale of the method species are allocated to one of three levels of conservation priority; green (low), amber (medium) and red (high). Lapwings were given an amber-listing (a population decline of 25-49% over 25 years) following the downward trend in the U.K. population (Gibbons *et al.* 1996).

The accelerating decline shown by the latest survey indicates that the conservation priority for lapwing in Britain needs to be re-assessed and, perhaps, its status upgraded. A national decline in numbers of 50% or more over 25 years warrants a species being red-listed in BoCC (Birds of Conservation Concern). At present re-assessment is complicated by the situation in Scotland, which holds a large proportion of the U.K. population. A recent (RSPB) survey of mainland Scotland has shown that the lapwing population declined by 13% from 1992 to 1997. This decline was not, however, statistically significant (Wilson *et al.* in press).

1.2.3 The causes of the population decline

Each of the surveys have shown that for lapwings in the U.K. farmland is the primary breeding habitat . It is also apparent that, since World War Two, agricultural practice has undergone major change. As a farmland bird species lapwings are likely to have been affected by such change.

Since the 1940's agricultural change has affected both farmland habitats *i.e.* changes in the extent of farmland types (*e.g.* grassland and tillage) or types of crops (*e.g.* ley grass or cereals) and the way crops are grown or managed (Shrubb 1990). These changes have involved the advent of chemical farming with a massive reliance on agrochemicals for conventional systems and the enhanced concentration of farming types. This has led to regional specialisation in arable and livestock with continual cereal cropping replacing traditional rotations (O'Connor and Shrubb 1986, Hudson *et al.* 1994). The widespread use of pesticides has allowed a switch from spring to autumn sowing which also caused an increase in cereals (at the expense of grassland and spring sown root crops). The introduction of new crops, such as oilseed rape, are also mainly autumn sown (Shrubb 1990). Grasslands have been improved and are more intensively managed. This has led to a switch from hay to silage production, and higher stocking rates (Shrubb and Lack 1991).

The lapwing's preference for spring tilled land was shown by all four surveys with more pairs breeding in this habitat than any other. The selection of spring tillage is clearly linked to hatching success as nests in this habitat suffer less from predation, trampling (by stock) and desertion (Shrubb and lack 1991). Between 1960 and 1987, however, the area of spring tillage in England and Wales decreased by 68% (with a corresponding increase in autumn tillage) becoming particularly scarce in the southern and south midland counties (Shrubb and lack 1991). Shrubb (1990) showed that the CBC index for lapwings for the primarily cereal growing counties of England and Wales showed a marked decline between 1962 and 1983. This decline correlated very closely with the reduction in area of spring cereals in those counties over the same period. Even though hatching success in autumn tillage is as high as spring hatching success, all the surveys have shown that this habitat is avoided for nesting and that this avoidance has become more pronounced (Shrubb and Lack 1991, Wilson *et al.*, *in litt*). O'Connor and Shrubb (1986) thought autumn sown cereals had grown too high by April to be used much by Lapwings. The increased use of fertilisers on cereals led to yields increasing by a third (from 4 to 6 tonnes ha $^{-1}$) between 1960 and 1980. In 1987 the reason that autumn tillage was avoided more than in the past was a result of the increased intensive management which had caused more rapid crop development (Shrubb and Lack 1991).

It has been shown that it is not just the spring tilled area that is important to lapwing productivity. Galbraith (1988b) showed that lapwings need pasture, a short grazed sward providing the best brood rearing habitat, next to good nesting habitat (*i.e.* spring tillage). In such circumstances chick production was high enough to maintain numbers. Shrubb and Lack (1991) showed that not only was there selection for nesting in spring tilled fields abutting grass rather than those separated from it, but also that there was a significant relationship between the preference shown by lapwings for permanent grass in a region and the ratio of spring tillage to permanent grass. The modern polarisation of farming types between eastern (arable) and western (livestock) Britain has affected the grass to tillage ratio. In 1987, 60% of spring till in England and Wales was in the East Midlands and East Anglia where 21% of agricultural land was grass. These being regions where the CBC index since 1970 has shown the greatest decline and where lapwings are now thinly distributed. In northern England, where the lapwing population is concentrated, there was only 12.5% spring tillage but 58% of farmland was grass. A moderate area of tillage in a large area of grass means that many pairs find the best breeding areas, *i.e.* the most profitable nesting sites close to the most productive chick rearing area. The change in the proportions of agricultural practice regionally has resulted in a geographic shift of the population to the North (Shrubb and Lack 1991).

The changes associated with the modern agricultural revolution have also affected grassland as well as tillage. One of the main changes to have occurred has been the switch from hay to silage (Shrubb 1990). Lister (1964) predicted that lapwings would avoid silage for nesting as it would be too high and dense in April. Silage fields are more intensively managed receiving 211kg ha^{-1} of nitrogen fertiliser compared to only 91 kg ha^{-1} for hay. The 1987 survey showed that lapwings do not like using silage for nesting (Shrubb and Lack 1991). In 1962 just 2% of ley and permanent grass was silage, by 1985 this had increased to 26% (MAFF[2] fertiliser practice surveys 1962 and 1985 in Shrubb and Lack 1991). This not only restricted the area of grass available for nesting but increased lapwing dependency on stocked fields where nest losses increase due to trampling and desertion. More intensive management has also affected unimproved grasslands. Baines (1990) showed that improvement of upland rough grazing (which held almost a quarter of all pairs in the 1987 survey) to more homogenous pasture decreased lapwing productivity below the level required to maintain numbers.

Another major change has been an increase in stocking rates. Increased stocking rates have also involved an increase in related activities, such as rolling, harrowing and manure spreading, all of which can cause nest losses (Beintema *et al.* 1985, Shrubb 1990). The 37% increase in stocking densities in England and Wales between 1962 and 1985 provided a consistent background to the rise in grassland nest losses (Shrubb 1990).

A smaller area of poorer quality breeding habitat resulting in a decrease in breeding success may not be the only reason for a decline in numbers. It is also possible that

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[2] Ministry of Agriculture, Fisheries and Food.

changes in the survival of fully-grown birds may have contributed to the recent population decrease. Peach *et al* (1994) have shown, however, that the survival rate of lapwings has actually increased over the period of decline, with adult life expectation increasing from 2.4 years (1909-52) to 3.5 years (1961-89). In addition, they found no evidence to suggest that first-year survival has declined sufficiently to have made a contribution to the decline in the lapwing population. These results imply that it is poor chick production that has been the most likely contributory factor in the decline in the British breeding lapwing population.

The many changes in farmland habitat and agricultural management that have occurred in recent decades have, thus, combined to affect not only the availability and distribution of lapwing breeding habitat but also its quality. Furthermore, there have been no effective measures to counteract these effects in the wider countryside, where nearly all lapwings breed. In the space of one human generation the decline has taken lapwing from being considered common with a population of about half a million individuals to becoming a candidate suitable for red-listing - a species warranting the highest conservation priority.

Britain has not been the only European country where lapwing breeding numbers have been diminishing. Population declines resulting from low productivity have been found during several studies of lapwings breeding on intensively farmed arable land in continental Europe *e.g.* in Switzerland (Matter 1982), in western and northern Germany (Beser and Helden-Sarnowski 1982, Kooiker 1984) and in Denmark (Ettrup and Bak 1985).

1.3 Previous studies of farmland lapwing

1.3.1 Nest site selection and hatching success

Surveys in the U.K. have established farmland as the most important breeding habitat for lapwings. In 1987 in England and Wales a total of 96% of lapwings bred on land farmed for crops or livestock. Although, there was some geographic variation (from 90% in the South-east to 98% in East Anglia and the North) farmland was found to be the primary nesting habitat in each region (Shrubb and Lack 1991). Farmland was also preferred by lapwings in Scotland with an estimated 85% of the Scottish population breeding on agricultural land (from Galbraith *et al.* 1984, Thom 1986).

Within farmland there is a strong preference for tillage (land cultivated annually) with 40% of pairs nesting on tilled land in the 1987 survey (Shrubb 1990). The majority (81%) of tillage pairs preferred spring tillage (mostly cultivated fields without an emergent crop and stubble fields). Spring tillage (fields cultivated in the spring) has been the most strongly and consistently favoured nesting habitat in all U.K. surveys. Autumn tillage (fields cultivated in the autumn) has been consistently avoided and the selection of grass habitats variable (Shrubb and Lack 1991). In a Swiss study, Imboden (1970, 1971) found that preferred nest sites were on the dark, bare arable ground of spring sown fields. He found, however, that, due to agricultural practices, up to 30% of pairs nested in meadows where hatching success was decreased. Galbraith (1988b & 1989b) also found a preference for tillage in a study including Scottish arable land (45% cereals and 49% grass). In Galbraith's arable study area lapwings showed a significant preference for nesting in cereals with a tendency towards spring cereals. Spring cereal fields held 68% of nesting territories but comprised only 34% of the area under crops. Furthermore, Galbraith's Scottish study and the 1987 BTO survey of England and Wales both showed that spring tillage that abutted pasture was preferred over other spring-tilled fields (Shrubb and Lack 1991). Berg *et al.* (1992) studying lapwing at a site dominated by spring cereals (*c.* 71% tillage and 25.4% grass) in central Sweden also found a preference for nesting in tillage. Grassland was avoided being used less commonly than expected by chance. Blomqvist and Johansson (1995), however, studying a coastal population of lapwings in south-western Sweden found that arable land (*c.*43% of study area) and pastures (*c.*57% of study area) were used to a similar extent for nesting. This study does seem to show, however, the predilection of lapwings for spring sown land within tillage as 96% of nests were in spring cereals. The few remaining arable nests were sited in autumn tillage but it is not stated how much of the arable area was autumn sown.

The preference for tillage appears to be linked to hatching success. Shrubb (1990) showed that in England and Wales clutch size and brood size at hatching was significantly larger in tillage than in grass. There would seem to be a paradox, however, as the favoured nesting habitat, tillage, is also where lapwing experience high rates of nest loss due to farming activities (Berg *et al.* 1992). The nesting season of lapwing coincides with spring cultivation and as many birds prefer to nest in spring tilled fields losses can be extensive (*e.g.* Shrubb 1990, Galbraith 1988b). Farming activities in central Sweden accounted for 85% of all nest losses and were, by far, the most important factor causing breeding failures. In fact, Berg *et al.* (1992) showed, that despite such losses, total hatching success (first clutches in unsown and second clutches in sown fields) in tillage was higher than in all other habitats (*i.e.* grassland and fallow). This was due to a higher re-laying frequency in tillage and a higher hatching success in second clutches. The optimal nesting habitat was, therefore, being chosen. In grassland, however, nest losses to farming operations, while they still occur, are seldom but grassland nests suffer a much higher predation rate than in tillage (*e.g.* Galbraith 1988b, Baines 1990, Shrubb 1990). Predation can determine breeding success, particularly in areas of improved grassland where a uniform sward can make eggs more conspicuous to predators (Baines 1990).

Galbraith (1988b) found that significantly fewer spring cereal than rough grazing clutches were depredated in his Scottish study area. He concluded that the substrate of bare, spring tilled fields provided camouflaged concealment of unattended eggs conferring protection against predators. In Sweden, however, Berg *et al.* (1992) and Blomqvist and Johansson (1995) found no significant difference in predation rate between nests sited on arable land and on grass. Blomqvist and Johansson (1995) thought the predation rate in their study area too low to influence nest site choice between arable and pasture fields. Berg and his colleagues found that predation was related not to habitat but to colony size and breeding density. In this study the risk of predation decreased not only with increasing nest density but also with increasing colony size. Berg *et al* (1992) also found that nest survival was higher at sites far (>50m) from trees indicating that birds were important nest predators. In their study, they found that lapwings minimised predation risk by breeding in aggregations and nesting far from perches for avian predators. Galbraith (1988b), however, found no relationship between hatching success and breeding density in his Scottish study where predation (not farming activity) was found to be the most important factor causing nest losses in both arable and rough grazing areas. This may be due to mammalian rather than avian predators robbing nests in the Scottish study. If foxes are the most common predator it may be disadvantageous to breed in large colonies (Berg *et al* 1992).

Another reason why lapwing prefer to nest on bare tilled land may be that it provides good feeding conditions during the pre-laying and nesting periods. Females need rich foraging areas in the vicinity of nests during the high energy demand periods of egg formation and incubation (Norton 1972, Erckmann 1983). Blomqvist and Johansson (1995) found that female lapwing caught more large prey items on arable fields than on pastures. They also found, as did Berg (1993), that females close to egg laying foraged close to their future nest sites with those nesting on arable land producing larger eggs (and, therefore, more viable offspring) than those nesting on pastures.

Hatching success on grass is also decreased by trampling by livestock and livestock-induced desertions, both factors absent in tillage. Shrubb (1990) concluded from his analysis of B.T.O nest record cards for England and Wales that the advantages of nesting in tillage (such as easier nest replacement, less predation and no stock) for lapwings outweigh the disadvantage of losses from cultivation activities. The nesting advantages of tillage, however, ultimately depend on the proximity to pasture for chick rearing. Without ready access to pasture, fledging success is often too low to maintain numbers in arable populations (Galbraith 1988b, 1988c).

1.3.2 Chick rearing and fledging success

In common with other Charadriiformes, lapwing chicks are precocial and mobile usually within 6 hours of hatching. Chicks, therefore, are able to abandon the vicinity of the nest and can be led by their parents to more suitable rearing areas (*e.g.* Ennion 1949). Among the first to study the different nesting and chick foraging requirements of lapwing was Redfern (1982). He found differences in brood behaviour between two lapwing colonies in Scotland. Adults in a colony sited in rough grazing (a short grass sward with clumps of rush (*Juncus*)) moved their chicks only a short distance after hatching, rearing them within their natal habitat. Parents hatching chicks in a blanket-bog area, however, led their offspring away from nest sites to areas of pasture where they remained until fledging. Redfern thought that blanket bog areas (where most pairs nested) were better for nesting as unattended eggs were well camouflaged which decreased predation risk. He also noted that these areas were free of livestock and, thus, nest trampling. After hatching chicks moved from what Redfern considered faunistically impoverished natal sites to the better feeding areas provided by pasture. Galbraith (1988b), in his study of lapwings breeding in Scottish farmland (rough grazing and arable), investigated food availability in chick rearing habitats. Galbraith found that at his rough grazing site unimproved land was the preferred nesting habitat, but most chicks left that habitat soon after hatching and moved quickly to adjacent improved rough grazing where the sward was shorter. At his arable site chicks hatched in cereal fields (the preferred nest sites) and mostly moved to permanent pasture. Galbraith found that the habitats to which the chicks moved had more abundant invertebrates than those where they were hatched.

Galbraith also showed that, in addition to food availability, the height of vegetation was an important influence on post-hatching chick movements. In one year of Galbraith's study crop growth was retarded by adverse weather which resulted in arable chicks remaining in their natal spring cereal fields. In northern England Baines (1989) found that the increasing height of grass and crops caused chicks, initially reared in meadows and arable fields, to move into adjacent pastures where they mostly stayed until fledging. Investigating food availability he concluded that this factor was not responsible for chick movements as all of the fields used by lapwing had adequate levels of chick prey (Baines 1990).

Galbraith (1988b and 1988c) found that chick survival and fledging success was influenced by the proximity of pasture to the nest field. Fledging success was highest at the rough grazing study site as chicks could accomplish post-hatching movements quickly, pasture being located immediately adjacent to natal areas. Arable chick survival depended on how far chicks had to move to pasture. Fledging success was higher for those with direct access, whereas for chicks that had to cross intervening crop fields to reach pasture high mortality was experienced. With many pairs nesting in cereal fields distant from pasture, breeding success for arable farmland lapwing was low. Galbraith concluded that modern management changes within his arable study site, characterised by a reduction in livestock and pasture and more emphasis on cereal production, had only recently resulted in it becoming less suitable for breeding than it once was. Lapwing, therefore, continued to use arable farmland for breeding. Blomqvist and Johansson (1995) also found that mortality was higher for chicks that undertook long post-hatching journeys. In their study the distance between nest sites and chick rearing areas was on average three times longer for lapwing nesting on arable land than for those on pastures. Chick survival between the two habitats, however, did not differ, even though arable chicks were taken to pasture to be reared. The conclusion of Blomqvist and Johansson was that nest site selection and chick production involved a trade-off between the benefits of nesting close to rich (arable) feeding grounds for adults (allowing females to produce larger eggs) and the costs of moving long distances between nest sites and brood rearing areas.

The studies that have looked at nest site selection and chick rearing have, therefore, demonstrated that chicks do move from one habitat to another suggesting that the optimum conditions for nesting and brood-rearing for lapwings are different. Traditional farming provided these conditions as a mixed agriculture provided a habitat mosaic. Over the last few decades, however, the role of political policy has greatly influenced the nature of farmland.

1.4 Arable farming and the Common Agricultural Policy

1.4.1 The CAP and the 1992 reform

Agriculture was included in the common market provisions of the European Economic Community (EEC) when first established in 1957. Agriculture within the EEC was to be governed by a Common Agricultural Policy (CAP), and when the U.K. joined the EEC in 1973 British farming was brought under the influence of the CAP.

The CAP had several objectives. These were primarily to increase agricultural productivity by promoting technical progress and by the optimal use of the factors of production and to ensure a fair standard of living for the agricultural community by increasing the earnings of persons engaged in farming. In addition, the CAP aimed to assure the availability of supplies ensuring those supplies reached consumers at reasonable prices (Robson 1997). These objectives were to be achieved by guaranteeing artificially high prices for major commodities and protecting farmers within the community from international competition (Potts 1997). After the CAP began there followed an intensification of production, involving ever increasing quantities of agrochemicals applied to each hectare of land. In Britain, for example, since the early 1950's an increase occurred in the mean levels of nitrogen applied by almost 900% on winter wheat and 500% on spring barley (Church 1981, Chalmers *et al.* 1990). Research and development (stimulated by the safe economic environment of guaranteed prices and public subsidy) helped create higher yielding crops and animals that were more responsive to agrochemicals (Sotherton 1998). Concomitant improvements in the mechanisation of production meant a virtual revolution in farming techniques also allowing an increase in scale of production (Potter 1997).

This intensification process caused a restructuring of agriculture throughout the European Union (EU[3]) affecting both cereal production and pastoral farming. Farmers could escape from grass/cereal rotations allowing continuous cropping, livestock became separated from the crops needed to feed them; mixed farms gave way to specialised farms, and mixed farming regions have given way to specialised regions (Potts 1997). In the U.K. the west is now predominantly grass whilst the east has effectively become an arable belt (O'Connor and Shrubb 1986). Landscapes became simplified through the removal of trees, hedges, small woods, ponds and the 'improvement' of semi-natural wet grasslands (Carter 1982, Potter 1997). The U.K. Government's 1990 Countryside survey showed that even in the early 1980's 28,000 km of hedgerow were being removed each year (Barr *et al.* 1993).

The greater use of farm chemicals, the main instrument of intensification, was also having environmental consequences, increasing pollution and enabling less fertile land to be brought into production (*e.g.* Baldock 1990, Ward and Aebischer 1994, Campbell *et al.* 1997). The number of chemical active ingredients approved for use in pesticides in 1960 was 71, in 1970 it was 214 and by the early 1990's it had risen to 600, with those 600 active ingredients formulated in some thousands of different products (O'Connor and Shrubb 1986, Campbell *et al* 1997). In 1993/94 the average U.K. cereal field received 2.7 of fungicides and 0.7 of insecticides and molluscicides (British Agrochemicals Association 1995). Before 1972 there wasn't a single fungicide approved for use in the UK with no approved molluscicides before 1960 (O'Connor and Shrubb 1986). All of these changes to farming have brought about a massive decline in biodiversity in the countryside (Potts 1986, 1991).

Further to the environmental repercussions of the CAP there were also those connected to production. Within the EU the volume of agricultural production from the early 1970's to early 1990's increased at an annual rate of 1.5%. The number of consumers, however, increased at only a fraction of these rates resulting in surpluses that required expensive disposal policies (Robson 1997). Furthermore, guaranteed prices meant that farmers could continue to produce without suffering a reduced price as a result of over-supply.

Reform of the CAP became inevitable not only as public awareness of environmental degradation grew and pressure from the environmental lobby increased but also because of the effect on the EC budget of increasing commodity stocks, particularly those of cereals and beef (Floyd 1992).

In 1992 a number of measures to reform the CAP (the MacSharry Reform) were introduced that not only included proposals to reform the production side of agriculture but also to encourage farmers to use less intensive and more environmentally friendly methods (Rayment *et al.* 1997). These included cuts in support prices and the introduction of livestock quotas and compulsory arable set-aside (*i.e.* taking land out of food crop production) to help reduce surplus production. The 1992 reform also included the Agri-environment programme (Regulation 2078/92 - as one of three 'accompanying measures') allowing extensification and environmentally sensitive farming practices. In England the two main agri-environment schemes, both operated by MAFF, are Environmentally Sensitive Areas (ESAs) and the Countryside Stewardship Scheme (CSS). ESAs are designated geographical areas selected for their national environmental significance whereas the CSS targets particular landscape types associated with traditional farming systems, high biodiversity or historic value, or amenity potential generally outside ESAs (Ovenden *et al.* 1998).

Although an effort to integrate environmental concerns into agriculture was made in the 1992 reform (particularly with the Agri-environment regulation) the root of the CAP

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[3] In 1986 the EEC became the EC (the European Community). In 1992 the EU came into being, including the same member states as the EC but embracing wider responsibilities. The terms EU and EC are often

problem (commodity subsidies) was not addressed (Dixon 1993, Rayment *et al.* 1997). Making set-aside obligatory (as a condition of receiving compensatory payments for cuts in support prices of cereals and oilseeds), however, made set-aside a prominent feature of the British countryside (Wilson *et al.* 1995). Between 1988 and 1993, when set-aside was a voluntary option for farmers, only 2.4% (155,255 ha) of the arable area of the U.K. was managed as set-aside. In 1994/95 this proportion had more than quadrupled to 10% (662,000 ha) of the arable area, representing 2.7% of the total U.K. land area (from data in Robson 1997). The importance of set-aside can be judged from the fact that in the mid 1990's the area under set-side in the U.K. was equivalent to the area (2.8%) occupied by nature reserves (RSPB 1995).

1.4.2 Set-aside

Set-aside exists not as a land-use policy but as a supply control measure to reduce the over-production of the food crops it replaces, this permitting reductions in the costs of agricultural price support in the EU (Floyd 1992). In 1992, CAP reforms greatly reduced the production support prices for cereals and oilseeds (helping reduce food prices) but farmers became eligible for 'Arable Area Payments' (AAPs) (Pain and Peinkowski 1997). Farmers could benefit from AAPs only if 15% of their land area growing the target crops was rested or set-aside from production. In 1988, when first introduced, set-aside was voluntary but it effectively became compulsory in 1992 when AAPs were made conditional on entering the scheme (Robson 1997). The increased financial attractiveness of the scheme resulted in substantial changes to the arable landscape of the U.K. The small area which existed under voluntary set-aside rocketed to well in excess of half a million hectares over the course of a single harvest (Wilson et al. 1995).

The 1992 CAP reform introduced three set-aside options (MAFF 1993):

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used interchangeably, although there are differences in technical meaning.

1. Rotational set-aside (RSA); eligible land must be set-aside for one growing season (15 January to 31 August), only becoming usable for set-aside again after five years. The land set-aside must represent 15% of the total area under AAPs.
2. Non-rotational set-aside (NRSA); land must remain as set-aside for at least five years and must represent 18% of the total area under AAPs.
3. A combination of RSA and NRSA; where land can be set-aside for 1,2,3,4 or 5 years in any combination with 18% of the total area under AAPs.

After the initial introduction of the scheme the proportion of land eligible each year was reduced annually so that for the years of this study the percentage of land that could be set-aside was 15% in 1994/95, 10% in 1995/96 and 5% in 1996/97.

Within each option there were various management rules which for RSA were intended to "help ensure that land was kept in sound agricultural condition without damaging the environment" (MAFF 1993). In summary the rules for RSA were:

- A green cover must be established (to minimise nitrate leaching) by allowing natural regeneration (*i.e.* regeneration of crop volunteers and 'weeds' from the soil seed bank) or sowing a suitable (wild bird) cover including grass, mustard or mixes of two crop groups (*e.g.* cereal and brassica), rendering them unharvestable.
- The cover must be cut short by 15 August or destroyed by 31 August.
- Fungicides, insecticides and fertiliser must not be applied.
- Selective herbicides may be used for weed control but non-selective herbicides should not be sprayed before 15 April to retain cover until that date.
- Land may be cultivated after 1 May to control weeds or after 15 July to prepare for the following crop.

The relevant MAFF quote for NRSA is somewhat different." .... that land is kept in sound agricultural condition and that set-aside brings environmental benefit" (MAFF 1993). Management options for NRSA included establishing a grass cover and maintaining the sward with an annual cutting regime, natural regeneration with an annual cut, sowing wild bird cover (using two crop groups) and cropping for non-food purposes (*e.g.* biofuels).

Set-aside can be as whole-field blocks, but is also allowed to be distributed in smaller blocks (minimum 0.3ha, and 20m width). This enables the relatively unproductive strips around field margins to be set-aside while the remainder is kept in production.

The management options from 1992 were considered to be an improvement on those connected to the 1988 voluntary scheme when most set-aside was managed by neglect and the resulting "tumbledown" criticised by farmers and conservationists alike (Sotherton *et al.* 1992). The initial management of obligatory RSA put in place for 1992/93 involving cultivation (for weed control) between 1 May and 1 June also led to widespread criticism following damage to wildlife, especially to ground nesting birds during the breeding season (Sotherton *et al.* 1994). Such management resulted in direct destruction of nests (*e.g.* Manosa 1993) or through increased predation (*e.g.* Poulsen and Sotherton 1992). Management rules continued to evolve and (by the first year of this study – 1995) the option of cultivation in May had been removed, weed control (by cultivation or application of a non-residual herbicide) being allowed after 15 July. Even though management options increased in flexibility after 1993/94, the most widely adopted practice for RSA has been to allow fields to regenerate a vegetative cover in the absence of agrochemical inputs (Sotherton 1998).

1.4.3 Birds and farming: the wider countryside

The importance of farming under the CAP and the seriousness of any affect of intensification can be realised when it is considered that the utilized agricultural area of the U.K. takes up 75.6% (*c.*18,450,000 ha) of the total land area with about 6,600,000 ha (35.7%) of this area under arable regimes (data from Eurostat 1995 in Pain and Dixon 1997). In the U.K. the area given over to cereals occupies 17% of the total surface area; 16 times the combined area given over to all local and national nature reserves (Potts

1991). It follows that farming is not only the most important land-use in the U.K. but also that the arable ecosystem is a most important part of the British countryside (Potts 1997).

The lapwing is not the only bird species living in the wider countryside to have undergone a recent substantial population decline. Many other farmland birds have also declined (*e.g.* Fuller *et al* 1991, Gibbons *et al.* 1993, Evans *et al.* 1995, Crick *et al* 1998). The U.K. grey partridge population decreased by 73% between 1968 and 1991 (Fuller *et al.* 1995). The decline largely being attributable to poor chick survival as increased pesticide use on cereal crops led to a reduced insect food supply for chicks (Potts 1986). In the whole of Europe the decline in numbers of grey partridge since the 1930's has been estimated as equivalent to the loss of over 16.5 million pairs (Potts 1997). The numbers of Corn Bunting (*Miliaria calandra*) in the U.K. declined by at least 60% between the early 1970's and early 1990's (Donald *et al* 1994). Evidence points to increased rates of adult mortality, resulting from agricultural changes reducing winter food supply through the loss of winter stubbles, as the most likely factor causing the population decline (Donald 1997). Another widespread species, the skylark (*Alauda arvensis*), declined in numbers by 51% between 1968 and 1995 on U.K. lowland farmland, a loss of approximately 3 million breeding birds (Siriwardena *et al.* 1998). Skylarks appear to require structurally diverse crop mosaics for successful breeding and the loss of these through continuous cropping, autumn sowing and abandonment of rotations has reduced breeding productivity in lowland farmland (Wilson *et al.* 1997). Fuller and his colleagues (1995) showed that of 28 species classified as farmland birds in Britain the distributions of 24 (86%) contracted between 1970 and 1990. Of the 18 farmland species for which it was possible to assess population change, 15 (83%) were less abundant in 1990 than in 1970 and seven of these had experienced population decreases of at least 50%. Their analysis also showed that farmland species underwent an appreciably larger contraction of distribution than species associated with any other habitat and that, in contrast to farmland species, woodland species tended to increase. The declines in farmland birds became evident in the mid- to late 1970's, a period when several fundamental changes were taking place in British agricultural practices (Fuller *et al.* 1995). Siriwardena and colleagues (1998), calculating population trends from smoothed CBC indices, identified the major downward turning point for U.K. farmland birds as the mid-1970's. They suggested a change or suite of changes in the agricultural environment adversely affected many species' populations at that time. As the U.K. entered the (then) EEC in 1973 it would appear that many of these changes have been brought about by the CAP.

A similar parlous situation for birds has also been found throughout the EU where 41% of the utilized agricultural area is arable farmland. Within Europe 195 species (38% of the total) have an unfavourable conservation status, mostly because of substantial declines, with farmland containing more species with unfavourable status than any other habitat (Tucker and Heath 1994). Furthermore, as the main cause of decline has been the continuing process of agricultural intensification the decline of farmland species has been predominantly in western Europe (the EU) and not in central and eastern European countries (Tucker 1997).

The distribution and abundance of non-avian organisms has also been recorded as having changed on lowland farmland, particularly during the 1970's and 1980's. One of the best data sets available allowing an assessment of broad changes in the abundance of British farmland invertebrates is that of the Game Conservancy Trusts' (GCT) grey partridge study. Invertebrate population data has been collected from a 62km^2 farmland study site on the Sussex Downs since the study began in 1970 and covers the main period of agricultural change (Aebischer 1991). A summary of the long-term trends in invertebrate abundance as shown by the GCT partridge study is illustrated in table 1.4.3a.

The GCT survey recorded a severe long-term decline in total insect abundance. An interesting finding was that the trends were the same on all farms within the study area despite considerable differences in farming practice. It was suggested that this might be because invertebrate numbers were determined primarily by climate. Alternatively, this decrease might have been because the impact of modern cereal farming on invertebrates was so extensive that it affected even individual 'island' farms that were managed in a more traditional manner.

Table 1.4.3a Summary of long-term trends in British farmland invertebrate abundance. From Game Conservancy Trust data 1972-89 (Aebischer 1990, 1991, Aebischer and Potts 1990).

Invertebrate Category	Trend
All invertebrates[1]	**
Collembola	++
Aphididae	***
Aphid-specific predators[2]	0
Polyphagous predators[3]	**
Parasitoid hymenoptera	**
Carabidae	0
Bembidion lampros	++
Chrysomelidae	*
Gastrophysa polygoni	**
Staphylinidae	**
Tachyporus spp.	**
Symphyta	**
Predatory diptera	0
Aranae/Opilionae	**

0 = no change, * = small decline (<25%), ** = large decline (25-75%), *** = very severe decline (>75%), ++ = large increase (25-75%).

[1] excluding Collembola and Acari; [2] Coccinelidae, Neuroptera (lacewings), Syrphidae and Cantharidae; [3] Aranae, Opilionae, Staphylinidae, Carabidae, predatory Diptera and Dermaptra.

Whilst some individual species increased (*e.g. Bembidion lampros*) on the Sussex site, overall numbers of carabid beetles showed no change in status. Sampling errors for this group, however, may have been high as the sampling method used (suction sampling) was considered unsuitable for carabid beetles (Aebischer 1991). A study of Carabids in The Netherlands has indicated that there has been a substantial increase in the ranges of farmland tolerant Carabids since the end of the nineteenth century (Turin and den Boer 1988). The GCT's study showed that, unlike the ground beetles, the rove beetles declined substantially over the period of the study.

More recently studies have examined the short- and medium-term effects of pesticide applications on invertebrates, and these can be used in assessing possible long-term impacts. Most demonstrate severe impacts on non-target invertebrate populations followed by a gradual or rapid recovery. Various factors effect the extent to which populations recover, including their susceptibility to the chemical used, the persistence of the chemical, their dispersal and reproductive abilities, the proximity of the field to other populations and their life-histories (e.g. over-wintering strategy and habitat) (Campbell *et al.* 1997). Conversely, neither Moreby *et al.* (1994) nor Brooks *et al.* (1995) could detect any differences in overall invertebrate densities between organic and sprayed fields. In fact, the study of Moreby *et al.* (1994) demonstrated even higher densities of aphids on spayed rather than organic fields. Herbicides have also been shown to affect invertebrate populations, either by reducing the availability of insect food plants or through being insecticidal themselves.

It would appear that there is considerable variability in the extent to which different invertebrate groups and species are affected by different chemicals. The limited data available, however, suggests an overall picture of stability or decreasing abundance for farmland invertebrates (see Table 1.4.3a).

Wilson (1992) has reported that many species of arable weed have become very rare or even extinct in Britain since the 1960's with major declines in formerly nationally widespread species. As has been found with birds, the decrease has been with species found in arable rather than other habitats (Rich and Woodruff 1996). Similarly to insecticides on invertebrates, the effects of herbicides has varied with plant species. Few changes took place in the weed flora in an area of heavy herbicide use between 1962 and 1967 (Fryer and Chancellor 1970). This suggests that species were protected from the effects of herbicides through a long lived seed bank or that factors other than herbicide usage were more important in determining weed populations. Potts (1986), however, attributed the decline of many plant species between 1968-85 in his Sussex study area to the use of herbicides.

Available data for plants are very limited and many extensive studies have concentrated on distribution rather than abundance, and a massive decline in abundance can occur before a species actually disappears. It is possible or even likely that there has been a significant underestimate of the decline of arable weed species, especially as analyses has been carried out on a limited number of species and some surveys have ignored the effect of seed banks (Campbell *et al.* 1997).

Although not comprehensive, available data for plants and invertebrates in lowland farmland areas strongly indicates widespread and major declines in many groups or species. These declines, like those recorded for birds, have taken place during a period of considerable change in agricultural practices. One or a combination of factors may have caused the declines, such as changes in the timing of cultivation or increased use of inorganic fertilisers. A recent JNCC[4] review, however, suggests that pesticides are likely to be one of the most important factors influencing the gross levels of abundance of farmland plants and invertebrates (Campbell *et al.* 1997).

The results of work on birds and on other groups (*e.g.* Aebischer 1991 and Woiwood and Harrington 1994 for insects, Banaszak 1992 for bees, Stewart *et al.* 1994, Rich and Woodruff 1996 and Wigginton 1999 for plants) have shown the need for conservation measures in the wider environment and illustrates the importance that farmed land plays as an essential habitat for some wildlife. Indeed, the U.K. government has adopted the performance of breeding birds in the wider countryside as the only headline indicator specific to biodiversity amongst a range of key indicators in its strategy for sustainable development (HM Government 1996 & 1999). It would now seem that conservationists and environmental policy makers have turned their attention to farmland confirming the need for a new philosophy for nature conservation that accommodates the 'wider

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[4] Joint Nature Conservation Committee

countryside' as a priority (Pain and Dixon 1997). In order for this to be successful a thorough knowledge is needed of what farmland species require from their environments and how agricultural policy and intensification may affect them.

2.0 Study Aims

The broad objective of the study was to investigate the interaction between farming practice at the study site and lapwing breeding ecology. Recent surveys have shown (see 1.2.3) that farmland lapwings are currently undergoing a major population decline. A main objective was to establish if productivity was below that required to maintain the population. If so, whether increases in nest or chick survival (or both) were needed to promote productivity. The general aim was to establish the response of lapwing to intensive farming under current agricultural policy. With a knowledge of this response a further aim was to provide recommendations to enable farmers, if necessary, to achieve good agronomic practice in ways that are beneficial or, at least, not damaging to lapwings. Any recommended changes to agricultural practice being achieved through policy instruments such as the CAP, *e.g.* under a Countryside Stewardship Scheme (see 1.4.1).

More specifically the principal objectives were to evaluate:-

2.1 Nest site selection in relation to field type:

The uniformity of nest distribution over the study area was examined to establish if there was a preferential field type for nesting. The nature of a field (proportion of bare ground/crop height) is influenced by the timing of cultivation. The preference of breeding lapwing to nest on spring tilled land shown by some previous studies (see 1.2 and 1.3) was tested. The influences of field size, distance from pasture and the nature of field boundaries on nest site selection were also examined. A knowledge of nesting field preference would allow favourable manipulation of farming regimes to benefit lapwing.

2.2 Nest survival:

Populations are maintained by recruitment. Recruitment rates are related to productivity. For birds, productivity results from the number of eggs or nests that are successful and the number of chicks that survive to fledge. In this study, nest survival was calculated as a measure of productivity.

To test if differences existed between field types, nest survival was calculated for each field type. This allowed examination of the effect of farming operations. Sowing and rolling have been shown to be causes of complete failure for lapwings in spring farming areas (Berg *et al.* 1992). Not only the type but also the timing of agricultural operations have been shown to be important (Galbraith 1988b). The introduction of set-aside has created a novel habitat in the modern farmland environment (see 1.4). Breeding success between crop habitats and RSA were tested for differences.

Birds that fail on the first clutch may lay a replacement. Nest survival between first and replacement clutches was calculated to test for differences between hatching success.

2.3 Factors affecting clutch and egg size and the relationship between egg size and chick survival.

Clutch and egg size was calculated to test for differences between field types. If females, to reduce energy expenditure, obtained food for egg production within the vicinity of the nest, variation in food availability could result in clutch/egg size differences according to field type.

Lapwing have precocial, mobile and self-feeding chicks requiring a high female investment in eggs (Beintema & Visser 1989a). Detailed studies of several species have indicated that, within species, more viable chicks are produced from larger eggs (Perrins 1996). Such chicks may be structurally larger and/or heavier at hatching (Grant 1991 and references therein) and in some species may be more likely to survive (Galbraith 1988a, Thomas 1983). Calculation of egg size and monitoring of chick survival allowed this relationship to be tested to determine if this was the main contributor to chick production.

2.4 Factors related to predation:

2.4.1 The effect of predation on nests and chicks in different field types was examined. Predation of eggs can be a principal factor in limiting lapwing productivity (Baines 1990). Different field types confer different degrees of crypticity to nests and vigilance capacity to incubating birds according to the structure, type and amount of vegetation cover. The predation rates of nests and eggs in different field types were calculated and compared to test for between field type differences.

2.4.2 The effect of predation on different sized nesting aggregations was examined. Lapwings exhibit strong anti-predatory behaviour (Cramp and Simmons 1983) and experiments with artificial nests indicate that predation risk is lower inside than outside nest aggregations (Baines 1990). Calculation of predation rates for different breeding densities and nesting aggregations allowed the effects of any anti-predatory behaviour to be tested.

2.4.3 The effect of predation on nests at different distances from predator refugia and perches was examined. This was tested by measuring the distance between nests and predator vantage points/refugia and calculating predation rates. Irrespective of nest crypticity, clutch survival may be higher when nests are further from sources of predators (*e.g.* Berg *et al.* 1992).

2.5 Factors affecting chick growth, survival and brood movements:

2.5.1 The relative abundance of food in different brood rearing habitats was examined. Immediate chick mobility on hatching means that brood rearing can occur away from natal localities (*e.g.* Galbraith 1988a and 1988b). Higher prey availability or biomass in rearing fields could account for movements away from nests and brood distribution. Different sampling methods were used to assess surface and sub-surface prey availability (numbers and biomass) in different field types.

2.5.2 The diet of chicks was examined to determine what were important prey items and, by comparison with prey availability, to allow examination of any dietary selectivity.

2.5.3 The influence of foraging habitats on nest site selection was examined. Lapwings prefer to nest on ground with little or no vegetation (Klomp 1954) but close to fields which are suitable foraging sites for chicks (Galbraith 1988b). Pasture seems to be important for successful breeding because the production of chicks at arable sites has been correlated to the distance of the nearest pasture (Galbraith 1988b). Chick survival was calculated in relation to distance between nest site and rearing field type.

2.5.4 An increase in the risk of mortality might be associated with brood movements. The effect of moving from natal to rearing locality was investigated on chick growth and survival.

2.5.5 The influence of weather on chick growth and survival was examined. Poor weather may affect prey availability and/or cause the chilling of chicks. These effects may combine with predation and the timing of cultivation to impact upon fledging success.

These objectives evaluate how different field types affect overall breeding success and how this might change in the absence of particular field types or a change in their proportions and distribution. For example, the proportion of set-aside decreases yearly (see 1.4.2) with the concomitant increase in the area under crops.

3.0 Study area

3.1 Location and description

The study area was 12 km^2 of intensively cultivated farmland forming part of the Altcar Estate (owned by Leverhulme Estates). Situated in s-w Lancashire, within National Grid Square SD30, the site was close to the coast with the western boundary approximately 3.7km from the mean high water mark of Liverpool Bay (Figure 3.1a). The flat, low-lying area was typified by peaty soils with a Grade 1 agricultural land use classification (MAFF 1988). The highest land was 7m a.s.l., although the majority of the land surface was between 2 and 5m a.s.l. (Ordnance Survey). To the south the area was bounded by the River Alt and to the west by a public road which also formed the Lancashire/Sefton county boundary. The "Cheshire Lines" dismantled railway (a public footpath) formed the eastern and much of the northern boundaries, with the Estate boundary making up the remaining northern boundary. Surrounding land use was similar to that of the study area except to the west which was urban (the town of Formby). Immediately to the east the landscape was not as flat, the land higher and less open with more hedges and trees on field boundaries than the study area.

The northern part of the study area was traversed by a 'B' classification road along which farms, a sewage treatment works and some houses were situated. There were also 42 ha of woodland within the study area, although 93% of this was constituted by two plantations (Figure 3.1b). One of these was mainly coniferous with some peripheral birch (*Betula spp.*).This plantation was about 15 years old, although the area had been deciduous woodland before replanting. The other plantation was mature and largely deciduous, mainly oak (*Quercus robur*) with a rhododendron (*Rhododendron spp.*) understorey. Otherwise trees, bushes and hedges were scarce within the area except around farms and habitation with a few mature sycamore (*Acer pseudoplatanus*) and some isolated willow (*Salix spp.*), hawthorn (*Crataegus monogyna*) and elder (*Sambucus*

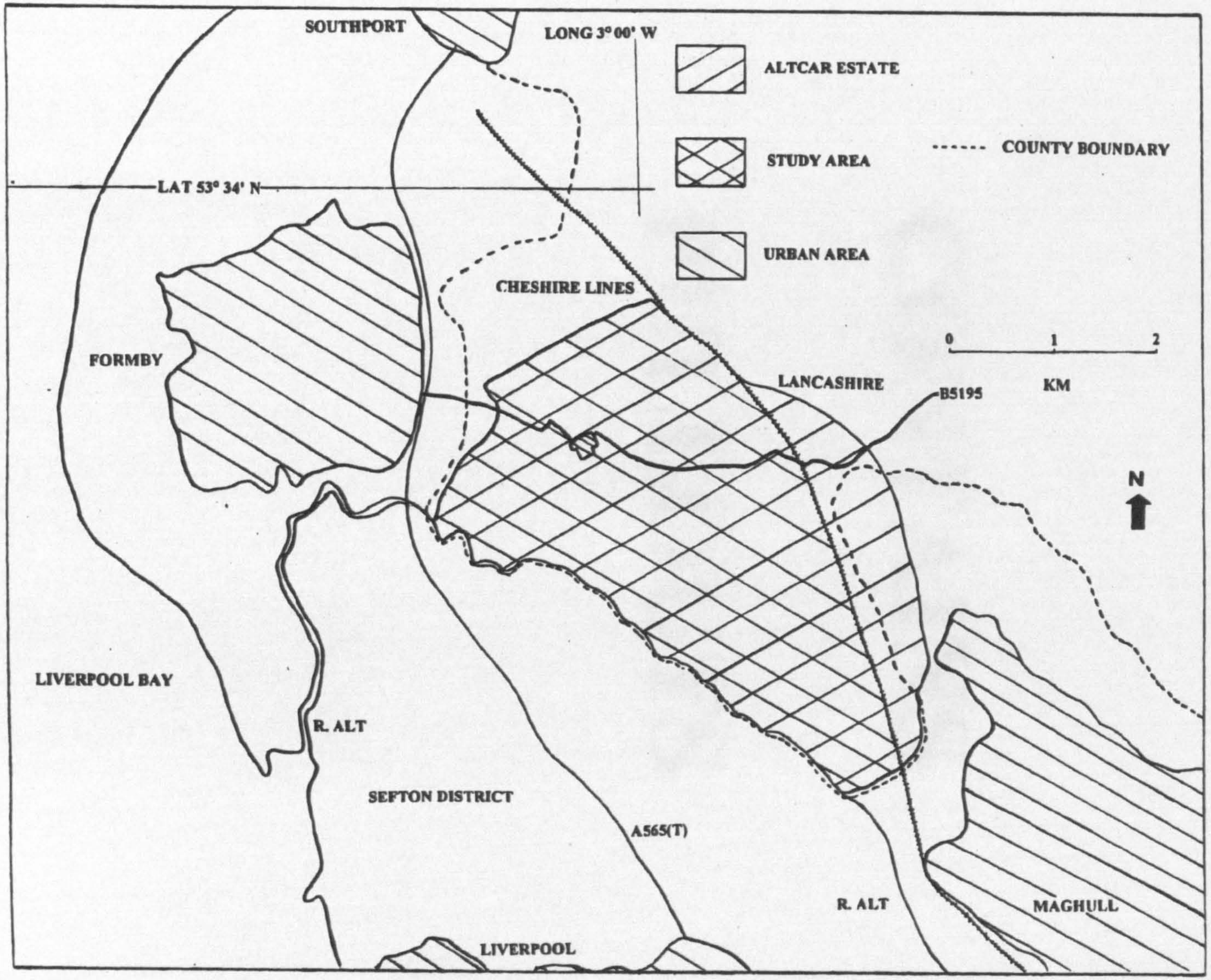
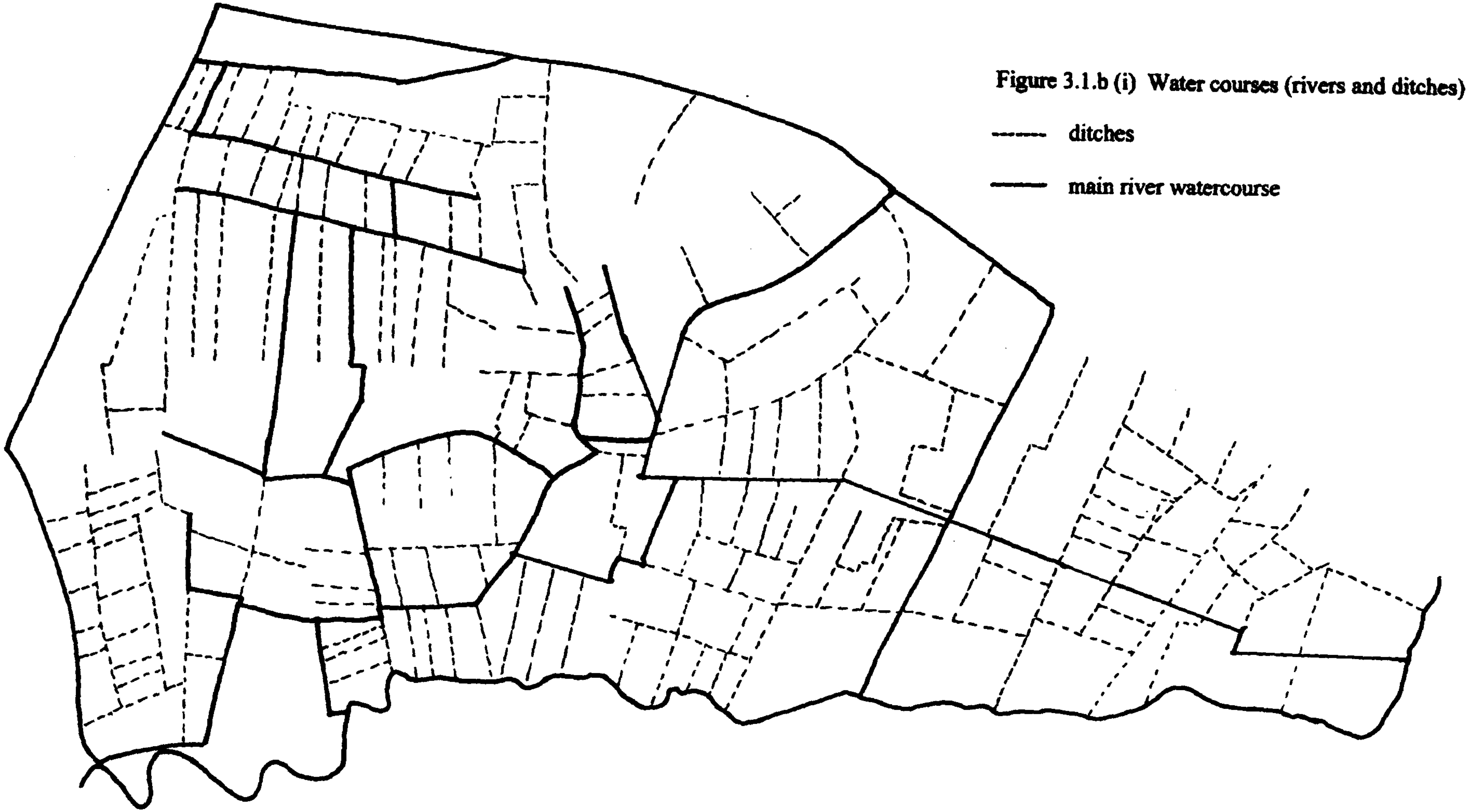


Figure 3.1a Geographical position of study area

VOLUME CONTAINS CLEAR OVERLAYS

OVERLAYS HAVE
BEEN SCANNED
SEPERATELY
AND
THEN AGAIN OVER
THE RELEVANT PAGE

Figure 3.1.b (i) Water courses (rivers and ditches)



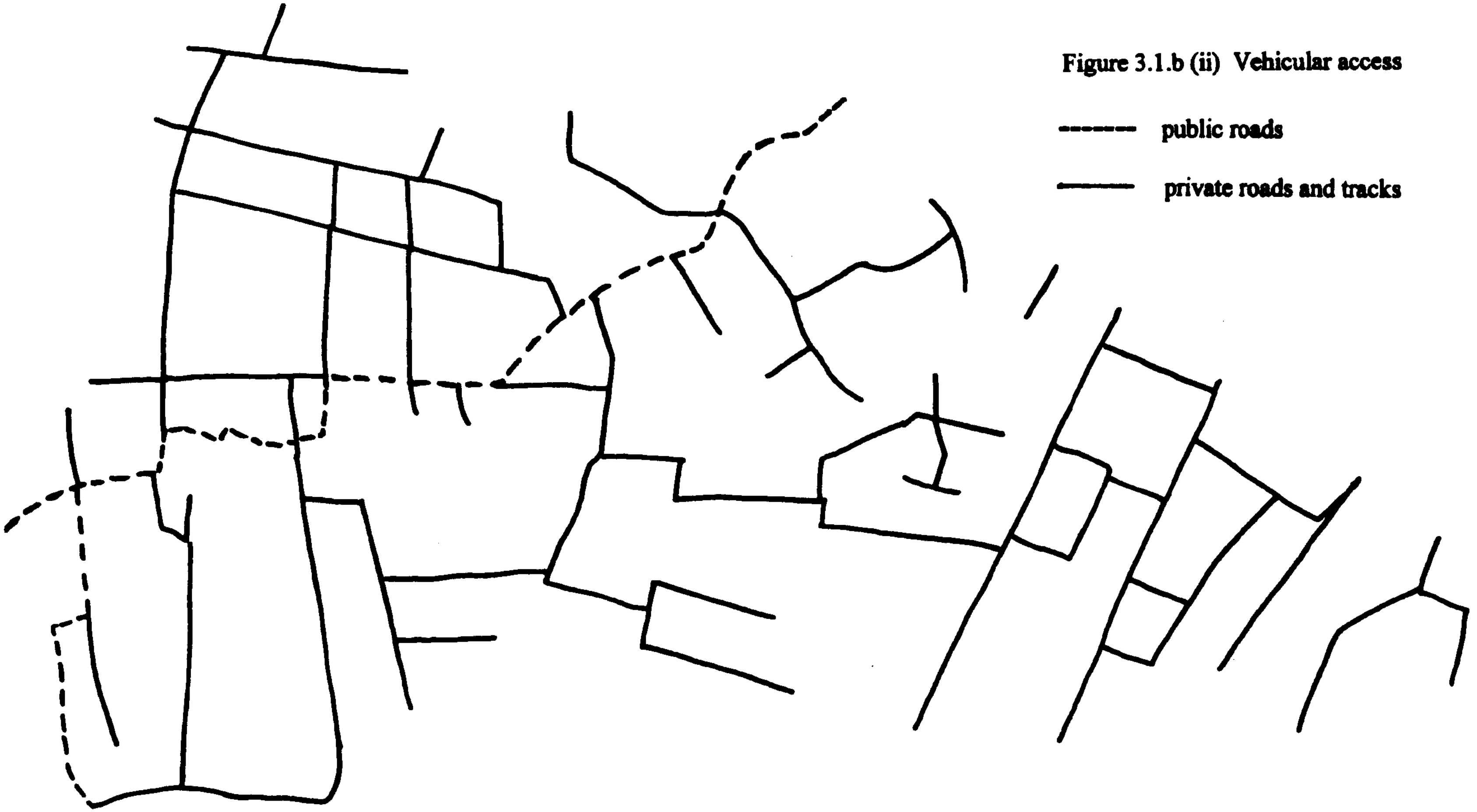


Figure 3.1.b (ii) Vehicular access

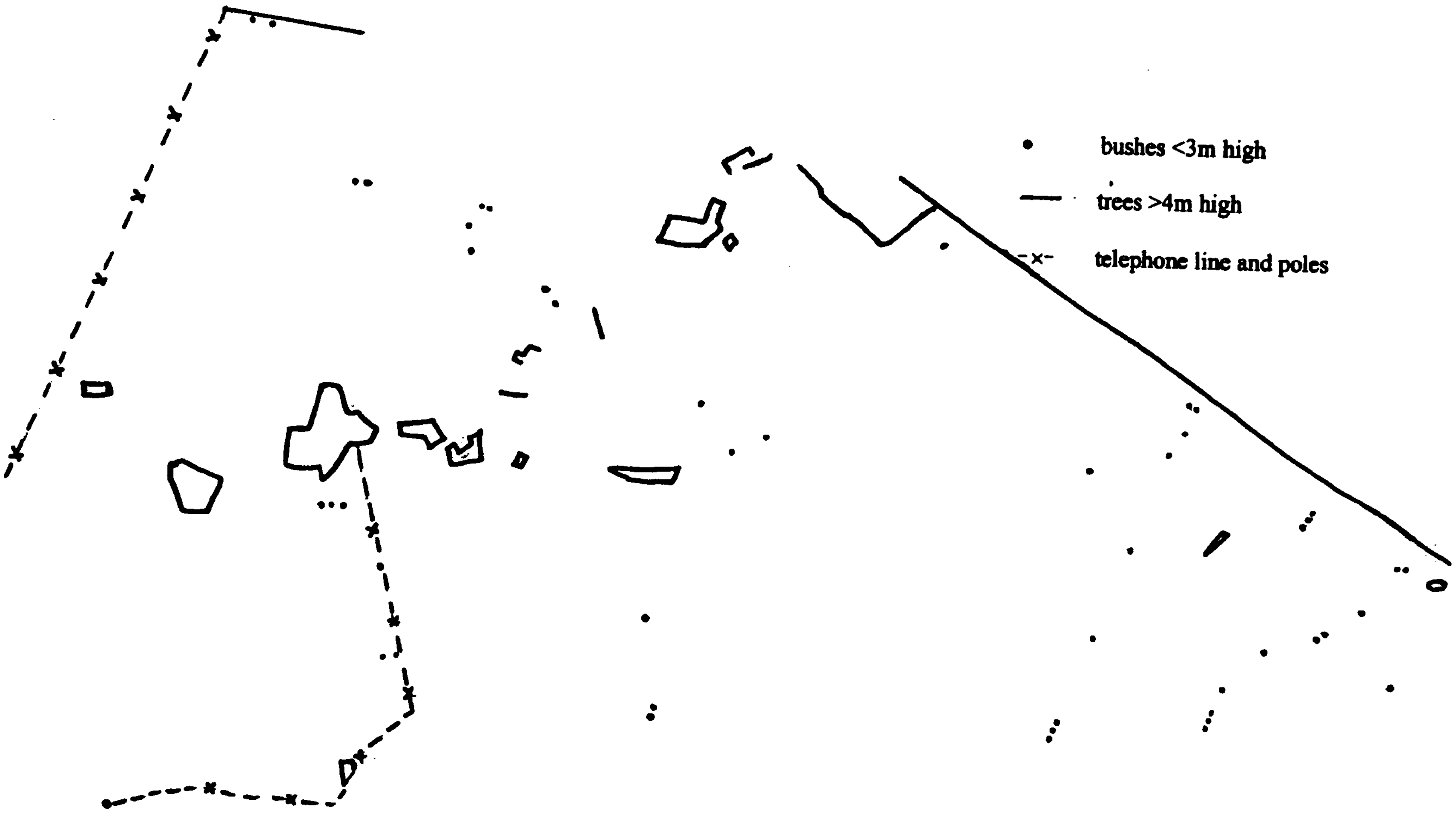


Figure 3.1.b (iii) Location of perches for avian predators outside of woodland

Figure 3.1b The study site at Altcar showing field boundaries

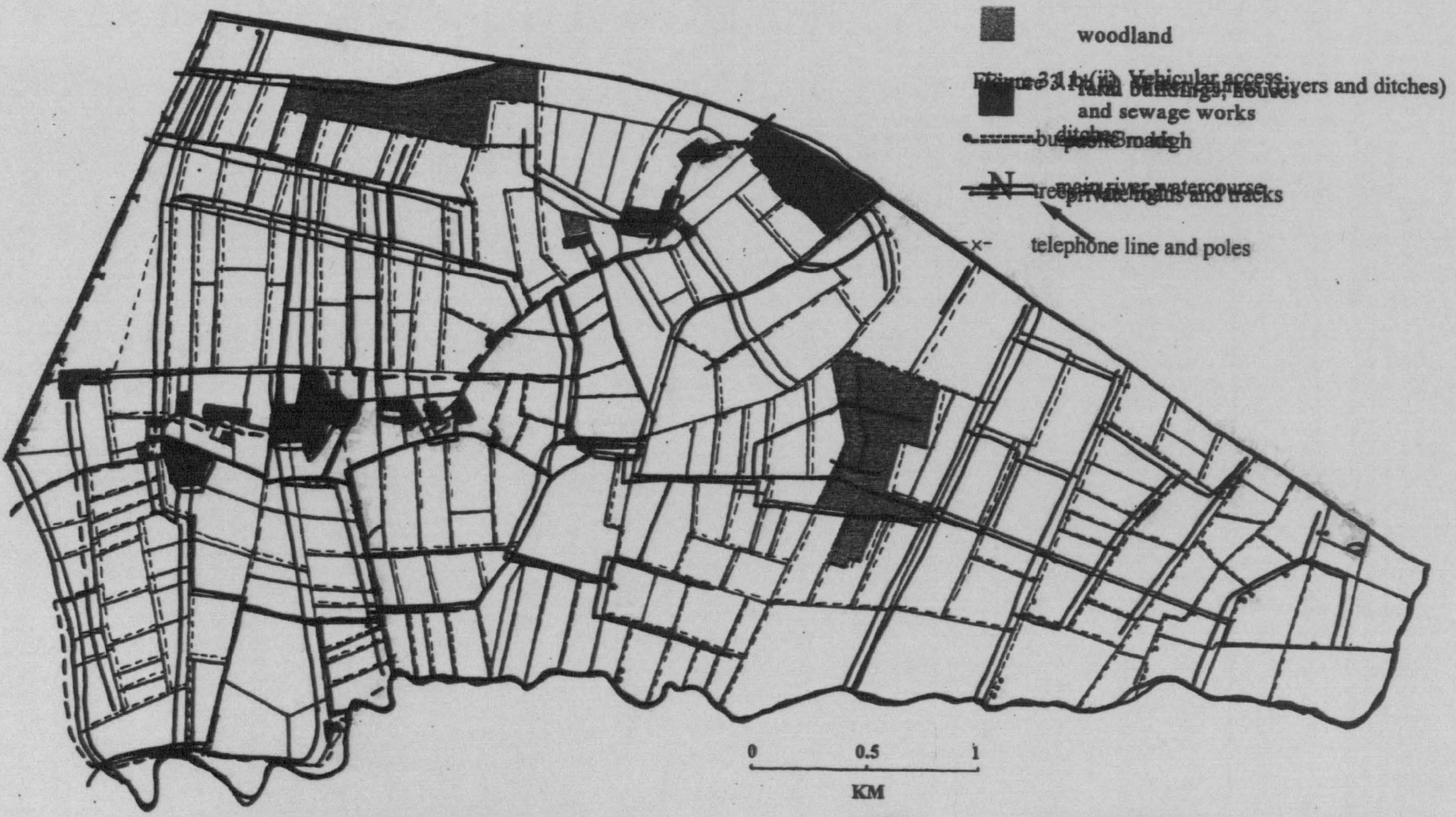


Figure 3.1b The study site at Altcar showing field boundaries Figure 3.1.b (iii) Location of perches for avian predators outside of woodland

nigra) bushes up to 3m high situated on field boundaries. Fields were, however, typically bounded by ditches (Figure 3.1b(i)). This feature together with the flat, level topography gave the landscape a very open character (Plates I).

All of the study area was accessible through a network of unmetalled lanes, which allowed almost every field to be viewed from a vehicle (Figure 3.1b(ii)).

3.2 Geology and land history

The study area formed a typical part of the Amounderness Plain which stretches from the Ribble estuary south to the Liverpool conurbation. The underlying geology of the plain consists of Permo-Triassic age rocks including older sandstones and younger mudstones overlain by glacial deposits of sand, gravel, clay and alluvium (English Nature 1996). Retreating glaciers left badly drained mires and wet hollows which filled with moss and sedge peat. During the 1800's there were extensive drainage operations which produced the highly fertile soils on which the intensive agricultural industry is based today (English Nature 1996). Peaty areas are known as 'mosses' or 'mosslands' with only a few remnant undrained areas still extant (*e.g.* Martin mere – a WWT[5] nature reserve).

Outside the Amounderness Plain in Lancashire the topography changes to include the valleys and hills of the forest of Bowland and the Pennines. The landscape is more wooded, hedges and stone walls feature on field boundaries and the agriculture is predominantly livestock.

3.3 Farming

The study area formed *c.*80% of the Altcar Estate on which there were 21 farm tenants. All the cropped land was farmed in a conventional, intensive fashion. Between 1995 and

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[5] Wildfowl and Wetlands Trust

Plate I. Landscape of the Altcar study site.

1997 most of the farmed land was under autumn and winter sown crops (48.5% of the cropped area; Table 3.3a), mostly cereals (wheat (*Triticum aestivum*) and barley (*Hordeum distichon*)) with some oilseed rape (*Brassica napus*). Much of the remainder (36.6% of the cropped area) was spring farmed, mostly with potato (*Solanum tuberosum*) and cereal (34% and 37% of the spring farmed area respectively). Spring cereals were sown between mid-March and the end of April and potatoes were drilled from the end of April to mid-May. Other spring farmed vegetables included carrots (*Daucus carota*) and brassicas (of the *B. oleracea* group), both sown in May, and legumes such as field beans (*Vicia spp*) and peas (*Pisum spp.*), which together accounted for 19% of the spring farmed area. Beans were sown in the first half of April and peas in March. Rye grass (*Lolium spp.*) cultivated for silage accounted for 6% of the cropped area. Set-aside (rotational and non-rotational) and permanent pasture occupied 6.2% and 2.7% of the cropped area respectively. Pasture was grazed solely by sheep except one field (of 3.7ha) which was grazed by both cattle and sheep.

Table 3.3a Proportions (%) of different crop and field types in the study area from 1995 to 1997.

Crop/Field-use	Percentage of cropped area
Autumn sown[a]	31.5
Winter sown[a]	17.0
Spring sown	36.6
Silage grass	6.0
Permanent pasture	2.7
NRSA	1.5
RSA	4.7

[a] refers to 1996 and 1997 only. In 1995 no differentiation was made between autumn and winter sown crops but combined these represented 46% of the cropping area.

The two categories of set-aside were non-rotational (*i.e.* fixed) set-aside (NRSA) and rotational (or annual) set-aside (RSA). NRSA meant the same field remained uncropped (without any special management) and RSA was where a field was only permitted to be diverted (or set-aside) from crop production for one growing season in every six. A field that was to be RSA effectively became such after harvest of the crop (*e.g.* in July/August for cereal fields), remaining uncultivated over the autumn, winter and following (growing season) spring until the preparation period of the next crop (usually autumn sown cereal). In a spring farmed area, therefore, RSA fields did not differ from spring cultivated (*i.e.* unsown) fields until sowing time. Generally no management was allowed on RSA (see 1.4.2) and fields were allowed to regenerate naturally until mid-July when mowing or an application of (a total) herbicide was permitted. NRSA fields, however, were taken out of production for at least five years. There were several management options for NRSA but in the study area such fields were (mostly) grassland or had wild bird cover (*i.e.* had been sown with two crop groups – see 1.4.2).

3.4 Game management and predators

In addition to the estates' agricultural activities there were commercial sporting interests. These were shooting common pheasants (*Phasianus colchicus*) and grey partridges (*Perdix perdix*) and hare coursing, involving wild brown hares (*Lepus capensis*). Both grey partridge and pheasants bred wild on the estate but pheasants were also bought as poults, reared and released. Hare coursing took place annually in mid-February with the Waterloo Cup, the largest event of its kind in the U.K. Two pasture fields were used for the hare coursing activities, both originally permanent although one of the fields was reseeded in April 1996. Smaller fields adjoining the large coursing fields were also kept as pasture as these were used for spectator parking. This resulted in nearly all the pasture within the study area being distributed in two clumps where hare coursing occurred.

The estate employed two gamekeepers to maintain the sporting interests. They were active in their control of vermin species, particularly foxes (*Vulpes vulpes*), stoats (*Mustela erminea*) and corvids, due to the relatively high breeding densities of grey partridge. An indication of fox presence (*e.g.* spraint, kills or observation) on the estate was dealt with immediately (by shooting the fox) with additional help, if needed, brought in for beating cover. Fox deterrents (sprays) were used in the vicinity of partridge nests. Corvids, mainly carrion crows (*Corvus corone*) and magpies (*Pica pica*), were shot (on sight) and trapped (with Larsen traps). Tunnel traps were used throughout the estate for stoats with animals also being shot. Brown rats (*Rattus norvegicus*) were also trapped and (around farm buildings) poisoned. Weasels (*Mustela nivalis*) and farm or feral cats *(Felis domestica*) may also have been present but were not seen by the author or gamekeepers during the course of this study.

All of these species legally classed as vermin are also predators of lapwing capable of taking eggs, chicks and, in the case of foxes and stoats, incubating adults. There were other potential avian predators of lapwing, pheasants, partridge and hare present on the estate that were legally protected: sparrowhawk (*Accipiter nisus*), kestrel (*Falco tinnunculus*), tawny owl (*Strix aluco*), long-eared owl (*Asio otus*) and barn owl (*Tyto alba*) bred within the study area (*pers. obs.*). In addition, an adult pair of buzzards (*Buteo buteo*) and three to five immature and adult female Marsh Harriers (*Circus aeruginosus*) were resident (*i.e.* built nests, hunted and roosted) in the study area over the lapwing breeding period. Other raptors seen frequently in the study area either on passage or over wintering were hen harrier (*C. pygargus*)[6], peregrine (*F. peregrinus*) merlin (*F. columbarius*) and short-eared owl (*A. flammeus*). There were sight records of all of these species for March, April and May, except hen harrier which was not seen after the beginning of April. Other bird species which might predate the eggs and (small) chicks of lapwing that were commonly recorded in the study area were lesser black-backed gull (*Larus fuscus*), herring gull (*L. argentatus*), common gull (*L. canus*) and black-headed gull (*L. ridibundus*). These species mostly passed over the study area (usually in the lower air space) daily from breeding and roosting locations on the coast to inland feeding sites. The cultivation associated with spring farming activity, however, also brought gulls (particularly the smaller species, such as *L. ridibundus* and *L. canus*) into the study area. On such occasions they sometimes formed flocks with jackdaw (*C. monedula*) to follow farm machinery engaged in activity causing disturbance to the field surface.

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[6] A montagu's harrier (*C. macrourus*) was also seen on two occasions in May 1997.

3.5 Comparison with other breeding lapwing study areas

The Altcar study area resembles in some ways the arable study area used by Galbraith (1987, 1988a,b,c,d, 1989a, 1989b) in the Carse of Stirling. Both were flat, near to sea level and intensively cultivated. There were, however, areas of afforestation surrounding his study area but the nature of his site's field boundaries, field size and soil type are not known. Galbraith does indicate that hedges and trees bounded at least some, if not all of the fields of his study area. By area Galbraith's study arable site consisted of 45% cereals, 30% meadows (for hay and silage) and 19% pasture. In contrast, Galbraith's rough grazing study site was enclosed hill land situated at 150m asl. Located in the Midland Valley of Scotland Galbraith's study sites were approximately 3^0 further north than Altcar.

The study areas used by Baines (1988, 1989, 1990) and Thompson *et al* (1994) were located in upland, northern England (the Eden Valley, Cumbria and Upper Teesdale, Co. Durham) between 300 and 500m asl, the altitudinal limit of most agricultural practices (Baines 1988). By area these study sites consisted of 67% pasture, 29% meadows used for hay/silage production and 4% arable (mainly spring cereals). The fields were enclosed (typically by dry stone-wall) but mean field size is unknown. Both areas are approximately 1^0 north of Altcar.

The Swedish study site of Berg (1992, 1993, 1996) and Berg *et al* (1992, 1994) was predominantly spring tilled arable (71%). Much (25%) of the remainder being grassland, approximately half of this described as permanent pasture and half as sown grass. Most of the remaining area consisted of scrub. Fields were bounded by trees and hedges and an unknown areas of forest were located within the 59km^2 study area. Berg's study area was nearly 7^0 further north and 19^0 to the east of Altcar.

The coastal study sites of Blomqvist and Johansson (1995) were all located in southwestern Sweden. They were predominantly composed of pasture (57% of total area) with arable (including unknown proportions of autumn and spring cultivated land) making up the remainder. Field sizes, types of field boundary and the occurrence of trees and scrub in the area is unknown. These coastal sites were approximately 4^0 further north and 16^0 to the east of Altcar.

4.0 Nest site selection, nest survival and hatching success

The influence of both the nesting and chick stages on the productivity of the Altcar lapwing population were examined. This chapter deals with the influence of the nesting stage.

It has been shown that lapwing have a preference for nesting on spring cultivated fields (Shrubb 1990) particularly those fields that abut pasture (*e.g.* Galbraith 1988b, Shrubb and Lack 1991). This nest site preference has, however, not always been found to be the case (*e.g.* Blomqvist and Johannson 1995; see 1.2.3 and 1.3.1). In this chapter nest site selection is examined in relation to field type and distribution to determine if the timing of cultivation and crop distribution influences nesting field.

Factors, such as cultivation activity and predation, that influence nest survival and hatching success may determine the selection by lapwings of nesting field type (Shrubb and Lack 1991). Nest or egg predation rates may be influenced by the nature of the field substrate (*e.g.* Klomp 1954), distance of nest to predator vantage points or cover Galbraith 1988b, Berg *et al.* 1992) and the size and density of lapwing breeding aggregation (Berg *et al.* 1992). These factors are examined to determine their influence on nest survival and hatching success.

If nest site selection is associated with a particular farming regime cropping practices could be manipulated to favour breeding lapwing.

4.1 Methods

4.1.1 Field use

Each year prior to the commencement of nesting (mid-March) the crop type or use of each field within the study area was determined by visiting all fields. This survey allowed the differentiation between 'autumn sown' and 'winter sown' crops and the identification of unsown areas. Much of the cereal and temporary grass grown within the study area was sown in autumn (September to November). By the following February/March these autumn sown crops were well established with very little or no bare ground apparent between plants. Autumn sown fields contrasted with cereal fields sown in the winter (December to February) as the winter cereal was less developed, being shorter and more sparse (bare ground being more evident). 'Winter *farmed*' land incorporates both 'autumn *sown*' and 'winter *sown*' crops as each are cultivated over the winter period. Fields not winter farmed were unsown and would be RSA (rotational set-aside) or, mostly, sown with a crop in the spring (April/May). In the early spring unsown fields were characterised by lacking a crop and having a bare substrate, having little or no living (green) vegetation due to post-harvest application of herbicide. If unsown fields had been cropped with cereal in the previous season, they contained stubble. Visits were again made in June when the determination of crop type (*i.e.* spring sown crops) of all fields was possible. There were two categories of spring sown crop. The different categories were based on the nature of the crop in addition to management and harvest method. 'Combinable' crops included cereals, oilseed, linseed (*Linum usitatissimum*) and silage. 'Vegetable' crops included potato, field beans, carrots, peas, leeks (*Allium porrum*) and brassicas (mainly of the *Gemminifera* group, *i.e.* brussel sprouts). 'Spring farmed' land incorporates the unsown and spring sown field categories.

RSA fields were identified during nest searches but it was also apparent during the second field use survey which were the season's RSA fields, these being the only uncropped fields where vegetation was naturally regenerating.

Fields which contained lapwing nests, therefore, were classified according to the sowing date and the nature of the crop or field. Winter farmed fields consisted of autumn and winter sown crops. Spring farmed fields incorporates unsown fields which were then spring sown. Spring sown fields were either planted with combinable crops (mainly cereals) or vegetables (mainly potatoes), these categories differing in their cultivation and management methods. RSA was not cropped during the breeding season, fields largely remaining uncultivated.

Field and other plot sizes (*e.g.* woodlands, farms, etc) were obtained from 1:2500 Ordnance Survey plans (1970) obtained from West Lancashire District Council. Some emendation of boundaries was needed as some fields had increased in size (from infilling ditches) since the original surveys. Also the number and size of fields each year varied slightly as sometimes fields were planted with two crops. In such cases the cropping unit was considered a field and field sizes were estimated by pacing to the new boundary and converting paces to metres. Otherwise fields were defined by their physical boundaries.

Positions of all predator refugia and vantage points (*e.g.* trees and bushes) not on the O.S. plans were mapped during surveys and their heights estimated (Figure 3.1b(iii)).

4.1.2 Nest finding

Nest finding was carried out from mid-March until the end of June and all fields within the study area were checked for nests. The crop/field type of each nest found was recorded. Nests were found by observing incubating birds from a vehicle with the aid of a pair of 8x30 binoculars or a 20x telescope. Territorial males (*i.e.* birds in courtship, anti-predatory/antagonistic display or acting as sentinel) also indicated nesting locations.

Accessibility was such that areas searched for nests were mostly within 300m of the vehicle and most fields could be searched from at least two sides. The method was improved by the flat nature of the terrain. Systematic search on foot was made when a nest was suspected but hidden due to undulation in the ground surface or crop growth. Quite often nests were located by following adults disturbed from the nest when they returned to resume incubation. This was particularly the case for nests in autumn sown cereals, where the crop hid incubating birds even early in the season. Disturbance was not uncommon and could be caused by nearby farming activity or the proximity of potential predators which induced mobbing behaviour from nesting lapwing. Such behaviour was usually precipitated by predatory species such as corvids (*Corvus spp.*) and gulls (*Larus spp.*) but was also frequently due to the presence on territory of pheasant, grey partridge and even brown hares, all three of which were commonly observed in the study area.

Nest positions were marked with upright garden canes pushed into the ground 20m or more from the nest site. Canes were long enough to be kept just above crop height in late season nests, usually, however, only 20-30 cm of the cane was exposed. Similar nest marking of lapwing in previous studies (*e.g.* Galbraith 1987) has shown that such a procedure does not influence nest survival by aiding predation. The canes were 1-2cm in diameter and dark green or brown making them very difficult to see by humans. Such canes were used deliberately in order not to influence the number of nests avoided by some farmers during spring cultivation. In the same way nest-cane distances were variable and did not indicate the direction of the nest to a finder. Minimum distances to the two nearest field edges were measured by pacing. Pace measurements were converted to metres by using the mean number of paces from 15 walked 200m lengths on arable ground. The mapped nest positions (on 1:2500 O.S. plans) enabled the following measurements to be made; distance from nearest nest, distance from nearest ditch and distance to nearest predator vantage point or refugia.

A feature of intensive management of all crops is the application of a variety of chemicals, such as fertilisers, pesticides and growth regulators. Pesticides include pre- and post emergent herbicides, insecticides, fungicides and molluscicides. The tracks created by tractors in order to apply these chemicals are used on each application. Repeated activity results in 'tramlines' running through the crop as no plant growth occurs on the compacted track surface. These linear features were particularly evident in cereal crops. Distances to nests from tramlines were recorded for nests in autumn and winter sown cereals, as tramlines were already obvious in these crops (as crops were well emerged) at the start of the nesting season (mid-March).

In the analysis of nest site selection the *G*-test with Williams' correction (Sokal and Rohlf 1981) is designated as G_{adj}. This test is used to analyze the deviation of observed to expected frequencies representing the null hypothesis.

4.1.3 Random control sites

The distance of lapwing nests to predator refugia and vantage and field boundary ditches was investigated by comparison with random sites. The distance to predator cover, perches and field boundary ditches was measured for 146 randomly selected control sites (originally 150 but four were discounted as they did not fall on farmland). A grid provided by the latitude and longitude on a 1:2500 map of the study area was used to locate the random sites. Co-ordinates were generated using the random data command on Minitab.

Random sites were also generated to investigate the position of nests in relation to distance from tramlines in autumn and winter sown cereal fields. Random sites were located in a hypothetical field with a length of 282m and a width of 155m, these being the average dimensions of the 29 autumn and winter sown fields used for nesting (SD (length) = 73m; SD (width) = 55m). The field was marked with nine pairs of tramlines, running parallel to the longest edge, spaced at every 15m with two metres between the tracks of each tramline. The distances between tramlines and tramline tracks were taken from measurements in the field. A 0.25 x 0.25m grid on a scaled down version of the 'field' was used to locate random sites. Co-ordinates for these sites were generated using the random data command on Minitab. The number of random sites matched the number of nests found each year in the winter farmed cereals (n = 43 and 59 for 1996 and 1997 respectively). Predatory mammals may use field boundaries as lanes to travel along, possibly increasing the chance of nest finding and predation. As lapwings might avoid nesting close to field boundaries (ditches) because of such a depredation effect (*e.g.* Galbraith 1988b) random sites located within 5m of a field edge were discounted (n =2 and 3 for 1996 and 1997 respectively) and regenerated (see 4.2.6iii).

4.1.4 Estimation of first egg dates

First egg (laying) dates were estimated for each clutch found in order to estimate hatch dates. This helped in monitoring nest survival and in the timing of nest visits to measure, weigh and ring neonates. This also helped in establishing whether clutches were first or replacements and in examination of any seasonal influence on nest survival.

The date on which the first egg of a clutch was laid and expected hatching dates were estimated by one of two methods (after Galbraith 1988b):

i. For clutches found before completion, the first and last egg dates were calculated on the assumption that the laying interval between successive eggs was 2 days. Variation has been noted in laying intervals from 1 (Klomp 1951) to 2.8 days (Heim 1974) but any errors incurred from assuming an interval of 2 days were likely to be small. The expected hatching date for each clutch was estimated as 25 days after clutch completion (Galbraith 1988a), but see 4.1.5 in case of variation in incubation period.

ii. The majority of nests were found once incubation had started, after the last egg had been laid and first egg dates and expected hatching dates were estimated from the mean egg density;

mean egg density = mean egg weight/mean egg volume (obtained from egg length × egg breadth^2 × 0.457 (K, the volume constant; see 5.1.1).

The following predictive equation was obtained from Galbraith (1988b);

days until hatching = 150.84 × mean egg density – 140.68 ($r = 0.905$, $P<0.001$) with a mean error of 2.3 days (SD = 1.876).

Weights were obtained using a battery powered portable balance to an accuracy of 0.1g. Once hatching date had been estimated the first egg date was calculated using the laying intervals and incubation period as above.

4.1.5 Nest and egg survival, hatching success

The number of eggs in a clutch was recorded when first found. In order to assess the fate of eggs in each clutch, nests were visited about every 4 days, increasing to every 1-2 days closer to hatching. Visiting lapwing nests on arable land has been shown not to influence their survival (Galbraith 1987) with similar results found for curlew (*Numenius arquata*) nests on arable farmland (Berg 1992). Apart from when egg measurements were taken, however, nests only needed to be approached to a distance of 1.5-2.5m to enable eggs to be counted. Nevertheless, a strategy of leaving confusing trails was adopted for nest visits. Occasionally, nests were empty and the presence of many, small eggshell fragments in the nest cup or lining was taken to indicate a successful hatch. This feature of vacated, successful nests has been used in other lapwing studies (*e.g.* Baines 1989; Galbraith 1988b, Green *et al.* 1987) and in studies on other waders (*e.g.* Nethersole-Thompson & Nethersole-Thompson 1942; Higgens & Kirsch 1975, Green *et al.* 1987). Nests that do not hatch young do not show this feature as it is associated with the hatching chick as it chips its way out of the shell. If a nest failed to hatch, an area within about 5m was searched for egg remains. The presence of damaged or broken eggs in or near the nest or the disappearance of one or more eggs signified predation (Green *et al.*

1987, Galbraith 1988b, Baines 1990). Whether eggs had disappeared or remains were found was recorded. Clutch destruction due to agricultural operations was obvious resulting in the flattening of the nest and its contents (as happened after rolling (Plate II)) or its complete disappearance as the ground was ploughed, harrowed or sown. Sometimes eggs were found in successfully hatched nests. Eggs may be laid infertile or the embryo may die before development. The contents of such eggs were rotten or consisted of yolk and albumen. On the other hand, abandoned eggs containing fully developed chicks were the result of desertion.

Females of unsuccessful clutches will often lay a replacement (Klomp 1951). It has been found that lapwings and other charidrid plovers whose nests fail usually re-lay within 15 days in close proximity to the previous nest site (Ratcliffe 1976, Berg *et al.*, 1992). In this study, clutches were considered to be replacements by the original pair if a clutch was lost and another appeared within 15 days within 100m of the preceding nest. This criterion in determining replacement clutches has been used in other studies of lapwing breeding on arable land (*e.g.* Baines 1989; Berg *et al.*, 1992). Additionally, as breeding fields were very closely monitored to establish nest fates, all clutches found before the first known replacement clutch in each year were classified first clutches, while all nests found after the last known first clutch were considered replacement clutches. It is possible that there is a likelihood of error in this method of distinguishing between first and replacement clutches. Without a marked (*i.e.* identifiable) adult population (see below), however, it is difficult to calculate any likelihood of error. Under such circumstances, and as the method has been used in other recent studies of lapwing breeding ecology (e.g. Berg *et al* 1992, Hegyi and Sasvari 1998), it was considered a suitable technique for distinguishing between clutches.

To monitor the replacement of lost clutches attempts were made to mark breeding females (under BTO licence) using 'sponges' soaked in the red dye Rhodamine B ($C_{28}H_{30}N_2O_3$) and placed in nests. A similar technique for marking breeding adults was used successfully by Galbraith (1988b). In this study the method was unsuccessful as nest sponges (cotton wool) appeared to inhibit the resumption of incubation by parents once

Plate II. A lapwing clutch destroyed by rolling.

they had returned to the nest vicinity. Sponges were, therefore, removed to allow incubation to continue. The lack of success of marking breeding adults in this way may have been because little or no vegetation was used as a lining for the cup of nest scrapes as was the case in Galbraith's study. The lack of nest-lining material in this study made it difficult to 'hide' the sponge. Attempts to render sponges invisible by covering them with fine soil from the nest environs failed as parents picked the sponges out of the nest scrape prior to resuming incubation.

Since clutches were found at different stages of incubation nest and egg survival were calculated according to Mayfield (1961 & 1975) with standard errors and confidence intervals calculated using the methods of Johnson (1979) and Henslor and Nichols (1981). Mayfield developed a method of measuring nest success as a daily survival rate, defined as the probability, P, of a nest present one day surviving to the next. Success could be expressed as the percentage of hatched nests from a sample of nests. This method is less satisfactory as it may introduce bias as unknown nests that had been lost could not be included in the calculation of success.

P is estimated from the formula:

(i) $P = 1 - A\text{-}B/\Sigma\, T$

in which A is the number of nests, B the number of successful nests and T the number of 'nests days' (*i.e.* the sum of all daily totals of nests present during the observation period), a unit of exposure combining nests and time. One nest-day is the equivalent of one nest under observation for one day. Where the exact day of failure of a nest was unknown, it was estimated as the mid-point between the last day on which the nest was known to be active and the day on which it was found to have failed. Nest can be replaced by egg or chick to give egg-or chick-days allowing P to be similarly calculated for egg and chick survival. The inverse of P gives a daily mortality rate. As mortality factors were identified and quantified the daily rate of loss for each of the causes of nest/egg failure (*e.g.* daily predation rate) could also be estimated.

The standard error (v) of P can be calculated from the formula:

(ii) $v = \sqrt{P(1-P)/\Sigma\ T}$

The daily survival rate can be converted to hatching success, the probability of surviving until hatching after 32 days (*i.e.* the laying and incubation period) and expressed as a percentage (*i.e.* $P^{32} \times 100$).

Survival and mortality probabilities were compared between two populations using the following equation:

(iii) $P_1 - P_2 / \sqrt{v_1^2 + v_2^2} > z_{\alpha/2}$.

This tests the null hypothesis that $P_1 = P_2$ against the alternative hypothesis (H_1) being that

(iv) $P_1 \neq P_2$.

Where P_1 and P_2 = daily survival probability of populations 1 and 2, v^2 the variance (se) of P, $> z_{\alpha/2}$ indicating the confidence interval.

It was, therefore, possible to test for differences in the survival/mortality rates between different sets of nests/egg (and radio-marked chick) data, *e.g.* between years and habitats and also between different subsets of nest/egg (and radio-marked chick) data, *e.g.* between crop and field types, first and replacement clutches, early and late clutches.

4.1.6 Density and heterogeneity of vegetation in nesting fields

To assess the crop and vegetation heterogeneity of nesting fields the height of the vegetation at the four corners of a $1m^2$ quadrat were measured (to the nearest cm). As it was found that field size was comparatively small (see 4.1.1 and 4.2.1) sufficient coverage was obtained by taking measurements from ten quadrats from each field.

Quadrats were thrown from a field corner or the field centre, the location determined randomly by the throw of a die. A heterogeneity index for each field type was calculated by the following formula:

(i) Heterogeneity index = $\Sigma(max - min)/\Sigma x$

Where max = maximum plant height in the quadrat, min = minimum plant height in the quadrat, and x = mean height of the vegetation in the quadrat. Low values of the index indicate uniformity of the vegetation and high values heterogeneous vegetation (Bibby *et al.* 1992). In order to avoid disturbance to lapwing measurements were carried out in June in fields where nesting had ceased. This made the assumption that the measurements made in June were related to those earlier in the year.

Vegetation density was measured by placing a 10cm wide board, marked into 1 × 1 cm squares, vertically into the vegetation in the centre of the quadrat (Bibby *et al.* 1992 and references therein). From a height of 15 cm above ground level (*i.e.* the eye level of the author when lying on the ground) and at a distance of 1m all the visible squares were counted from the ground to a height of 15cm. The number of all visible squares per field type were summed to give a density index (total number of squares – total number of visible squares/total number of squares). Low values of the index indicate plant growth is sparse and high values dense vegetation. Differences in visible square proportions between field types were examined by chi-square tests of association (with Yates' correction).

4.1.7 Weather data

Meteorological Office weather data were obtained to examine between year differences in mean daily rainfall and mean daily temperature during the breeding season. Daily rainfall (mm) and daily minimum and maximum temperature ($^{\circ}$ C) were supplied by coastal weather stations at Crosby and Southport, 5km and 8.5km from the study site respectively. Data from Crosby were used mostly but as some days were missing appropriate data were taken from Southport which was 18.5km to the north and shared a similar longitude. To validate the use of data from two stations meteorological differences were examined by carrying out t-tests on mean daily temperature and mean monthly rainfall for March-May 1996 and March and April 1997 (no data exists or was needed for May 1997 for Southport). No significant differences were found for any test.

4.2 Results

4.2.1 Field use

There was some change in the proportions of crop types over the period of study (Table 4.2.1a). This was mainly due to an increase in area of autumn sown oilseed and sown grass (for silage) at the expense of spring farmed cereal. During the period 1995-97 vegetable crops accounted for most (56.3%) of the spring farmed area. The proportion of spring farmed land under vegetables increased from 52% to 60.3% over the three years. The hectarage of vegetable crops remained quite stable, however, as it was the increase in winter farmed crops that caused the reduction in the area of combinable crops. There was also a 43% decrease in the area of permanent pasture between 1995 and 1997. This was almost entirely due to the loss of one field through reseeding in April 1996. Over the two years 1996 and 1997 RSA accounted for 4.8% of the study area, although there was a 25% reduction in area from 1996 to 1997 due to changes in agricultural policy (see 1.4.2).

Table 4.2.1a Areas (ha) and proportions (%) of different crops grown in the study area from 1995 to 1997.

	1995		**1996**		**1997**	
Crop	**ha**	**% Area**	**ha**	**% Area**	**ha**	**% Area**
Autumn sown: Cereal	460[a]	40.3[a]	294	25.8	229	20.1
Oilseed rape	64	5.6	57	5.0	146	12.8
Winter sown cereal	?	?	179	15.7	213	18.7
Total winter farmed crop	**524**	**45.9**	**530**	**46.5**	**588**	**51.5**
Spring sown: Cereal	199	17.4	155	13.6	117	10.3
Oilseed rape	16	1.4	0	0	14	1.2
Linseed	0	0	18	1.6	12	1.1
Silage	0	0	15.4	1.3	10	0.9
Total Combinable crop	*215*	*18.8*	*188.4*	*16.5*	*153*	*13.4*
Potato	144	12.6	144	12.6	143	12.5
Field beans	28	2.5	33	2.9	22	1.9
Carrot	30	2.6	26	2.3	27	2.4
Brassica	25	2.2	24	2.1	23	2.0
Leek	5	0.4	7	0.6	6	0.5
Peas	0	0	11	1.0	10	0.9
Total Vegetable crop	*232*	*20.3*	*245*	*21.5*	*231*	*20.3*
Total spring farmed crop	**447**	**39.2**	**433.4**	**38**	**384**	**33.7**
RSA[b]	55	4.8	61	5.4	47	4.1
NRSA[b]	17	1.5	17	1.5	17	1.5
Silage grass	56	4.9	73	6.4	81	7.1
Permanent pasture	42	3.7	26.6	2.3	24	2.1
TOTAL	**1141**		**1141**		**1141**	

The remaining area was composed of; woodland = 42.4 ha; farms, houses and sewage works = 17 ha. Winter farmed crops combines autumn and winter sown crops. Spring farmed crops represent those crops (combinable and vegetable) sown in the spring.

[a] No differentiation was made between autumn and winter sown crops in 1995, therefore, the figure refers to winter farmed cereal. [b] RSA represents rotational set-aside; NRSA represents non-rotational set-aside. Permanent pasture was grazed and were fields that had been under grass for more than 5 years.

Field size and number varied little between years with 227 fields in 1996 (mean size ± SD = 4.99 ha ± 3.24) and 229 fields in 1997 (mean size ± SD = 5.0 ha ± 3.50). On average field size was small. For both years combined the mean field size was 5 ha (SD = 3.40 ha). This was 43% smaller than the average size of English and Welsh (grass and tilled) fields calculated by Shrubb and Lack (1991).

4.2.2 Nest site selection

i. Nest site selection according to habitat and crop type

Lapwing nests (n = 485) were not uniformly distributed at the study site (Figure 4.2.2a), as the number of lapwing nests in 1 km^2 squares deviated significantly from an expected (or uniform) distribution (*i.e.* an equal number of nests in all squares, *G*-test for goodness-of-fit between observed and expected values, $G_{adj} = 160.2$, $P<0.001$, d.f. =10). It was, therefore, valid to investigate the pattern of nest distribution.

Breeding adult lapwing have been shown to be highly site-faithful (*e.g.* Thompson *et al.* 1994). Testing for nest site selection, therefore, was carried out within years to avoid any effect of philopatry. In both 1996 and 1997 the same preference was exhibited. Spring farmed land and RSA were used most often as nesting habitat, while pasture and winter crops were used less commonly than expected (Table 4.2.2a; *G*-test for goodness-of-fit between observed and expected values, G_{adj} (1996) = 142.5; $P<0.001$, d.f. = 4; G_{adj} (1997) =116.9, $P<0.001$, d.f. =4).

Table 4.2.2a Distribution of lapwing nests in relation to habitat distribution. The number of nests expected represents a random nest distribution with respect to habitat.

Habitat	**1996**			**1997**		
	Area (%)	**No. nests**	**No. expected nests**	**Area (%)**	**No. nests**	**No. expected nests**
Permanent pasture	2.3	1	5.6	2.1	0	5.1
Winter farmed	52.9	54	128	58.6	70	142.4
Spring farmed	38	139	92	33.7	150	82
RSA	5.4	48	12.9	4.1	23	10
NRSA	1.5	0	3.6	1.5	0	3.6
Total		242			243	

1995 was excluded as nest data were incomplete.

The location of all 485 nests (1996 and 1997 combined) departed significantly from the random with respect to habitat distribution (Figure 4.2.2b; *G*-test for goodness-of-fit between observed and expected values, $G_{adj} = 257.6$, $P<0.001$, d.f. = 4). The two preferred habitats held 76% of all nests although they only constituted 41% of the study area. NRSA was not used as a nesting habitat.

The strong avoidance of winter farmed fields was not exhibited by all winter crops (Figure 4.2.2c). Winter farmed crops are sown in two periods, autumn and winter. The strongest avoidance by lapwings was shown towards autumn sown oilseed (no nests in either year) and autumn sown cereal and silage. The early, autumn sowing date of the crops results in these crops being well emerged and dense at the beginning of lapwing territory establishment, this being particularly true of the oilseed rape. Similarly, the 14 ha of NRSA (grassland and wild bird cover (see 1.4.2)) had a tall (>20cm), dense sward during nesting. The harvesting of row crops in late autumn and early winter delayed the sowing of some cereal until late autumn/early winter. This winter sown cereal was preferred for nesting to autumn sown cereal and silage (*G*-test for goodness-of-fit between observed and expected values,; G_{adj} (1996) = 28.8; $P<0.001$, d.f. = 1; G_{adj} (1997) = 9.1, $P<0.01$, d.f. = 1; Table 4.2.2b).

Table 4.2.2b Distribution of nests in autumn and winter sown crops. Expected nests represent their distribution if random with respect to habitat.

	1996			1997		
Crop	**Area (%)**	**No. nests**	**No. expected nests**	**Area (%)**	**No. nests**	**No. expected nests**
Autumn sown cereal and silage	67.2	17	36.3	59.3	29	41.5
Winter sown cereal	32.8	37	17.7	40.7	41	28.5

Spring farmed fields and RSA provided a different nesting substrate to other field types. Before spring farming activities field surfaces were bare with stubble, if the previous crop had been cereal. Very little or no living vegetation was evident in these fields due to the post-harvest application of herbicide. Spring cultivations produced bare fields with crop

Figure 4.2.2a Frequency distribution of 485 lapwing nests in the study area.

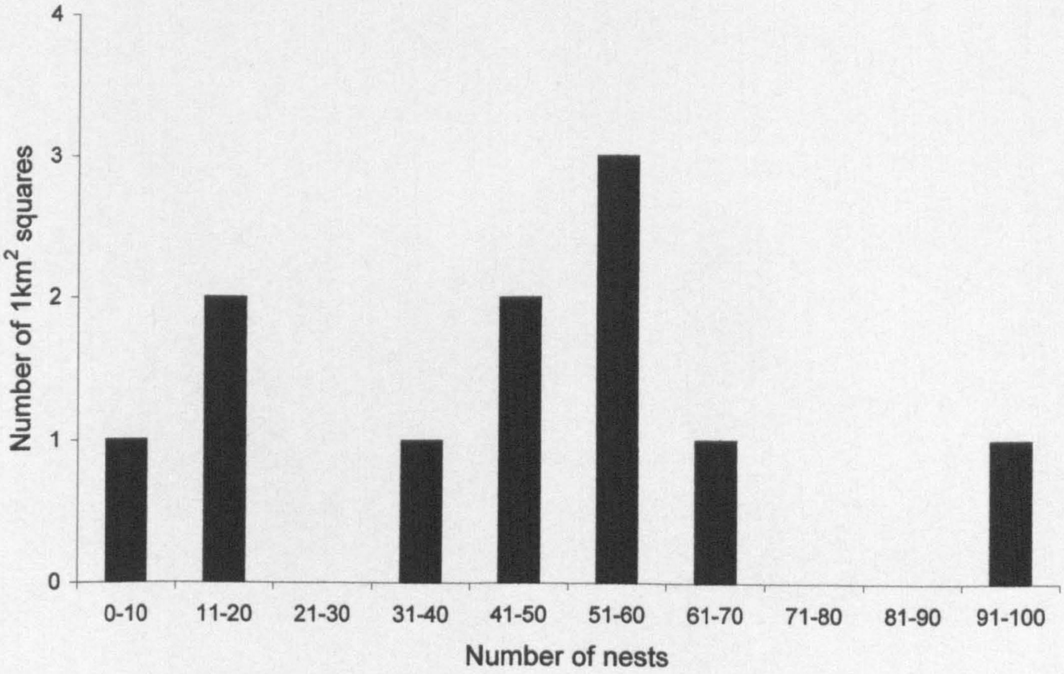


Figure 4.2.2b Lapwing nest site selection - proportional distribution of 485 nests (1996 & 1997 combined) in relation to habitat distribution. Expected proportion of nests if their distribution was random with respect to habitat.

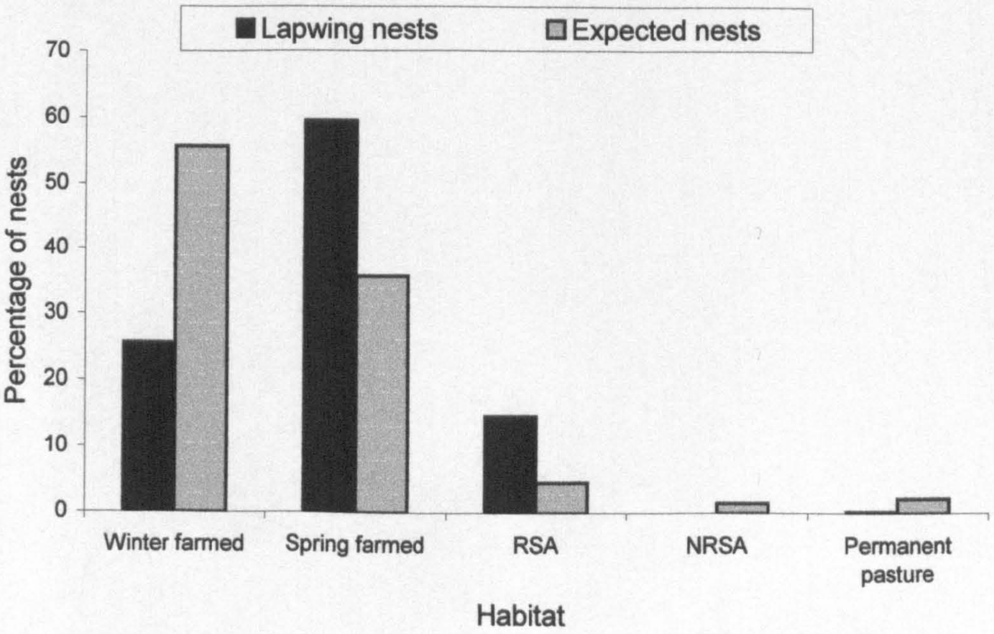


Figure 4.2.2c Distribution of lapwing nests in autumn and winter sown crops (1996 & 1997 combined). Expected nests if their distribution was random with respect to habitat.

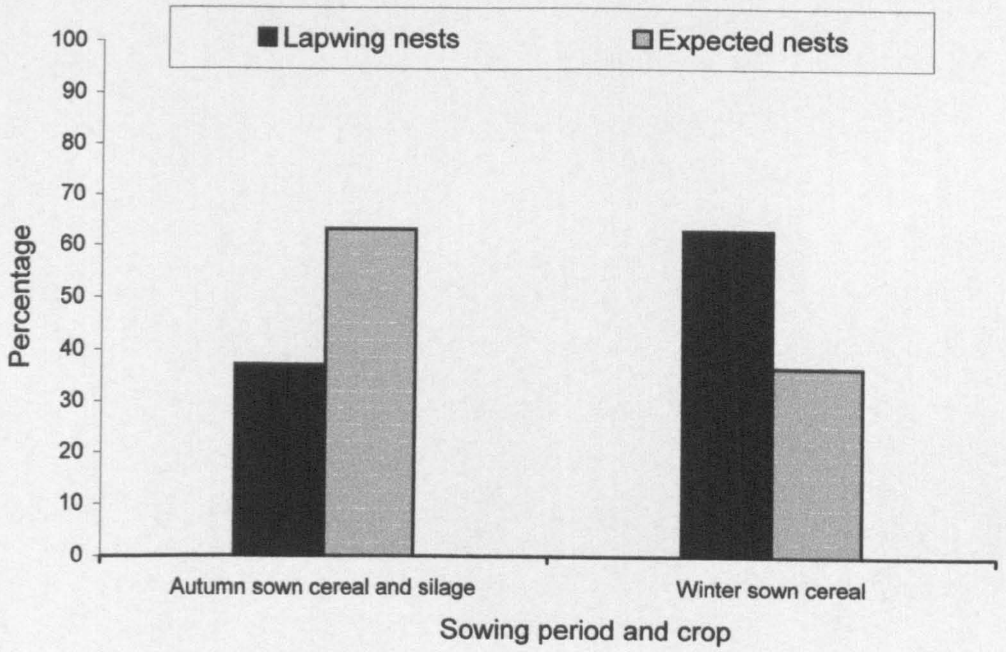
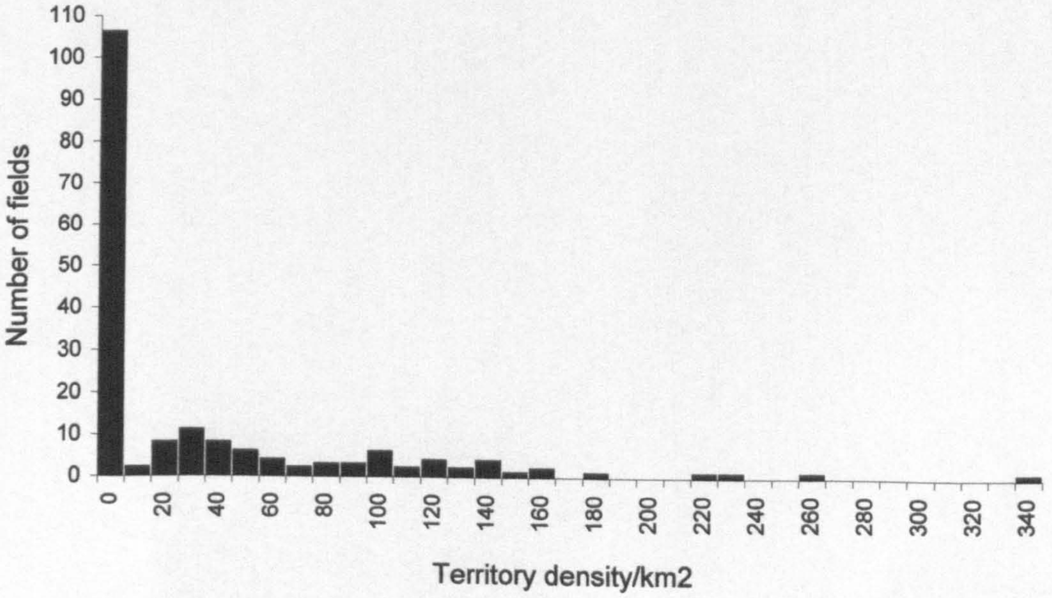


Figure 4.2.2d Lapwing territory density/km^2 in spring farmed and RSA fields (1996 & 1997 combined). n = 179 fields.



emergence soon after sowing. RSA was unmanaged with field vegetation (arable 'weeds' and volunteer crops) regenerating naturally. In contrast to crops, RSA sward growth was not uniform and the area of bare ground was greater throughout the nesting period. Over the two years RSA fields held 15% of all nests, although the habitat occupied only 5% of the area.

Preference for crop type within the spring farmed category could not be tested. Most nests (61%) on unsown land failed, mainly through cultivation activities. The great majority (90%) of nests in unsown fields were first clutches. At least 81% of nests in spring sown fields were estimated to be replacement clutches. Many nests on spring sown land were started on bare till (*i.e.* prior to crop emergence). Furthermore, there was a tendency for females to use the same fields for re-laying as 66% of nests in spring sown fields were located in the same fields as first clutches on unsown land.

ii. Other factors affecting nest site selection

Despite lapwing preferring to nest in RSA and spring farmed fields not all such fields were used and territory densities varied from field to field (Figure 4.2.2d). For example, in 1996 nine of the 14 RSA fields (64%) were used for nesting. In 1997, only 5 (*i.e.* 42%) of 12 RSA fields had lapwing territories. Three variables were significantly correlated with territory density (Table 4.2.2c). Lapwings preferred to nest in large fields that had previously been spring farmed and were distant from trees.

Table 4.2.2c Spearman rank correlation between lapwing territory densities in spring farmed and RSA fields and four variables (probability values were obtained from two-tailed tests).

	r_s	*P*	No. of fields
Years field spring farmed*	0.41	<0.001	182
Field area	0.18	<0.02	182
Distance to predator vantage	0.15	<0.05	182
Distance to pasture	-0.13	ns	182

* Crop distribution known for 1995 to 1997, therefore, the maximum a field could score in 1996 was 1 year.

The rank correlation between breeding density in spring farmed and RSA fields and distance to permanent pasture was not significant (Table 4.2.2c).

iii. Density and heterogeneity of vegetation in nesting fields

The vegetation stand of crop fields used for nesting was more even than that of RSA fields (Table 4.2.2d). The vegetation structure of RSA fields used for nesting was more heterogeneous than either winter sown or spring sown cereals.

Table 4.2.2d The mean height (cm), heterogeneity and density of vegetation in lapwing nesting fields in intensive arable farmland. The more uniform the vegetation height the lower the heterogeneity index. High density index values indicate high plant density. Measurements were taken from 10 quadrats from four fields for each field type. n = number of samples from which each index was derived.

	n	Mean height (S.D)	Heterogeneity Index	n	Density Index
Winter sown cereals	4	29.3 (5.10)	0.75	4	0.94
Spring sown cereals	4	16.4 (4.90)	1.3	4	0.85
RSA	4	11.7 (14.2)	5.5	4	0.73

The vegetation of RSA fields was less dense and more uneven in height than that of cereal fields.

4.2.3 Nest survival

i. Differences between habitats

No significant difference was found in daily nest survival in each year between nests in autumn and winter sown crops (z = 1.06; ns in 1996; z = 0.91; ns in 1997 (see 4.1.5 equation (iii) for the calculation of z)), therefore, nests in these field types were combined in a 'winter farmed' habitat category. To investigate any habitat effects, nest survival was calculated for the three main nesting habitats (winter farmed, spring farmed and RSA) within the study area. Permanent pasture is excluded as the single nest in this habitat was too few to include in analysis. Nest survival in each of the three nesting habitats was different (Table 4.2.3a). For both years combined, nest survival was significantly higher in RSA (where hatching success was 88%) than in spring or winter farmed fields (z = 6.44; P<0.001 and z = 3.87; P<0.001 respectively). The hatching success in spring farmed fields (48.4%) was the lowest and although success in winter farmed fields was higher (57.2%) the difference between daily nest survival rate in these two habitats was not significant (z = 1.4; P>0.1).

Table 4.2.3a Lapwing nest survival and hatching success in three intensive farmland habitats (1996 & 1997 combined). P represents the daily survival rate (se, its standard error; see 4.1.5, equations (i) to (iii)).

Habitat	**Nests**	**Nest days**	**Losses**	**P**	**se**	**Hatching success (%)**
Winter farmed	118	2022	35	0.9827	0.0029	57.2
Spring farmed	296	4733	106	0.9776	0.0022	48.4
RSA	71	1241	5	0.9959	0.0018	88.0

The major factor responsible for nest losses in all habitats was farming operations, which accounted for 77.4% of all losses (Table 4.2.3b). Depredation was the secondary nest loss factor (14.4% of all losses), although in spring farmed and RSA fields nest desertion accounted for a similar level of nest failure. The most numerous losses were on spring farmed land where 72.6% of all nest losses occurred. In this habitat most first clutches were laid on unsown land, the majority of which were destroyed by spring cultivations.

Nearly 92% of breeding failures, therefore, were attributable to the two factors of farming operations and predation (Table 4.2.3b).

Table 4.2.3b Causes of nest loss (1996 & 1997 combined).

			Percentage of failures due to:		
Habitat	**Nests**	**Nests failed**	**Farm operations**	**Predation**	**Desertion**
Winter farmed	118	35	60	29	11
Spring farmed	296	106	84	9	7
RSA	71	5	60	40	0
Total	**485**	**146**	**77.4**	**14.4**	**8.2**

ii. Differences between years - the effects of farm operation timing

The overall nest survival of all three habitats did not differ significantly between the two years with a hatching success of 56.2% in 1996 and 54.8% in 1997 (with 242 nests and 3695 nest days in 1996 and 243 nests and 4301 nest days in 1997; $z = 0.19$; $P>0.1$). Differences in the probability of nest failure were consistent for spring farmed and RSA habitats with no significant difference in these habitats in nest loss between years ($z = 1.85$, $P>0.05$ and $z = 0.9$, $P>0.1$ respectively, Figure 4.2.3a). There was, however, some annual variation in hatching success which was shown most strongly by winter farmed habitats. Daily nest survival was significantly higher in this habitat in 1996 ($z = 2.93$; $P<0.01$) when the hatching success was 76% compared to 44.7% in 1997. The main reason for this difference was yearly differences in the timing of farm operations in relation to the timing of breeding of lapwings (Figure 4.2.3b). Early rolling of winter sown cereals in 1997 destroyed nests whereas in 1996 young hatched before the operation occurred.

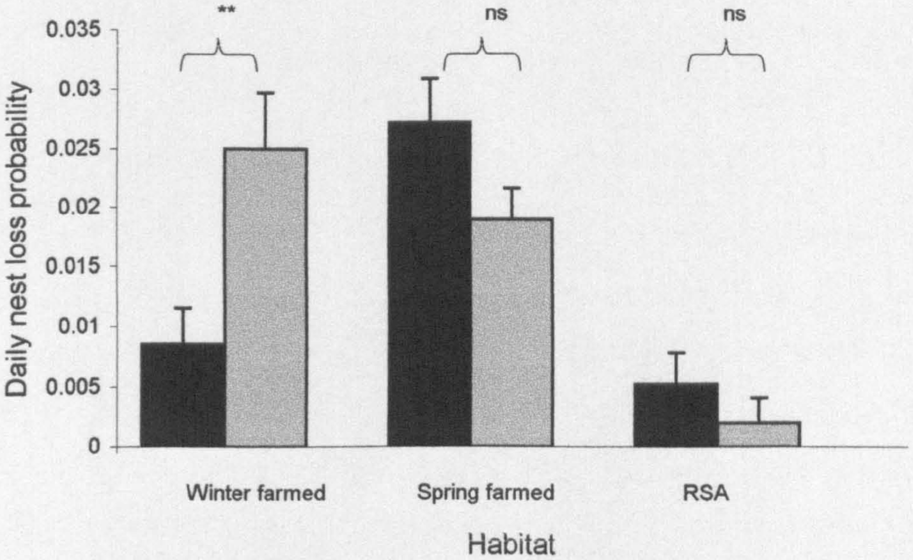
The effect of this different timing is illustrated by the fact that in 1996, due to nest losses incurred by spring sowing, the daily destruction probability was significantly higher in spring farmed than in winter farmed fields ($z = 5.11$; $P<0.001$; Figure 4.2.3b). In 1997, however, there was no significant difference in nest losses from farm operations between these two habitats despite the similar probability of nest destruction on spring farmed land ($z = 0.13$, $P>0.1$; Figure 4.2.3b). In addition, the proportion of replacement clutches in spring sown fields in 1997 was greater (80.4%) than in 1996 (65.3%). Lapwings that failed in winter crops in 1997 re-laid on spring sown ground as the advanced crop development stage prevented re-laying in the original crop type.

Furthermore, in 1996 there was no significant difference in nest survival between winter farmed habitats and RSA ($z = 0.84$, $P>0.1$), or in losses caused by farm operations ($z = 0.24$, $P>0.1$). In 1997 RSA had a significantly higher nest survival with a significantly lower nest loss by farming operations than other habitats ($z = 4.3$, $P <0.001$; $z = 3.27$, $P<0.002$; for RSA *v*. spring and winter farmed habitats respectively).

iii. Effects of spring farming

The preferred nesting habitats of spring farmed and RSA fields were similarly managed and did not differ in appearance until spring cultivation, *i.e.* lapwings were selecting unsown tillage for nesting. Most nests (56.2%) in unsown fields were destroyed by spring farming activities (Table 4.2.3c), although some nests were deliberately avoided by the farmer during cultivation (see 4.2.5 iv.).

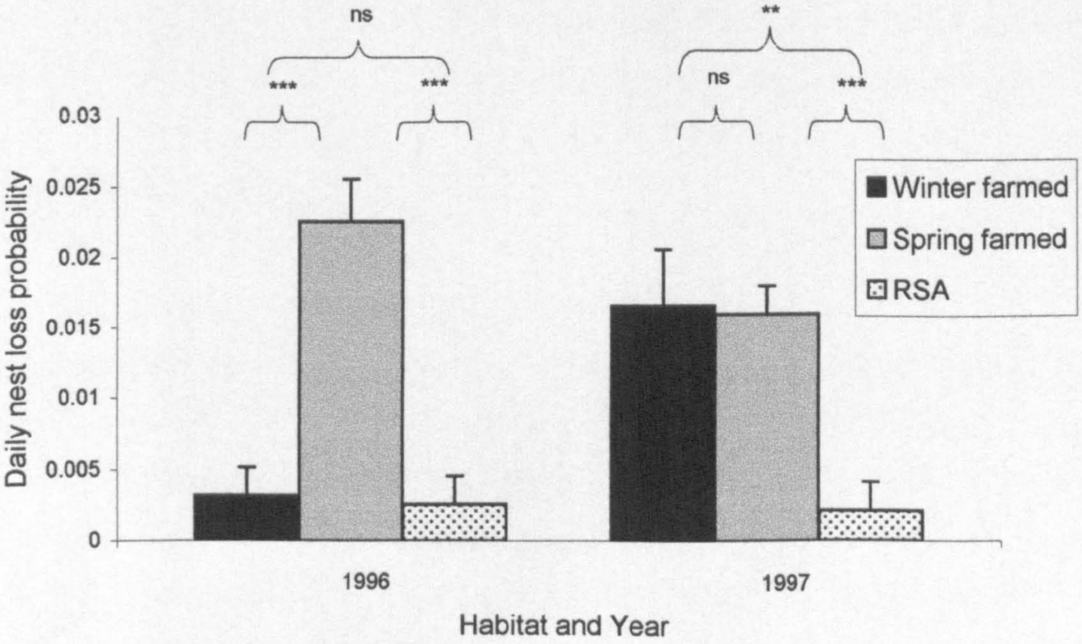
Figure 4.2.3a Daily nest loss probability in winter farmed, spring farmed and RSA habitats in 1996 (dark bars) and 1997 (light bars).



The number of nests and nest days in 1996 were as follows: winter farmed 54 nests and 937 nests days; spring farmed 140 nests and 1987 nest days; RSA 48 nests and 771 nest days. In 1997: winter farmed 64 nests and 1085 nest days; spring farmed 156 nests and 2746 nests days; RSA 23 nests and 470 nest days.

**** indicates level of statistical significance significance, *P* <0.01; ns = not significant.**

Figure 4.2.3b Daily nest loss probability due to farm operations in three farmland habitats in 1996 and 1997.



For the number of nests and nest days for each habitat and year see Fig. 4.2.3a.
Level of statistical significance: ** = *P* <0.01, * = *P* <0.001, ns = not significant.**

Table 4.2.3c Causes of nest loss in spring farmed fields (1996 & 1997 combined).

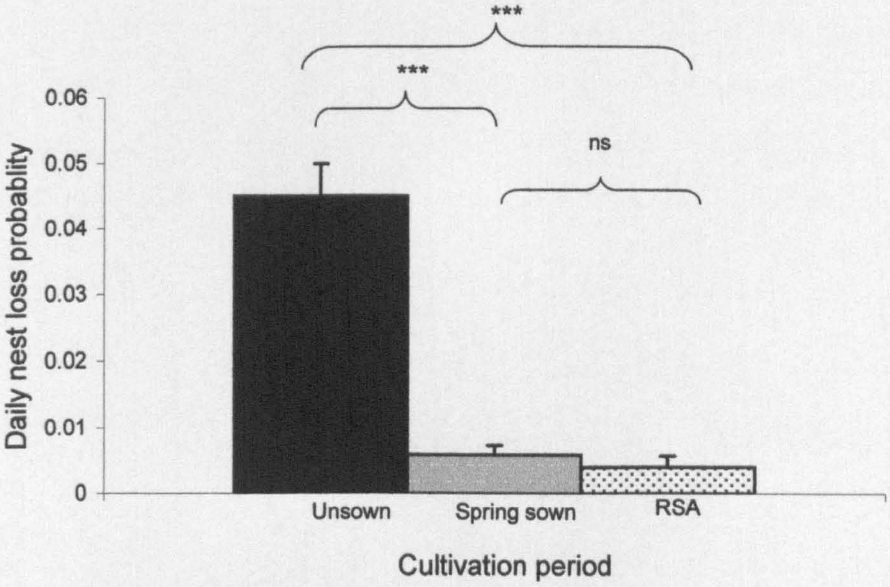
Category	Nests	Percentage of nests failed due to:			Number of failed nests
		Farm operations	**Predation**	**Desertion**	
Unsown	146	56.2	4.8	0.7	90
Sown	149	4.7	2.0	4.0	16

Nests in spring farmed fields fared better after sowing with only 4.7% lost to farming operations. The difference in daily nest loss probability between the two cultivation periods was very highly significant ($z = 8.59$; $P>0.001$; Figure 4.2.3c). This difference between cultivation periods also incorporates the difference between first and replacement clutches as most first clutches on spring farmed land were laid on unsown tillage (with 45% of all first clutches) and most replacements on sown tillage (with 73.8% of all replacement clutches). Nest survival in unsown and sown categories did not differ significantly between years for each category ($z = 0.42$, $P>0.1$ in unsown, with 73 nests each year and 915 and 1052 nest days in 1996 and 1997 respectively; $z = 1.8$, $P>0.05$ in sown, with 66 nests and 1058 nest days in 1996 and 83 nests and 1694 nest days in 1997). There was no significant difference in the risk of nest loss between spring sown and RSA fields ($z = 0.77$, $P>0.1$: Figure 4.2.3c), illustrating the effect of cultivation activities.

iv. Effects of cropping

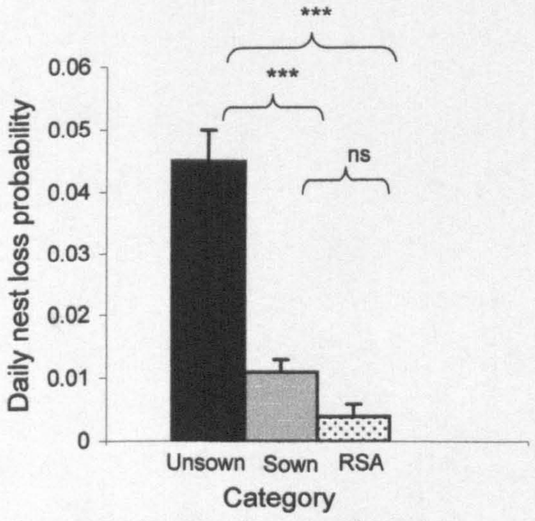
Overall, whether fields had been sown or not before laying determined nest success in cropped fields (Table 4.2.3d). The hatching success of nests in sown fields (*i.e.* autumn, winter and spring sown) was 71% whereas in unsown tillage (*i.e.* fields to be spring sown) it was 22.6%. The high 'unsown' nest loss resulted in the difference in daily survival rate between nests in sown and unsown fields being very highly significant ($z = 7.13$; $P<0.001$; Figure 4.2.3d(i)). In this study the hatching success of 'unsown' nests was elevated by human agent as some farmers deliberately avoided nests during sowing.

Figure 4.2.3c Daily nest loss probability in spring farmed and RSA fields (1996 and 1997 combined).



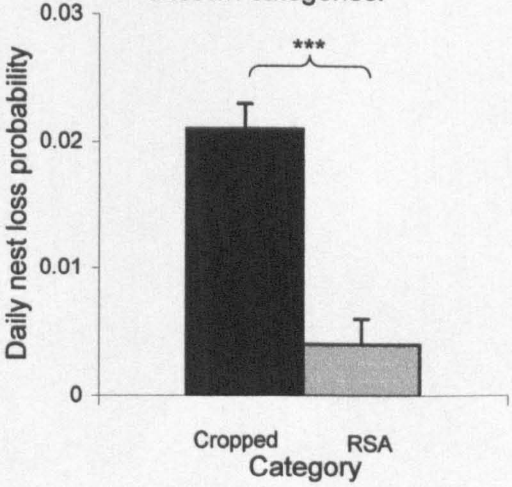
The number of nests and nests days for each category were as follows: unsown: 147 nests, 1981 nest days; spring sown: 149 nests and 2752 nest days; RSA: 71 nests and 1241 nest days.
*** indicates level of statistical significance, *P* <0.001, ns = not significant.

Figure 4.2.3d (i) Daily nest loss probability in three farmland categories (1996 & 1997 combined).



The number of nests and nest days for each category were as follows: unsown nests = 147, nests days = 1981; sown nests = 267, nest days = 4774; rsa nests = 71, nest days = 124. *** indicates level of significance, *P* <0.001; ns = not significant.

Figure 4.2.3d (ii) Daily nest loss probability in cropped fields and RSA (1996 and 1997 combined). Cropped fields represent sown + unsown categories.



The number of nests for the cropped category was 414 with 6755 nest days. See Figure 4.2.3d (i) for the number of RSA nests and nest days.
*** indicates level of significance, *P*<0.001.

Through this action 38 (25.8%) nests survived sowing. Of these nests 86.8% (33) hatched. It is not known if the proportion of nests avoided during sowing increased during the period of investigation. Nests in RSA had a significantly higher probability of survival than nests in sown tillage ($z = 2.99$, $P<0.01$) and cropped ('sown' and 'unsown' nests combined) fields ($z = 6.71$, $P<0.001$, Table 4.2.3d), as nest loss was significantly lower in RSA (Figure 4.2.3d(ii)).

Table 4.2.3d Survival and hatching success of lapwing nests in three different farmland categories (1996 & 1997 combined). P represents the daily survival rate (se , its standard error).

Category	**Nests**	**Nest days**	**Losses**	**P**	**se**	**Hatching success (%)**
Sown Tillage	267	4774	51	0.989	0.00149	71
Unsown Tillage	147	1981	90	0.955	0.00468	22.6
RSA	71	1241	5	0.996	0.00180	88

v. Survival of first and replacement clutches

Overall 302 nests (62.3%) were classified as first clutches (see 4.1.5), 158 (32.6%) as replacement clutches with the remaining 25 (5.2%) being unclassified (Table 4.2.3e). There was between year consistency in the rate of nest loss in both first and replacement clutches with differences in daily survival not being significant (first clutches: $z = 1.06$, $P>0.1$; replacement clutches: $z = 0.70$, $P>0.1$). For both years combined there was a large difference in daily survival rates between first and replacement clutches which was significant ($z = 4.91$, $P<0.001$). Overall, daily survival probability was higher in replacement than in first clutches.

Table 4.2.3e Daily survival rates of first and replacement clutches in intensive farmland lapwing nests.

Clutch	**Nests**	**Nest days**	**Losses**	**P**	**se**
1996 First	154	2373	50	0.9789	0.00295
Replacement	72	1085	12	0.9889	0.00318
1997 First	148	2450	63	0.9743	0.00320
Replacement	86	1671	14	0.9916	0.00223
Total First	302	4823	113	0.9766	0.00218
Replacement	158	2756	23	0.9916	0.00184

A total of 62.6% (189/302) of females hatched a first clutch. Only 62% (70/113) of the replacement clutches were known second clutches, *i.e.* laid within 15 days and 100m of the failed first clutch (Table 4.2.3f).

Table 4.2.3f Daily survival and hatching success of known second clutches of lapwing breeding in intensive farmland. Second clutches are those laid within 15 days and 100m of the first failed clutch. P represents the daily survival rate (se , its standard error).

	n	**Hatch**	**Fail**	**Unknown fate**	**Nest days**	**P**	**se**	**Hatching success (%)**
1996	36	26	8	2	532	0.9812	0.0059	54.5
1997	34	25	9	0	621	0.9860	0.0047	62.7
Total[a]	70	51	17	2	1153	0.9840	0.0037	58.8

[a] Data were pooled as there was no significant difference in survival rates between 1996 and 1997 (z = 0.64, P>0.1).

The proportion of all nesting females to hatch a known second clutch can be estimated as 13.6% (the proportion of females with unsuccessful first clutches × the proportion of first clutches replaced by a second × the hatching success of known second clutches / 0.374 × 0.6195 × 0.588 = 0.136). The addition of the proportion of females succeeding in first clutches (0.626) gives an estimated proportion of 76.2% of all females succesfully hatching a clutch. This figure must be considered as a minimum as it is not known how many of the remaining replacement clutches (*i.e.* those laid over 100m away and after 15 days from the failure of the first clutch) were re-nesting attempts from initial failures within the study area as no females were marked. The remaining replacement clutches may also represent subsequent nesting attempts distant from the original territory. This may have been the result of the inability of females to quickly re-attain satisfactory breeding condition or crop growth or cultivation activity rendering original nesting sites unsuitable. Excluding unclassified clutches, there were 28.5% more clutches classed as replacements than there were failures of first clutches (Table 4.2.3e). If replacement of failures was 100% then the proportion of all nesting females succesfully hatching a clutch was 91.1% ($0.374 \times 1.0 \times 0.763 = 0.285 + 0.626 = 0.911$). The classification of clutches indicates that between 76% and 91% of all females were successful in hatching a clutch. The situation is difficult to determine as there were no marked females in this study to monitor the replacement of lost clutches (see 4.1.5). Female lapwing have been known to lay three or even five clutches in a single season (Klomp 1951, Berg *et al.* 1992). There did appear, however, to be some redistribution of nests after initial clutch destruction. For example, in one spring farmed field where there had been no first clutches or any breeding behaviour, eight replacement clutches were laid in May. There had been no similar nest loss of first clutches in neighbouring fields to account for the replacements.

There was variation between field types in loss of first and replacement clutches. Most nest losses (55.5%) occurred in first clutches in unsown spring farmed land (Table 4.2.3g). In contrast to other habitats, nest loss in spring sown fields and RSA was highest in replacement clutches. Indeed, in RSA all losses were incurred by replacement clutches. In this habitat, most nest losses were through farm operations with 2 nests destroyed by late season (mid-June 1996) herbicide application and one by cultivation activity (in mid-May 1997) when part of the field was sown as game crop.

Table 4.2.3g Lapwing nest loss in first, replacement and unclassified clutches in different field types in intensive farmland (1996 and 1997 combined). Unsown and spring sown constitute spring farmed land.

				Percentage of failures to:		
Habitat	**Clutch**	**Nests**	**Losses**	**Farm operation**	**Predation**	**Desertion**
Winter farmed	First	105	31	64.5	22.6	12.9
	Replacement	8	1	0	100	0
	Unclassified	5	3	33.3	66.7	0
Unsown	First	133	81	90	8.75	1.25
	Replacement	9	6	100	0	0
	Unclassified	5	3	100	0	0
Spring sown	First	25	1	100	0	0
	Replacement	116	14	42.9	14.2	42.9
	Unclassified	9	1	0	100	0
RSA	First	39	0	0	0	0
	Replacement	25	5	60	40	0
	Unclassified	7	0	0	0	0

Nearly all losses (91%) through desertion occurred in well-grown cereals. These desertions were in well developed crops in the last quarter of the incubation period with three nests found with chicks that had died during hatching.

vi. Weather

Lapwing nest losses to farm work on arable land have been shown to be correlated with weather (Shrubb 1990). Shrubb showed that greater March rainfall delayed cultivations into the peak lapwing nesting period which increased nest losses. As farming operations were responsible for the majority of nest failures between year weather differences were examined. There were between year differences in weather parameters of March and April in 1996 and 1997 at the study site (Table 4.2.3h).

Table 4.2.3h Mean daily temperature (^{0}C) and rainfall (mm) in 1996 and 1997.

		1996	1997
		Mean (SD)	Mean (SD)
Daily temperature	March***	4.75 (1.68)	7.75 (1.52)
	April ns	8.50 (2.70)	9.00 (2.60)
	May**	9.20 (3.10)	11.9 (3.30)
Daily rainfall	March	0.96 (2.85)	1.10 (1.9)
	April	1.82 (4.12)	0.90 (2.0)
	May	1.10 (2.10)	2.60 (4.8)

Asterisks indicate significance levels of *t*-tests between years: ** = P<0.01, *** = P<0.001, ns = not significant.

A *t*-test on the mean daily temperature of March 1996/97 showed that March 1997 was significantly warmer than March 1996 (t = -7.38, P <0.001, d.f. = 59). Additionally, there were 4 days with frost in March 1996 and none in March 1997 and 2 days with frost in April 1996 and none in April 1997. Temperatures in April were similar each year (t = -0.86, P>0.1, d.f. = 55) but May was significantly warmer in 1997 than in 1996 (t = -3.34, P<0.01, d.f. = 59). The greater mean daily rainfall in April 1996 resulted in the monthly total (54.6mm) being twice that of April 1997 (26.6mm). Conversely, the total rainfall of May 1996 (35.4mm) was less than half that of May 1997 (79.6mm).

4.2.4 Clutch size

i. Clutch size estimation

As survival rates were higher in replacement clutches (which constituted at least 32.6% of all nests) differences in clutch size between first and replacement clutches were investigated. It is possible, however, that clutch size may alter through the incubation period due to partial predation of eggs. The clutch size of a nest when found, therefore, may be lower than that at the time of clutch completion. To determine if measured clutch sizes differed from those at the beginning of incubation, nests were divided into two period categories, assuming egg predation risk to be greater the longer the nest is available to predators. Clutch size was then examined by comparing the mean clutch size of nests found within the first five days of incubation to those found later in the incubation period.

Table 4.2.4a The mean clutch size of lapwing nests found in the first five days of incubation and those found later. n = the number of clutches examined.

	Clutches found in first five days of incubation			**Clutches found after five days of incubation**			**t-test between incubation periods**
	n	**mean**	**s.e.**	**n**	**mean**	**s.e.**	
1996	77	3.896	0.044	88	3.932	0.048	$t = 0.55$; $P>0.5$; d.f.=162
1997	155	3.90	0.025	54	3.796	0.061	$t = 1.71$; $P>0.05$; d.f.=71

There were no significant differences in the mean clutch size of nests between the two periods in both years (Table 4.2.4a). Also the frequency of four egg clutches between the two periods for both years combined did not differ ($X^2_1 = 0.182$; $P>0.50$). It was, therefore, taken that the clutch size of nests when first found was a reliable indication of clutch size at the time of clutch completion.

For both years combined 88.4% of clutches had four eggs, 8.2% had three, 2% had 2, 1.1% had one and one clutch had six eggs.

ii. Differences between first and replacement clutches

Differences in clutch size between first clutches and replacements were not statistically significant in both years (Table 4.2.4b). Overall, the size of first clutches was 3.91 (s.e. = 0.03) and the size of replacements was 3.86 (s.e. = 0.04).

Table 4.2.4b Mean clutch size of first and replacement clutches of lapwings breeding in intensive lowland farmland. n = number of clutches measured.

Clutch	**n**	**mean**	**s.e.**	**t-test between clutches**
1996 First	101	3.92	0.044	$t = 0.19$; $P>0.8$; d.f.=117
Replacement	54	3.91	0.055	
1997 First	117	3.91	0.030	$t = 1.39$; $P>0.1$; d.f.=149
Replacement	83	3.83	0.045	

The mean clutch size in 1996 (3.92 eggs) was not significantly larger than that of 1997 (3.88 eggs; $t = 0.85$; $P>0.3$). Overall, clutch size was 3.89 (s.e. = 0.02).

iii. Differences between arable habitats

As there were no significant differences in mean clutch sizes between first and replacement clutches and between years, clutch and year data were pooled to examine the effect of different habitats on clutch size. Clutches on sown land (winter farmed and spring sown fields) were compared to clutches laid on unsown land (unsown spring farmed fields and RSA). There was no significant difference in clutch size between habitats (Table 4.2.4c).

Table 4.2.4c Clutch size of lapwing nests in sown and unsown fields in intensive lowland farmland (1996 and 1997 combined).

Habitat	**n**	**mean**	**s.e.**	**t-test between habitats**
Sown	218	3.90	0.023	$t = 0.61$; $P>0.5$; d.f.=227
Unsown	137	3.88	0.039	

Sown represents nests in winter farmed and spring sown fields; Unsown includes nests in RSA and unsown spring farmed fields.

4.2.5 Hatching success

i. Egg loss in sown tillage and RSA

Investigation of hatching success in sown fields and RSA was also undertaken by examining egg loss. In addition to farming operations, other nest loss factors caused partial nest failures which were important in terms of overall breeding success. In cultivated fields, for example, 14% of breeding failures were due to partial losses resulting from infertility or embryo death (Table 4.2.5a). Egg survival, therefore, gave a more accurate assessment of breeding success than nest survival. Breeding failures in unsown fields were excluded from this analysis as some nests were destroyed before clutch size could be established. Examination of nest survival (see 4.2.3) elucidated breeding success in that field type.

Table 4.2.5a Causes of egg loss in lapwings breeding in intensive lowland farmland (1996 & 1997 combined).

		Percentage of failures due to:			
Habitat	**Eggs lost**	**Farm operations**	**Predation**	**Infertility/ embryo death**	**Desertion**
Autumn sown	55	43.6	41.8	7.3	7.3
Winter sown	96	59.4	25.0	3.1	12.5
Spring sown	91	30.8	16.5	30.8	22.0
RSA	22	54.5	31.8	9.1	4.5
Unsown*	239	85.4	11.3	0.84	2.5

*The numbers of eggs lost is an underestimate as 21 nests were destroyed by farming operations before clutch size could be established, however, 'unsown' losses are included to allow comparison with the other categories.

Overall the risk of egg loss was significantly lower in RSA nests than in clutches laid in both winter farmed and spring sown fields ($z = 8.7$, $P<0.001$ and $z = 3.07$; $P<0.01$ for winter and spring categories respectively; Table 4.2.5b). As the risk of egg loss was significantly higher in both crop categories (Figure 4.2.5a), daily egg survival was significantly higher in RSA than for all sown tillage ($z = 7.22$, $P<0.001$).

The causes and rate of egg loss, however, varied between habitats between years (Table 4.2.5c). Egg survival was significantly higher in RSA than in sown tillage in both 1996 and 1997 ($z = 3.18$, $P<0.002$; $z = 6.9$, $P<0.001$ for 1996 & 1997 respectively). In 1996 this was due to RSA egg survival being significantly higher than that of both winter farmed ($z = 2.1$, $P<0.02$) and spring sown fields ($z = 3.18$, $P<0.002$). Although in 1997, daily egg survival rates of RSA nests were significantly higher than for eggs in winter farmed crops ($z = 9.3$, $P<0.001$), the risk of egg loss did not differ between RSA and spring sown crops ($z = 1.72$, $P>0.05$). This resulted from an increase in hatching success in spring crops in 1997 due to a lower rate of infertility/embryo death than in 1996 (see below).

Farm operations caused a very large decrease in hatching success in winter sown crops in 1997, where the between year difference in daily egg survival was significant ($z = 8.85$, $P<0.001$; Figure 4.2.5a). Thus, in 1996 there was no significant difference in egg survival between spring sown and winter farmed land ($z = 1.11$, $P>0.1$). In 1997, however, egg survival was significantly lower on winter farmed land than in spring sown fields ($z = 8.67$, $P<0.001$). In addition, egg survival was significantly higher in winter than in autumn sown crops in 1996 ($z = 2.6$, $P<0.01$). In 1997 the converse was true, egg survival was significantly higher in autumn than in winter sown crops ($z = 5.4$, $P<0.001$). In 1996 'winter sown' hatching success was comparable with that of RSA (the field type with the highest hatching success) as there was no significant difference in egg survival between the two field types ($z = 0.49$, $P>0.1$). In 1997, however, RSA hatching success was almost seven times greater than that of winter sown eggs. Egg survival was, thus, significantly higher in RSA than in winter sown fields ($z = 9.27$, $P<0.001$) in 1997.

In spring crops, however, hatching success was higher in 1997 than in 1996, the between year difference in egg survival probability being significant ($z = 2.65$, $P<0.01$; Figure 4.2.5a). The hatching success for eggs from RSA and autumn sown crop nests was similar for each field type in each year (Table 4.2.5c) with no difference in daily egg survival between years for each habitat (for RSA: $z = 0.72$, $P>0.1$; for autumn sown: $z = 1.02$, $P>0.1$). In 1996 hatching success was, therefore, comparable between spring and autumn sown eggs when egg survival in these two field types did not differ ($z = 1.2$, $P>0.1$). In 1997, however, egg survival was significantly higher in spring than in autumn sown fields ($z = 4.1$, $P<0.001$).

Table 4.2.5b Survival and hatching success of lapwing eggs in three habitats in intensive lowland farmland (1996 and 1997 combined). P represents the daily survival rate (se , its standard error).

Habitat	**No. eggs**	**Egg days**	**Egg loss**	**P**	**s.e.**	**Hatching success (%)**
Winter farmed	468	6642	151	0.9773	0.00183	48
Spring sown	565	10403	91	0.9913	0.000913	75.5
RSA	276	4806	22	0.9954	0.000974	86.3

The winter farmed and spring sown categories represent sown tillage.

ii. Differences between habitats – infertility and desertion

Egg failure rates through infertility were highest in nests in spring sown fields (Figure 4.2.5b), the differences between spring and winter crops and spring crops and RSA being significant ($z = 2.45$, $P<0.02$ for winter crops and $z = 3.89$, $P<0.001$ for RSA). There was no significant difference, however, for infertility rates between RSA and winter crops ($z = 1.33$, $P>0.1$). This habitat difference also reflects the difference between clutches with 67.6% of infertile eggs occurring in replacement clutches. In addition, there was a between year difference with infertility rates being higher in spring sown crops in 1996 ($P = 0.005 \pm 0.0011$) than in 1997 ($P = 0.0014 \pm 0.0005$), the difference being significant ($z = 2.79$, $P<0.001$).

The probability of losing eggs through desertion was higher in crop fields than in RSA (Figure 4.2.5b) with differences being very highly significant (winter crops and RSA: $z =$

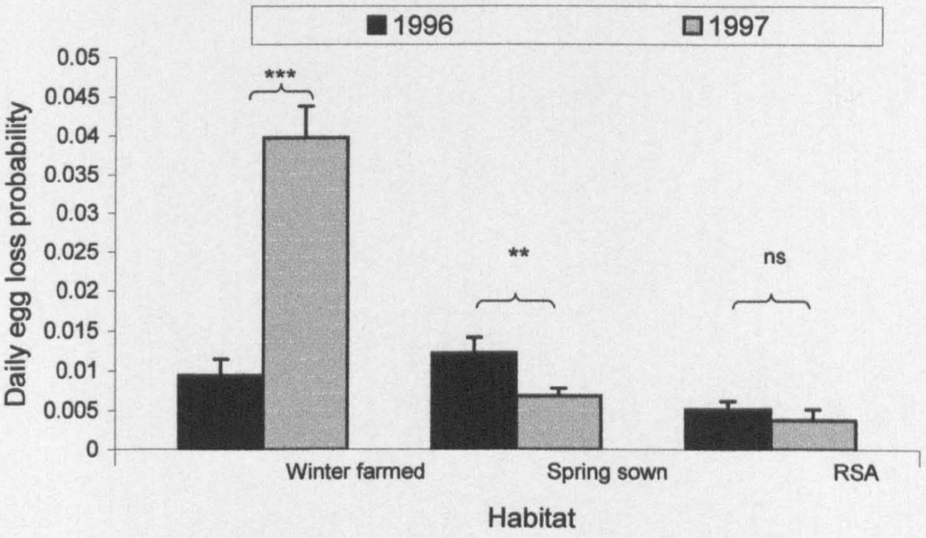
3.45, $P<0.001$; spring sown crops and RSA: $z = 3.53$, $P<0.001$). There was no significant difference in desertion rate between winter farmed and spring sown crops for both years combined ($z = 0.69$, $P>0.1$). Desertion rates were similar in both years in spring sown crops ($z = 0.11$, $P>0.1$). They differed significantly, however, between years in winter farmed crops ($z = 2.33$, $P<0.02$), being higher in autumn sown crops in 1996 (no desertion in 1997) and higher in winter sown cereal in 1997 (no desertion in 1996).

iii. Differences between different spring crops

Two categories of crops were spring farmed. These were combinable crops, mainly cereals (34.5% of spring farmed area) with some oilseed and linseed (5.6% of spring farmed area). The remaining 60% was given over to vegetables, mostly potato (36% of the spring cropped area) with some field beans, carrots, brassicas, peas and leeks (23.9% of the spring farmed land). There was no between year difference in the proportion of nests in each category (chi-square test of association (Yates correction applied) on the frequency of nests in each spring crop category: $X^2_1 = 3.32$, $P>0.05$).

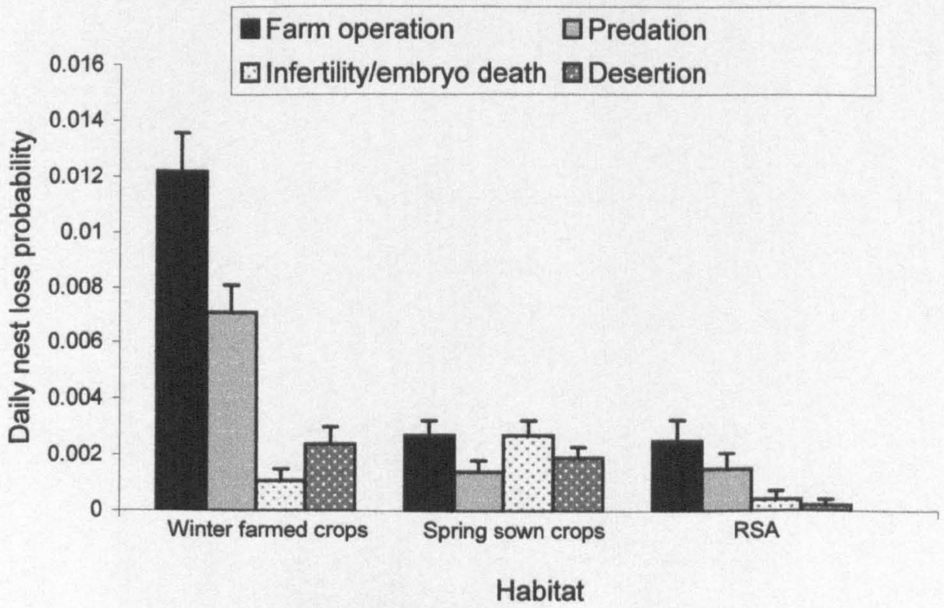
Hatching success in spring sown fields was related to crop category (Table 4.2.5d). In both years hatching success was higher in combinable than in vegetable crops as egg survival was significantly higher in combinable crop nests (1996: $z = 3.17$, $P<0.002$; 1997: $z = 5.35$, $P<0.001$). The rate of egg loss, however, was significantly lower for both categories in 1997 ($z = 3.27$, $P<0.002$; $z = 2.17$, $P<0.05$ for combinable and vegetable crops respectively). Eggs failed due to infertility, farm operations, predation and desertion (Figure 4.2.5c), although only the daily egg predation rate did not differ between the two categories ($z = 1.78$, $P>0.05$). The rate of egg loss by all other factors was significantly higher in vegetable than in combinable crops ($z = 2.62$, $P<0.01$; $z = 3.38$, $P<0.001$; $z = 2.69$, $P<0.01$; for infertility/embryo death, farm operation and desertion respectively).

Figure 4.2.5a Daily egg loss probability for lapwings breeding in three intensive farmland habitats in 1996 and 1997



The number of eggs and egg days for each habitat were as follows: winter farmed 1996: eggs = 216, egg days = 3725; 1997: eggs = 252, egg days = 2917; spring sown 1996: eggs = 246, egg days = 3999; 1997: eggs = 319, egg days = 6404; RSA 1996: eggs = 184, egg days = 2933; 1997: eggs = 92, egg days = 873. Significance levels: ** = *P* <0.01, *** = *P* <0.001, ns = not significant.

Figure 4.2.5b Daily egg loss probability due to farm operations, predation, infertility and desertion for lapwing nests in crop fields and RSA (1996 & 1997 combined).



For the number of eggs, egg days and egg losses see Table 3.3. See text (4.2.4 and 4.2.5) for details of statistical differences between the different causes of egg loss.

Table 4.2.5c Egg survival for lapwings breeding in RSA and crops differing according to sowing period in an area of intensive farmland.

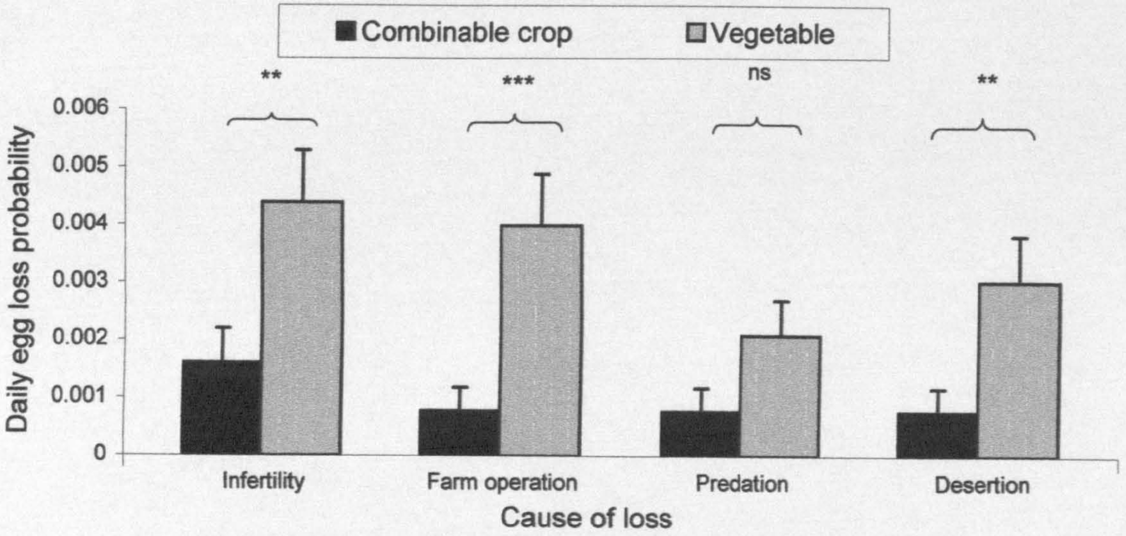
1996			**No. eggs fail to:**							
Habitat\Crop	**No. eggs**	**Egg Days**	**Infertility**	**Farm operation**	**Predation**	**Desertion**	**Total no. losses**	**P**	**se**	**Hatching success (%)**
RSA	184	2933	2	8	5	0	15	0.9949	0.00132	84.9
Autumn sown	68	1109	2	4	9	4	19	0.9829	0.003897	57.6
Winter sown	148	2616	1	5	10	0	16	0.9939	0.001524	82.2
Spring sown	246	3999	19	16	5	8	48	0.988	0.001722	67.9
1997										
RSA	92	1873	0	4	2	1	7	0.9963	0.00141	88.8
Autumn sown	91	1596	2	20	14	0	36	0.9774	0.003717	48.1
Winter sown	161	1321	2	52	14	12	80	0.9394	0.005971	13.5
Spring sown	319	6404	9	12	10	12	43	0.9933	0.001021	80.6

Table 4.2.5d Egg survival for lapwings breeding in two different crop categories in intensively cultivated spring sown fields.

			No.eggs fail to:							
Crop	No. eggs	Egg Days	Infertility	Farm operation	Predation	Desertion	Total losses	p	se	Hatching success (%)
<u>1996</u>										
Combinable	134	2381	8	4	1	4	17	0.9929	0.001721	63.4
Vegetable	112	1618	11	12	4	4	31	0.9808	0.003412	53.8
<u>1997</u>										
Combinable	124	2749	0	0	3	0	3	0.9989	0.00064	96.5
Vegetable	195	3655	12	9	7	12	40	0.9891	0.001721	70.4

Combinable crops (cereals and oilseed) are harvested with combines, and managed differently to vegetable crops.

Figure 4.2.5c Daily egg loss probability from four factors for lapwings breeding in two categories of intensively cultivated spring sown crops (1996 &1997 combined).



For the relevant number of eggs, egg days and eggs lost see table 4.2.5d
Level of significance: ** = P <0.01, *** = P <0.001, ns = not significant.

iv. Hatching success for human intervention nests

Some farmers deliberately avoided nests when cultivating unsown fields (a preferred nesting habitat), even though the farmers seemed well aware that females would probably lay a replacement clutch if their first was destroyed. If a farmer saw a nest during a cultivation operation, the nest was driven around. Sometimes not all nests in a field were spotted and so some were destroyed. Extant nests were then similarly avoided during any subsequent cultivation operations resulting, once sowing had been completed, in these nests remaining on islands of unsown land within (bare) tilled fields. It was observed that farming operations in spring sown crops after sowing were sometimes carried out by contractors. No heed was given to lapwing nests during these 'contractor' operations and any nests that had not hatched were destroyed. It was also evident that the 'islands' holding nests became very conspicuous in the freshly sown fields which may have made them more susceptible to predation. It was possible, therefore, that the hatching success of nests deliberately avoided during spring sowing was decreased and that avoiding nests was of no benefit to productivity.

The survival of eggs in 'avoided nests' was compared to the survival of eggs in all 'other nests' in sown fields and RSA to investigate any differences in hatching success (Table 4.2.5e). In both years hatching success was higher in 'avoided nests' than in 'other nests'. In 1997 the daily survival probability of 'avoided nests' was significantly higher than for 'other nests' ($z = 2.26$, $P<0.05$), although in 1996 there was no difference in survival rate between the two categories ($z = 1.33$, $P>0.1$).

Table 4.2.5e Survival of lapwing eggs in nests avoided during sowing operations, eggs in other nests in all sown fields and RSA and eggs in spring sown nests. P represents the daily survival rate (se , its standard error).

Nest type	**No. nests**	**No. eggs**	**Egg days**	**Eggs lost**	**P**	**se**	**Hatching success (%)**
Avoided 1996	19	74	1452	9	0.9938	0.0021	82
1997	18	68	1479	13	0.9912	0.0024	75.4
Other 1996	168	646	10657	98	0.9908	0.00093	74.4
1997	170	663	11194	166	0.9852	0.00114	62
Spring sown 1996	66	246	3999	48	0.9880	0.0120	67.9
1997	83	319	6404	43	0.9933	0.00102	80.6

Nests in unsown fields that were not avoided during cultivation or did not hatch before sowing operations were destroyed. Nests in spring sown fields were mostly replacement clutches, females re-laying after the destruction of their first clutch in unsown fields (i.e. 'spring sown nests' mostly replaced nests that were not avoided by farmers). Further investigation, therefore, compared the survival of eggs in 'avoided nests' with those of eggs in nests in spring sown fields (*i.e.* nests in the same fields containing 'avoided nests' but after sowing). In 1996 the hatching success of eggs in 'spring sown clutches' was lower than that of 'avoided nests' with the latter having a significantly higher daily survival probability ($z = 2.16$, $P<0.05$), in 1997, however, there was no difference between survival rates ($z = 0.81$, $P>0.1$) for eggs in these two groups. The difference between the categories in 1996 was due to significantly higher rates of infertility/embryo death in spring sown fields in 1996 ($z = 3.11$, $P<0.01$; test between eggs in 'avoided' and spring sown clutches) and desertion (see below). There were no significant differences in egg survival in spring sown nests between 1996 and 1997 due to predation ($z = 0.1$, $P>0.1$), desertion ($z = 0.2$, $P>0.1$) or destruction from farming operations ($z = 0.2$, $P>0.1$). Although there were no differences in egg survival rates between 1996 and 1997 in avoided nests for sterility ($z = 0.013$, $P>0.1$) and predation ($z = 1.78$, $P>0.05$), there was a between year difference in egg survival due to desertion and destruction from farming activities. No eggs were lost to desertion in avoided nests in 1996 but in 1997 one clutch of four eggs was deserted. Farming operations accounted for the destruction of six eggs in avoided nests in 1996 but none in 1997.

To investigate any effect avoided nest 'islands' might have had on nests being robbed of eggs, predation rates were compared between categories. Examination of predation risk between eggs in 'avoided nests' and those in 'spring sown nests' and 'all sown and RSA nests' showed that there was no significant difference between the categories in each year (z = 0.12, 1.23 and 1.95, 0.92; NS in all cases; for avoided and spring sown nests and avoided and all sown and RSA nests in 1996 and 1997 respectively; Figure 4.2.5d).

4.2.6 Factors related to predation

i. Whole clutch and partial predation

Most egg loss through predation occurred as a result of whole clutches being taken (Table 4.2.6a). Partial predation of clutches accounted for 20.5% of all predated eggs with similar ratios in each year.

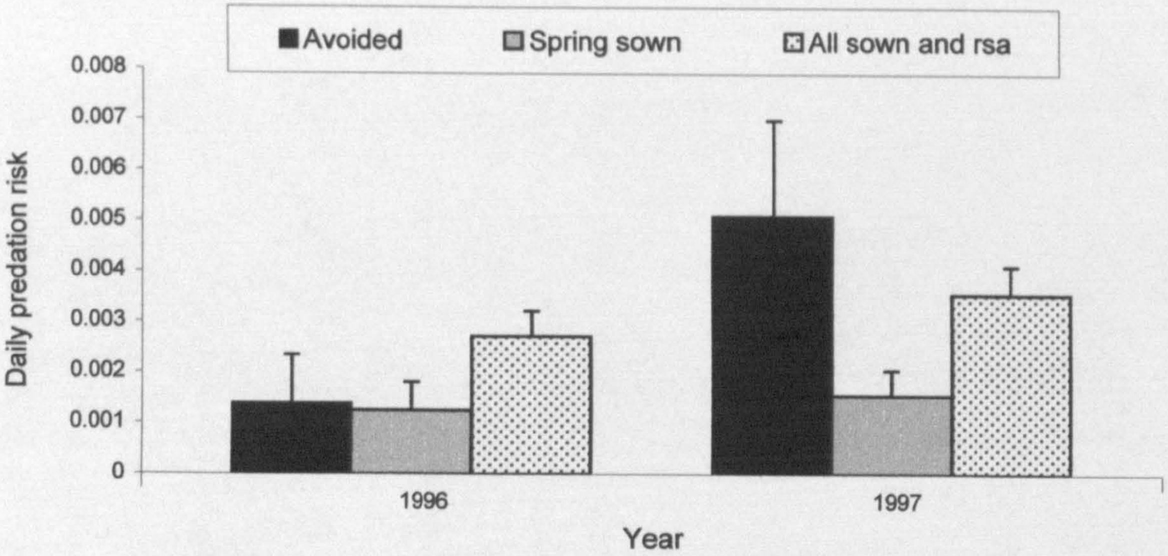
Table 4.2.6a Whole clutch and partial predation of lapwing nests in intensive lowland farmland. Figures in parenthesis give percentage loss.

	Whole clutches		Partial loss		Total	
	Nests	**Eggs**	**Nests**	**Eggs**	**Nests**	**Eggs**
1996	8	30	6	6	14	36
1997	9	40	5	12	14	52
Total	17	70 (79.5)	11	18 (20.5)	28	88

A chi-square test of association on the frequencies of nests with (*i.e.* including whole and partial clutch loss) and without predation showed that there was no between year difference in the proportions of nests that suffered egg depredation (X^2_1= 0.04, P >0.5).

Eggs or clutches mostly disappeared without trace with the remains of only one clutch of four eggs being found near a nest.

Figure 4.2.5d Predation risk for eggs in nests avoided during sowing, eggs in spring sown clutches and eggs in all nests in sown fields and RSA.



The number of predated eggs in the different categories were as follows: avoided nests: 1996 = 2, 1997=8; spring sown: 1996 = 5, 1997 = 10; nests in all sown fields and rsa: 1996 = 29, 1997 = 40. Egg predation rate did not differ significantly between any category: 1996; z = 0.12, P>0.1 for avoided and spring sown nests; z = 1.23, P>0.1 for avoided nests and sown and rsa nests; 1997: z = 1.95, P>0.05 for avoided nests and spring sown nests; z = 0.92, P>0.1 for avoided nests and sown and rsa nests.

ii. The effect of season.

Predation was examined in relation to first egg dates to investigate the effect of season. Predation risk to eggs was compared between clutches with first egg dates before and on the median first egg date and those after the median first egg date for all crop types combined. Median first egg dates differed between years (23 April in 1996 and 17 April in 1997) so each year was analysed separately (Figure 4.2.6a). In both years the daily probability of egg predation was significantly higher for clutches laid in the period up to and including the median first egg date than for clutches laid in the period after this date (for 1996: $z = 2.07$, $P<0.05$; for 1997: $z = 4.15$, $P<0.001$).

iii. Distance to predator vantage points and cover.

Although the majority of breeding failures was attributable to farming activity, at least 14.4% of failed nests were lost to predators. Examination of egg loss in sown tillage and RSA shows that 26% of failures were due to predation. Within the study area potential predators of lapwing eggs and newly hatched young were gulls, corvids, foxes, stoats, hedgehogs (*Erinaceus europeus*) and rats. Corvids are known to use perches in trees or bushes to locate nests and it has been shown in previous studies that lapwings avoid breeding close to such predator vantage points (*e.g.* Berg *et al*, 1992; Galbraith 1989b), especially if they contain crow nests (Elliot 1985). In this study it was found that lapwings did nest further away from such perches (mean 482 nests[7] ± SD = 226.3 ± 117.2m) than would be expected by chance (mean 146 random sites ± SD = 201.7 ± 137.8; Mann-Whitney test, $W = 156338$, $P<0.02$; see 4.1.3). In their Swedish study Berg *et al* (1992) showed advantage was conferred upon lapwings nesting further than 50m from trees or shrubs in that predation risk was decreased. In this study, of the 6 nests (2 in 1996 and 4 in 1997) situated within 50m of a predator vantage point none suffered predation. In fact, there was no predation recorded for all 39 nests (19 in 1996 and 20 in

1997) situated within 100m of trees or bushes. Predation risk, therefore, could not be shown to have increased due to proximity to avian predator vantage.

The ditches and ditch margins that formed field boundaries could provide cover for potential mammalian predators, particularly during the nesting period when fields were either bare or had short crops and such boundaries had rank vegetation. Rabbits (*Oryctolagus cuniculus*), rats, other small mammals as well as nesting grey partridge and pheasant used ditch banks which may have attracted mammalian predators. Also, the uncultivated, bare strips between crop and ditch/field boundary might be used as predator lanes. Avoidance of ditch boundaries, therefore, might be expected. It was found that lapwings nested further from ditch field boundaries (mean of 482 nests ± SD = 62.5 ± 3 5.5m) than would be expected by chance (mean of 146 random sites ± SD = 48.7 ± 35.8; Mann-Whitney test, W = 160725, $P<0.001$; see 4.1.3). It appeared advantageous for lapwings to nest distant from ditches (Figure 4.2.6b) as the risk of egg predation was significantly lower for nests further than 5m from ditches than for eggs in nests within 5m ($z = 2.3$, $P<0.02$; all habitats and years combined).

In the analysis of radio-marked chick mortality avian and mammalian predation are treated separately.

iv. Intensive cultivation – distance to tramlines

A feature of the intensive management of cereals is that fields possess 'tramlines' along which machinery travels in order to apply fertilizer, pesticides, growth regulators, etc to the growing crop. It was observed that a number of nests within autumn and winter sown cereals were situated close to tramlines and nest to tramline distance was measured for all nests found in these crop types. Nests in spring cereals were excluded as clutches are laid mostly before crops are well emerged and tramlines evident. Tramline-nest distance measurements revealed that 42.2% of all nests in winter cereals were situated within 1m

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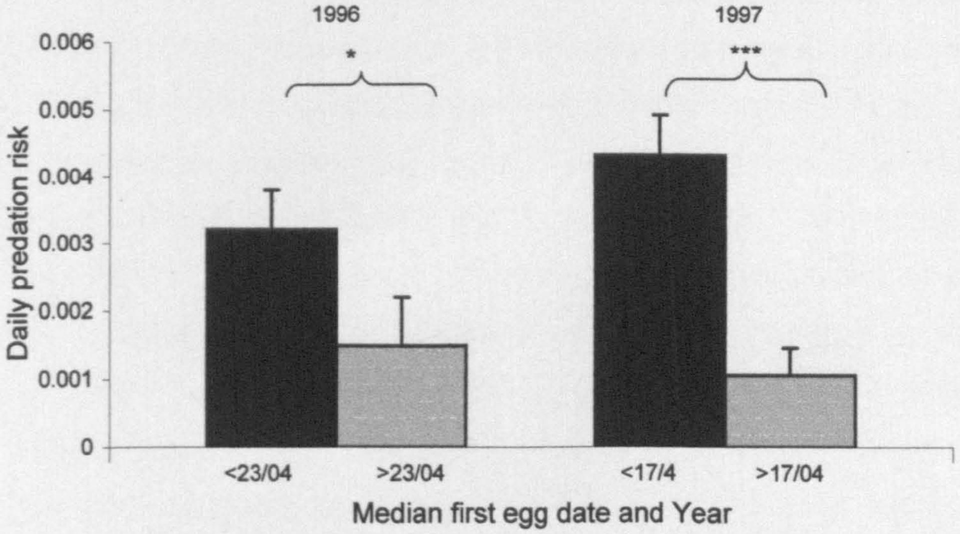
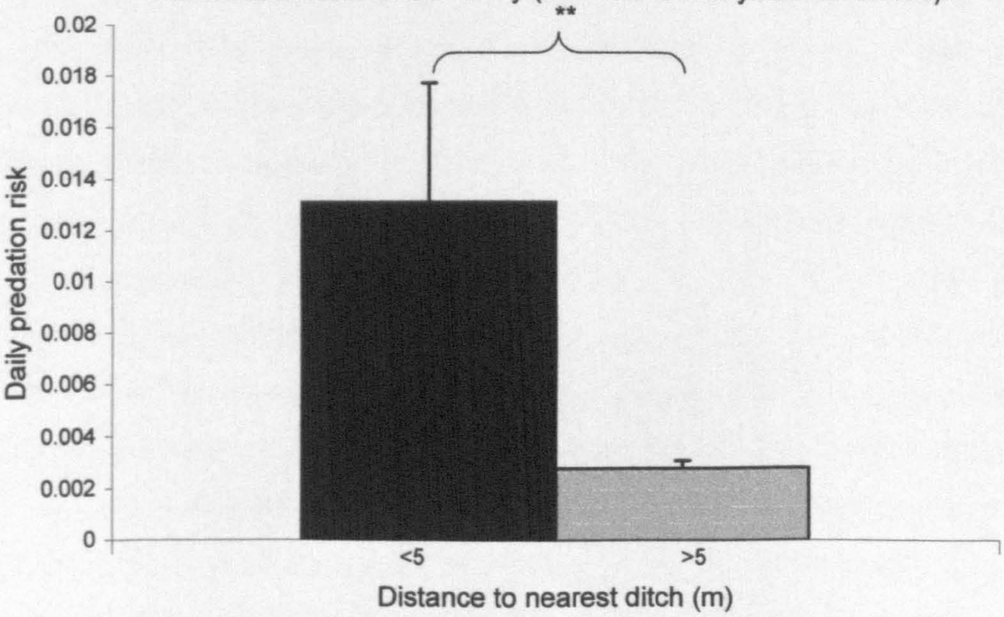
[7] The distance to trees and field boundaries was not measured for three nests.

Figure 4.2.6a Predation intensity in relation to season (up to and including median first egg date and after median first egg date).



The number of eggs, egg days and eggs predated for each date period were as follows: 18-23/04/96; eggs=565, egg days=9678, eggs predated=31; 24/04-29/05/96: eggs=233, egg days=3445, eggs predated=5 (34 nests were excluded from 1996 due to unknown first egg date period); 10/03-17/04/97: eggs 651, egg days=10651, eggs predated=46; 18/04-24/5/97: eggs=283, egg days=5673, eggs predated=6. Significance levels: * = P <0.05, *** = P <0.001.

Figure 4.2.6b Daily predation risk for lapwing nests within 5 metres of ditches and nests further away (all habitats and years combined).



The number of eggs, egg days and eggs predated in the two categories were as follows: <5m: eggs= 40; egg days=610; eggs predated=8: >5m: eggs=1680; egg days=28685; eggs predated=80. In total 37 nests were excluded all from the >5m category as in 1997 the distance to ditches was not measured for three nests and in 1996 farm operations destroyed 34 nests before clutch size could be established. There were no nests located exactly 5m from any ditch. Significance level: ** = P <0.01.

of a tramline. In fact, 44% of the nests close to tramlines were situated within the two wheel tracks. Tramlines remain bare and compacted throughout the nesting period (indeed, throughout the cropping period) and, therefore, present lanes along which potential mammalian predators may travel. It might be expected that nests close to tramlines suffered higher egg predation than nests further away either through increasing the facility by which nests were found or by increasing the likelihood of predators coming across nests incidentally. This was examined by comparing the predation risk of nests within 1m of tramlines to those further away. The daily probability of egg loss was, in fact, twice as high for eggs in nests further than 1m from tramlines (Figure 4.2.6c) and the difference was (just) significant ($z = 1.98$, $P<0.05$). This indicates that no disadvantage was incurred from nesting close to tramlines.

The high proportion of nests situated close to tramlines in autumn and winter sown cereals might indicate that there was selection for these sites. Such sites might be selected as they may significantly ease the post-hatching movement of chicks out of the natal crop. When the first chicks hatch these early sown cereals have already developed a dense sward, taller than young chicks. Hence, on hatching parents try and lead their families out of these fields to more favourable locations (see 5.2.4. i.). The susceptibility of chicks to chilling is increased by their down being wetted which may occur if they have to move through dense vegetation. The vegetation free tramline tracks would (and do; personal observation) provide passage out of the field also reducing the chance of chicks becoming wet and chilled. As there was no increased risk of predation to nests in the proximity of tramlines then an advantage in such nest sites may derive from successfully completing post-hatching movements out of natal winter farmed cereal fields. Sites close to tramlines might also facilitate the approach of adults when accessing nests for incubation. If adults used tramlines to take up incubation duties the length of approach trails (where the growing crop is flattened by being repeatedly walked on) to nests would also be shorter.

In order to investigate selection for nesting close to tramlines the number of nests found in autumn and winter sown cereals was compared with the same number of random sites.

If females were choosing to nest close to tramlines the number of nests close to (1m or less) tramlines and in between tramline tracks would be expected to be greater than that occurring by chance. As five nests (in two fields) were in the same location in each year the analysis was carried out for each year separately. As lapwings avoided nesting close to ditches where predation risk was higher (see 4.2.6. iii.) no random sites were located within 5m of the control field edges. Chi-square analysis (contingency tables with Yates' correction) was used to examine differences between the proportions of nests and random sites close to or distant from tramlines.

Table 4.2.6b The number of lapwing nests and random sites close to (≤1m) or distant from (>1m) tramlines and in between or outside tramline tracks in autumn and winter sown cereals.

	≤1m	**>1m**	**Chi-square**
1996	18	25	$X^2_1 = 2.0$; $P > 0.1$
Random	10	33	
1997	25	34	$X^2_1 = 1.83$; $P > 0.1$
Random	18	41	
	In between	**Outside**	
1996	9	34	$X^2_1 = 3.58$; $P > 0.05$
Random	3	40	
1997	10	49	$X^2_1 = 0.13$; $P > 0.5$
Random	9	50	

The proportion of nests (41.9% in 1996 and 42.4% in 1997) sited 1m or less from a tramline would appear high considering nests could be situated up to 7.5m from a tramline. The number of random sites in close proximity to tramlines was, however, similar to the number of nests in each year indicating no preference for nesting close to these plant free, linear features (Table 4..2.6b). In addition, there was no significant difference each year between the number of nests and random sites located in between tramline tracks. Lapwing, therefore, were also not choosing to locate nests in between tramline tracks.

v. Size of nesting aggregation

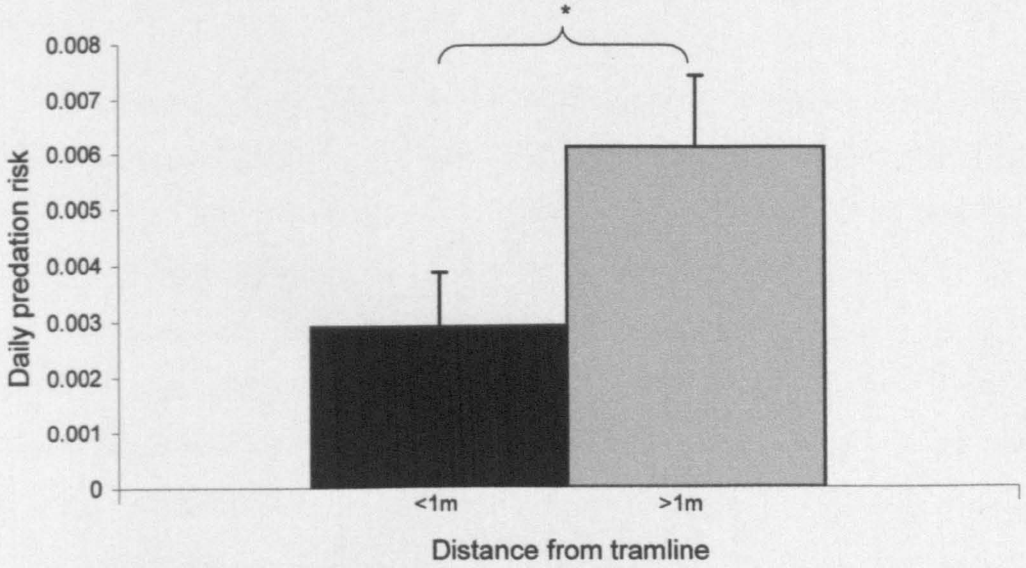
As lapwings are a group nesting species the effect of size of nesting aggregation or group on predation rate was investigated. A nest was defined as belonging to a particular nesting aggregation when situated within 200m (even if separated by a field boundary) of any other active nest, *i.e.* a nest incubated during the same time for at least one day (*c.f.* Berg *et al.* 1992). This linked nests several hundred metres apart to one particular nesting group if there were other nests between them. The great majority (86.2%) of the 485 nests belonged to large aggregations (>10 nests) with < 2% of nests solitary and few in small or medium-sized aggregations (Table 4.2.6c). The maximum number of nests in a large nesting aggregation in 1996 was 108 with a maximum of 93 nests in 1997.

Table 4.2.6c The number and proportions (%) of lapwing nests in different sized nesting aggregation categories.

Year	Solitary nests	2-5 nests	6-10 nests	>10 nests
1996	1 (0.4)	10 (4.10)	7 (2.9)	224 (92.6)
1997	7 (2.9)	25 (10.3)	17 (7.0)	194 (79.8)
Total	8 (1.6)	35 (7.20)	24 (4.9)	418 (86.2)

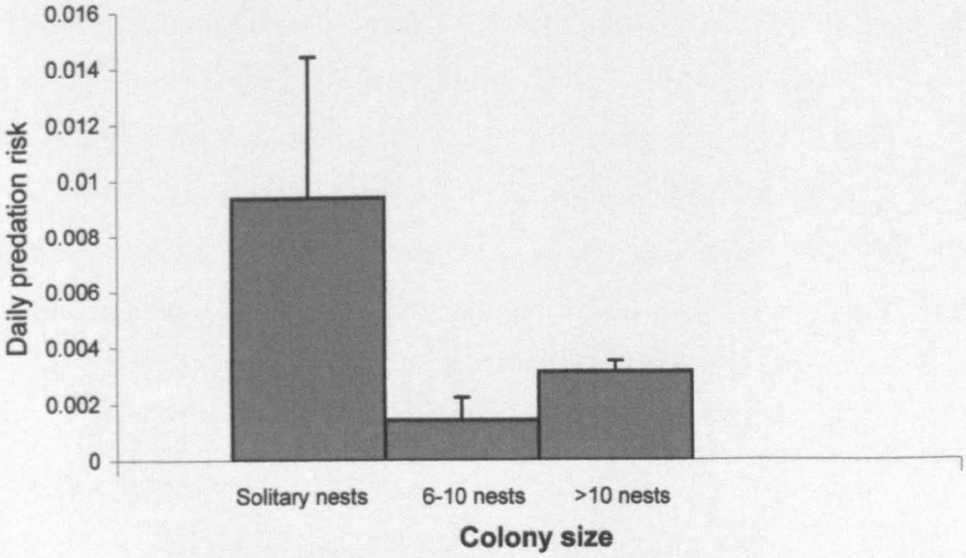
Although the daily predation rate was highest in solitary nests (Figure 4.2.6d) there was no significant difference in predation rate between eggs in single nests and medium and large nesting aggregations (z = 1.36, P>0.1 and z = 1.68, P>0.05 respectively). None of the 35 nests in the 12 small nesting groups had any eggs predated. There was also no significant difference in predation risk to eggs between medium and large nesting aggregations (z = 1.8, P>0.05).

Figure 4.2.6c Daily predation risk to lapwing eggs in nests <1m or >1m from tramlines in intensively farmed winter cereals (1996 & 1997 combined).



The number of eggs, egg days and eggs predated in the the two categories were as follows; <1m: 169, 3104 and 9 respectively; >1m: 235, 3463 and 21 respectively. * = $P < 0.05$.

Figure 4.2.6d Daily predation risk for lapwing eggs in nests belonging to different colony sizes (1996 and 1997 combined).



The number of eggs, egg days and eggs predated for the different colony sizes are as follows: single nests: eggs=27, egg days=426, eggs predated=4; 2-5 nests: eggs 132, egg days=2005, eggs predated=0; 6-10 nests: eggs=113, egg days=2107, eggs predated=3; >10 nests: eggs=1452, egg days=24865, eggs predated=77 (a 4 egg clutch is excluded from this category as the predation occurred during farming activity, the disturbance removing all lapwing from the vicinity negating any effect of colony size). There were no significant differences between the colony size categories.

vi. Breeding density

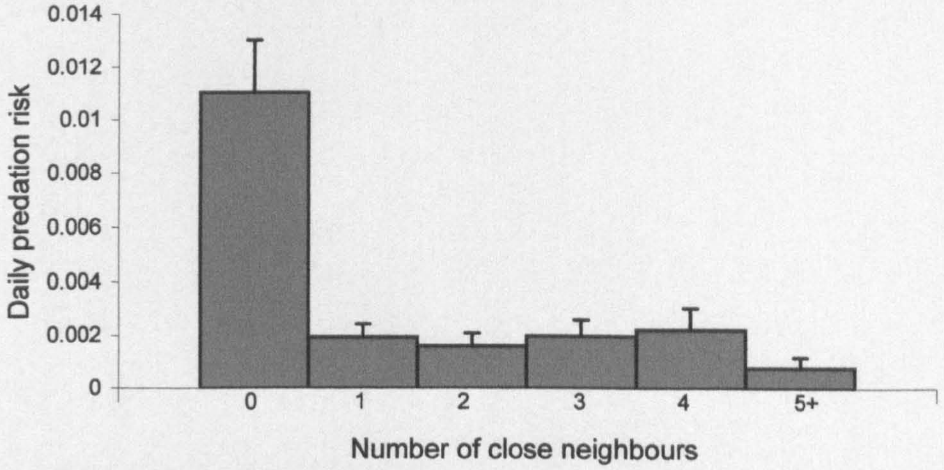
Within lapwing nesting groups there is a communal response to potential predators. The efficacy of this response might be expected to be greater with an increasing nest density within colonies. This was investigated by comparing the predation rate of eggs in nests with different numbers of close neighbours for all habitats/crop types for both years combined. Anti-predatory responses birds are invoked in breeding lapwing from distances of up to a 100m (Cramp and Simmons 1977 and references therein, Elliot 1985b). Close neighbours were, therefore, nests situated within 100m of the nest site and nests had 0-12 close neighbours, and were examined in the six categories of 0, 1, 2, 3, 4 and 5+ close neighbours.

Predation risk to eggs was highest in nests without any close neighbours and lowest to eggs in nests with five or more close neighbours (Figure 4.2.6e). The daily probability of predation for eggs in nests without close neighbours differed significantly from eggs in nests of all close neighbour categories (z scores between 0 and 1 to 5+ close neighbours were respectively 5.28, 5.45, 5.08, 4.84, 6.04; $P<0.001$ for each score). There was no significant difference in predation risk between any category with close neighbours ($P>0.1$ in each test). This indicates that in the colonies examined having a nest within 100m greatly reduces the likelihood of losing an egg to a predator. One close neighbour, however, is as efficacious in this respect as having five or more nests close by. Most nests had close neighbours with only 15% of nests without another nest within 100m.

vii. Predation in relation to habitat & crop type

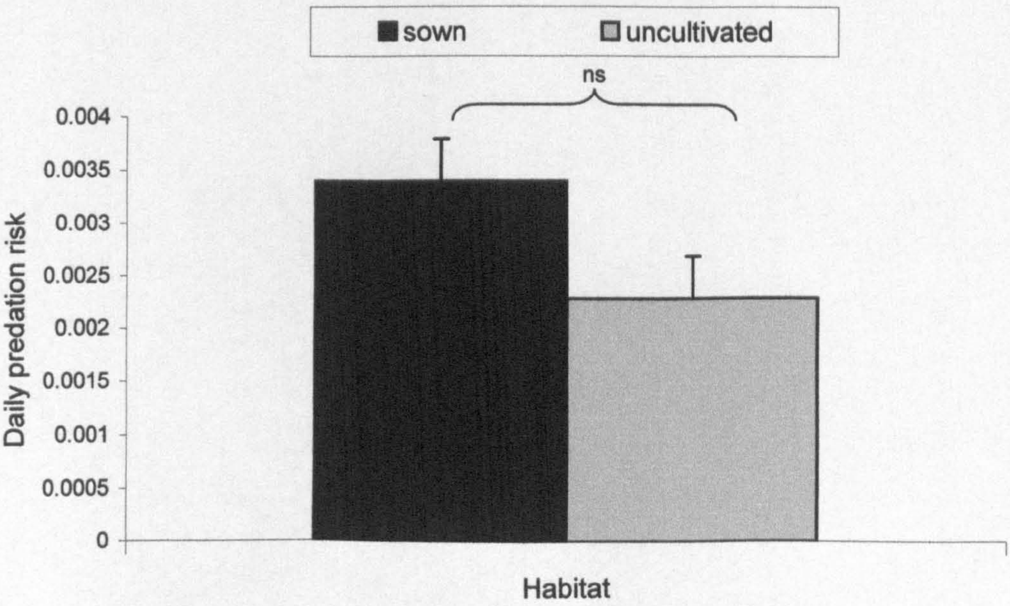
Predation was examined in relation to the two broad habitat categories of sown (including autumn, winter and spring sown fields) and uncultivated (RSA and unsown fields) tillage, *i.e.* with and without crop (Figure 4.2.6f). There was no significant difference in daily predation probability between these two habitats ($z = 1.76$, $P>0.05$).

Figure 4.2.6e Daily predation rate for lapwing nests with different numbers of close neighbours (nests within 100m of nest site). Data for 1996 &1997 combined.



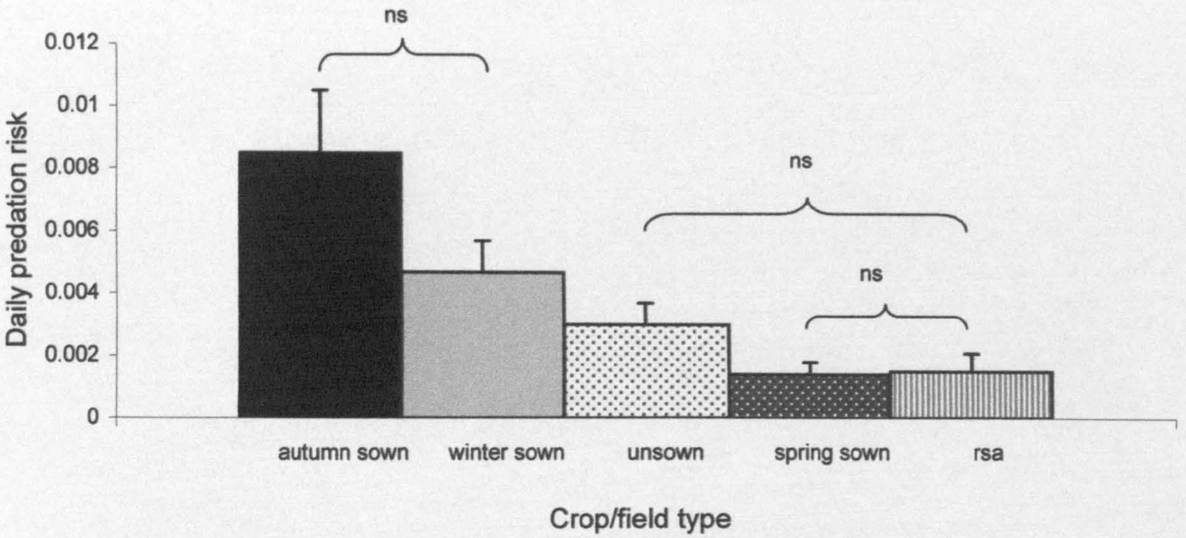
The number of eggs, egg days and eggs predated for the close neighbour (cn) categories were as follows: 0 cn: eggs=262, egg days=4075, eggs predated=49; 1 cn: eggs=425, egg days=6713, eggs predated=13; 2 cn: eggs=335, egg days=5649, eggs predated=9; 3 cn: eggs=231, egg days=4512, eggs predated=9; 4 cn: eggs=202, egg days=3575, eggs predated=8; 5+ cn: eggs=277, egg days=4923, eggs predated=4. There was a significant difference between nests without close neighbours and all other categories, *P*<0.001 in all cases.

Figure 4.2.6f Daily predation risk for lapwing eggs in two habitats in intensive lowland farmland.



Unsown represents rsa and unsown tillage (34 nests with unknown clutch size are excluded). Sown represents autumn, winter and spring sown tillage. The number of eggs, egg days and eggs predated for the two habitats are as follows: Unsown: eggs=695, egg days=11220, eggs predated=26: Sown: eggs=1033, egg days=18227, eggs predated=62.

Figure 4.2.6g Daily predation risk to eggs for lapwings nesting in different crop/field types in intensive lowland farmland (1996 & 1997 combined).



The number of eggs, egg days and eggs predated in the different categories were as follows; autumn sown crops: eggs = 159, egg days=2705, eggs predated = 23; winter sown crops: eggs=309, egg days=5119, eggs predated=24; spring sown crops: eggs = 565, egg days=10403, eggs predated=15; unsown tillage: eggs = 419, egg days=6414, eggs predated=19; rsa: eggs = 276, egg days=4806, eggs predated=7. Daily predation risk differed between winter farmed (autumn + winter sown) and unsown (P<0.01), spring sown (P<0.001) and RSA (P<0.001) categories.

The crops or field types within these habitats differed mainly in their period of cultivation which affected the stage of plant development and substrate appearance within fields during the nesting period. Such differences might impact upon a predator's ability at nest finding and even alter the chances of incidental predation. Egg predation for both years was, therefore, examined in the different crop and field types. The daily probability of predation was highest in autumn and winter sown crops (Figure 4.2.6g). These two winter farmed crop types had comparable predation rates as there was no between crop difference in predation risk to lapwing eggs ($z = 1.89$. $P>0.05$). Predation risk was very much lower in all other categories with significant differences between winter farmed crops and each of the three other field types ($z = 2.71$, $P<0.01$; $z = 4.85$, $P<0.001$ and $z = 4.34$, $P<0.001$; for tests between winter farmed and unsown, spring sown and RSA field types respectively). There was no difference between predation risk to eggs in RSA and the unsown or spring sown categories ($z = 1.7$, $P>0.1$; $z = 0.15$, $P>0.1$ respectively). Predation risk was significantly higher for eggs in unsown fields than for eggs in spring sown crops ($z = 2.07$, $P<0.05$), this increased risk accounted for by human agent. Some farmers made deliberate efforts to avoid nests during the cultivation operations of unsown fields, which normally completely destroyed nests. Such farm operations, which disturbed the field surface, sometimes attracted gulls (*Larus spp.*) and corvids (*Corvus spp.*) in considerable numbers (>30) which followed behind machinery feeding on any revealed prey items. In one instance, a nest that had been avoided during an operation was seen to be predated by tractor attendant birds whilst passing the nest site. If the predation risk to eggs for unsown fields is adjusted to account for this loss then there was no significant difference in daily predation probability for this category and spring sown crops ($z = 1.37$, $P>0.1$; adjusted number of eggs, egg days and eggs predated for the unsown category were 415, 6370 and 15 respectively). This indicates that the predation rate for unsown fields was influenced by the human activity associated with the field type and not the nature of the habitat.

Predation risk was compared between the two categories of spring sown crops. It was found that there was no significant difference between the daily predation probability for eggs in combinable crops (mainly cereals) and in vegetable crops ($z = 1.78$, $P>0.05$; Figure 4.2.5c, Table 4.2.5d).

As there was no difference in predation risk between the two broad habitats but large differences were found to exist between field types, the timing of cultivation would appear to be an important factor influencing predation. The risk of predation did not differ between sown and uncultivated (RSA and unsown) fields due to the inclusion of spring sown clutches (mostly laid on recently tilled, bare ground) in the sown category. Predation risk was higher in those fields (winter farmed crops) with a more advanced sward.

4.3 Discussion

i. Nest site selection

The most important aspect for lapwings in selecting nest sites in an area of farmland dominated by tillage would appear to be the crop phenology. The timing of sowing of a crop directly influenced the nature and appearance of the substrate of fields. The height and density of crops during the nesting period was also the result of the date sowing had taken place. Klomp (1954) considered that lapwings could judge the grey-brown or grey-green tints of fields in spring which enabled them to avoid fertile green fields where grass would become too tall later in the season and interfere with post-hatching chick mobility. This would explain why in this study lapwings preferred to nest on unsown land rather than in sown fields where crops had already emerged. Autumn sown cereal was used far less than expected according to the area of the crop with the faster growing autumn sown oilseed rape avoided completely. Furthermore, there was much greater selection for nesting in those cereals sown late in the winter rather than for those drilled in the previous autumn. Not surprisingly, winter sown cereal is less advanced than autumn sown when lapwings first arrive on territory in March. Winter sown cereal had not developed far beyond emergence, with (in contrast to autumn sown) much bare ground evident.

One way of avoiding the mobility problems facing recently hatched chicks in winter farmed fields would have been for adults to nest close to the unvegetated tramline tracks used for cultivation activities. There was a tendency for lapwings to nest close to these linear features, *i.e.* nearly half (42.2%) of all nests in winter cereals were close to tramlines, but this was no more than could be expected by chance.

A further reason why lapwings may choose nest sites with little or no vegetation is that they allow incubating birds clearer views of any approaching predator. Fields that already have tall vegetation could, therefore, be expected not to be used for nesting as they may increase the risk of predation to adults and eggs in addition to prohibiting easy chick movement once clutches have hatched. In this study, NRSA fields possessed tall vegetation during the breeding season and were avoided by nesting lapwings.

It is worth speculating on possible evolutionary aspects of nest site selection. Anthropogenic changes to the environment have been comparatively recent in evolutionary terms. Before humans started altering landscapes through farming and other activities lapwing may have relied on natural processes, such as flooding, to create ideal nesting habitat. The spate conditions caused by winter and spring rains may have removed vegetation from river banks and flood plains exposing bare substrate. Such sites would offer cryptic concealment to eggs and incubating birds as well as unimpeded views. It is likely that such locations would be in environments where ideal chick foraging habitats could also be found. Such a mechanism would have operated on lapwing nest site selection for a considerably longer period than any anthropogenic changes.

Pasture fields were also used less commonly than expected. This may be due to the fact that neighbouring spring farmed land provided better conditions for nesting as noted above. It might also have been the result of the high stocking rates (over 28 sheep ha^{-1}).

The last ten years saw a dramatic increase in sheep numbers in the locality (see 7.2). Shrubb (1990) noted lapwing breeding success on grazing land was reduced with high stocking rates. Given that a single cow may be more destructive in terms of nest trampling than a single sheep, Beintema *et al* (1982) showed that, in The Netherlands, 40% of lapwing nests were destroyed with only 1 cow ha^{-1}. In England, 60% of nests were trampled at 2 cows ha^{-1} (R. E. Green, quoted in O'Connor and Shrubb 1986). It is possible that shepherding activities could also be responsible for deterring breeding lapwing. It was observed that both vehicles and dogs were used to round up and move sheep. Vehicles were also used to move electric fences. Such activities could all cause nest failures especially as pasture fields were small (mean size ± S.D: 7.1ha ± 6.4) and grazing units (fields partitioned with electric fences) were even smaller. The small size of grazing areas would increase the chance of a vehicle or a running sheep or dog encountering and destroying a nest. Sustained failure on pasture could result in this habitat not being used for nesting by lapwing.

The nature of the field surface was not the only determinant of nest site choice. Lapwings preferred to nest in large spring tilled fields that had previously been spring farmed and were distant to trees. These results are consistent with previous work (*e.g.* Galbraith 1989b, Berg *et al.* 1992) which has also shown a preference for larger fields and sites distant from trees. Field size may be expected to exert influence if boundaries restrict the visibility of nesting birds or provide cover or vantage points for mammalian and avian predators. As the landscape of the study area was open without hedges on field boundaries and views from fields were unimpeded, choosing large fields for nesting is most likely an anti-predatory adaptation. Breeding birds avoided field edges as ditches provided cover for mammalian predators. Thompson *et al.* (1994) have shown that breeding lapwing are highly site faithful and in this study the same fields were occupied by breeding adults each year provided they were spring farmed. Breeding site-fidelity can confer an advantage of (nesting/chick rearing) site knowledge. As they noted in their study, however, it is not always possible for arable breeding adults to nest in the same or adjacent field in successive years as suitable nesting crops (*e.g.* those that are spring sown) are rotated with unsuitable ones (*e.g.* those that are autumn sown, such as oilseed rape). Unfavourable nesting conditions in the nesting field does not necessarily mean birds are not practising breeding site-fidelity as they may move to an adjacent or nearby field where nesting conditions are favourable. Such a situation was found in the two study areas by Thompson *et al.* (1994) where an appreciable number of birds breed in the field next to that in which they hatched. A similar situation is likely to have operated at Altcar as the area of spring tillage (the favoured nesting field type) was comparatively high. A potential cost of philopatry is that of inbreeding. Because lapwings are highly site faithful, with males and females equally likely to return to the breeding area, the risk of inbreeding amongst lapwing siblings, possibly born in different years, is considerable (Thompson *et al.* 1994). It is possible, however, that there are, as yet unidentified, behavioural mechanisms which prevent inbreeding from occurring.

In contrast to other British studies (Galbraith 1989b and Shrubb and Lack 1991) distance to pasture did not exert any influence on the location of lapwing nest sites. Galbraith (1989b) found that lapwings selected nest sites close to permanent pasture as it was the farmland habitat that provided the most plentiful supply of invertebrate food for broods. He showed chick survival was enhanced by reduced journey time from natal to feeding areas. Galbraith concluded, however, that possibly the primary factor forcing the movement of chicks from natal spring cereal fields to pasture was crop growth. At his Scottish study site cattle grazed pasture comprised 20% of the 'arable' area. In this study, permanent pasture was not only scarce, comprising just over 2% of the cropping area, but 74% of pasture was represented by one field. This scarcity and pattern of distribution may have influenced the nest site choice of lapwings in relation to distance to pasture. In addition, in this study the fact that lapwing did not nest near pasture could be due to spring farmed land (cereal and vegetable fields) providing adequate food and foraging areas for broods (see 5.2.6 ii).

ii. Nest survival and hatching success

The most important factor causing lapwing nesting failures was farming operations. The high hatching success in RSA compared to spring and winter farmed fields was a result of fewer and less disruptive farming activities as RSA was not cultivated for cropping. Consistency was found in the between year hatching success of RSA and spring sown fields. The differences in the timing of farming operations which caused differences in the yearly hatching success of winter sown fields was related to weather. The late rolling of winter sown cereals in 1996 which allowed more nests to hatch was a result of cold weather in March and wet weather in April. In addition, there were several frosts in both March and April in 1996. Cold weather retards crop growth, frost wilts young plant stems and wet weather softens and can waterlog the soil. All these factors combined to delay rolling of the winter sown crop in 1996 until after 26 April. The following March was significantly warmer with far less rain in April and no frosts in either month. In 1997 rolling was able to commence two weeks earlier than in 1996 with the consequent destruction of clutches, even though laying had commenced, on average, 6 days earlier than in the previous year.

It is difficult to compare hatching success across studies as it is often expressed as the percentage of nests or eggs found that hatch as opposed to the method used in this study where it is a function of daily nest survival rate. Even though the former method can overestimate survival (Mayfield 1961), the hatching success of RSA nests in this study (88%) was higher than that reported in all recent (since 1985) breeding lapwing studies (Table 4.3a).

Although hatching success was higher in RSA, there was no significant difference between the nest survival of sown tillage in central Sweden and that of RSA in this study (z = 1.44, ns). The success in sown tillage in Sweden, however, refers to replacement clutches whereas at least 55% of RSA nests in this study (Table 4.2.3g) were first clutches. The hatching success on arable reported by Shrubb (1990) is also likely to refer to second clutches.

Table 4.3a Lapwing studies with habitats where hatching success was recorded as over 60%. Hatching success is expressed as the percentage of nests that were found that hatched except for those studies marked with an asterisk where it has been calculated according to Mayfield (1961, 1975), *i.e.* $P^{32} \times 100$.

Study	Site	Hatching success (%)
This study*	Sown tillage	71
Berg *et al* 1992* (Sweden)	Sown tillage	78
	Grassland	67
Shrubb 1990 (England & Wales)	Spring cereal	71
	All cereals	70
	Bare tilth	69
Beser & Helden-Sarnowski 1984 (Germany)	Maize and grassland	84-100
Jackson & Jackson 1980 (England)	Rough grassland	70[a]

[a] Represents a nine year mean (S.D. = 12.96).

The Swedish arable study also shows the advantage that RSA has over fields that are managed as fallow over the breeding season. Nest survival in Swedish fallow was significantly lower ($z = 6.44$, $P<0.001$) than the natural regeneration RSA of this study. Berg *et al* (1992) showed that the farming operations that occur in fallow were the main cause of nest failure and reduced the hatching success in that arable habitat to 31%.

The fact that no nests were deserted in RSA is another reason why the hatching success in RSA was much higher than in cropped fields. Rapid cereal growth is aided by the application of agrochemicals. This shortens the laying season in these fields with few relays in winter farmed cereals and most replacement clutches laid on recently sown spring farmed ground. Furthermore, nest losses are increased through desertions in late first clutches in winter sown cereals and late replacements in spring cereals. Cold weather in March and April in 1996 retarded the development of winter sown cereals which were associated with a decreased desertion rate. Desertions were avoided in autumn sown crops in 1997 possibly due to earlier nesting in these crops (median egg date = 25 March) than in 1996 (median egg date = 1 April). Desertions were possibly a result of predation of the incubating adult as incubating birds in tall crops have severely restricted visibility.

Lister (1964), however, noted that lapwings leave a site when cereals reach 30cm tall, but improved cereal yields have increased the density and evenness of plant stands in the early stages of the growing season (O'Connor and Shrubb 1986). By the mid 1970's it was found that lapwings deserted dense crop stands when plants attained a height of *c*.9cm (Glutz *et al.* 1975, in Cramp and Simmons 1983). As none of the deserted nests in this study incurred egg loss, adults had probably abandoned nests because of the danger associated with minimal vantage in tall, dense crops and the difficulties in moving chicks, on hatching, through well developed cereals to better rearing fields. No nests were deserted in RSA where the plant growth was not only slower but also more uneven than in cereals. The sparser, more heterogeneous vegetation in RSA probably didn't interfere with the vigilance of incubating birds thereby decreasing the risk of desertions in replacement clutches.

Farm operations not only cause breeding failures directly through clutch destruction but also by increasing the rates of infertility and/or embryo death in eggs. The most intensive field management activities during the nesting period occur in spring sown fields where infertility/embryo death was highest. Similarly Galbraith (1988b) found a higher incidence of infertility/embryo death in clutches in arable fields than in clutches on rough grazing. In this study the highest risk of infertility/embryo death was in spring 'vegetable' fields. Cultivation activities in vegetable fields are more intensive and protracted than in other spring crops. For example, drilling potatoes (the commonest 'vegetable' crop) is a lengthy process involving several people. Post drilling activities (such as earthing-up potatoes) are also more intensive and frequent in 'vegetable' crops. In combinable crops once sowing is completed further activities are restricted to farm machinery passing quickly along tramlines spraying with the aid of a boom or hopper.

The higher the level of spring farming activity in a crop the higher the incidence of infertility/embryo death in eggs. What could explain this association between spring farming activity and infertility/embryo death? A possible reason is that insufficient nutrients are available for egg formation. A lack of calcium, for example, would decrease the quality of the eggshell. Shells which are too thin may lead to the death of the embryo

(Perrins 1996 and references therein). For such a factor to operate females in field types with high rates of infertility/embryo death would have to have been obtaining food for egg production in poorer foraging habitats than other females. This seems unlikely as egg size did not differ between sown and unsown habitats and the risk of infertility/embryo death was the same for clutches in RSA and autumn and winter sown fields. Furthermore, it is difficult to imagine vegetable field nesting females (where infertility/embryo death rates were highest) having more inadequate food resources prior to egg laying than females nesting in combinable crop fields as these crop categories share the same phenology.

Another putative reason is that farming activity disturbs incubating birds sufficiently to cause embryo death in unattended eggs. The rate at which an egg loses water and cools is a function of egg size. As egg size increases, the surface area : volume ratio decreases, meaning that larger eggs retain heat better and lose proportionately less water through evaporation (Drent 1970) and at a relatively lower rate (Carey *et al.* 1983). If a parent has to be away from a nest, larger eggs will cool and lose water more slowly than smaller ones. Too much cooling or water loss may lead to embryo death (Perrins 1996). Beser and Helden-Sarnowski (1982) found hatching success decreased in lapwing eggs which had become desiccated due to exposure to strong sunlight. In the current study, unhatched eggs that didn't contain developed chicks have been labelled as either infertile or embryo deaths because of the difficulty in distinguishing between these two causes of failure. It is possible, however, that such failures were largely the result of embryo death (as opposed to infertility) as the smallest eggs were in 'spring sown' replacement clutches in 1996 (see 5.2.2) where the highest rates of embryo death occurred. Additionally, the rate of cooling of unattended eggs may be affected by the ambient temperature. The cooler the weather, the faster the eggs cool with less time needed for embryo death. All embryo death in spring crop replacement clutches in 1996 occurred in clutches with first egg dates in May. Similarly in 1997, 80% of replacement clutches where embryo death occurred had first egg dates in May. Higher rates of embryo death in spring crops in 1996 might be due to May being much colder in 1996 than in 1997.

Further evidence for this may come from the comparison of those nests avoided by farmers and replacement clutches on spring sown land in 1996. Embryo death (and/or sterility) was a major cause of difference in hatching success between these two nest categories even though the nests were in the same fields. Eggs in avoided nests, where hatching success was higher, were, however, larger as well as being at a further incubation stage than the replacement clutches. Kania (1992) found that desertion rates of disturbed nests decreased with the age of the nest. It is, perhaps, also possible that parents of older nests return more quickly to their nests after a disturbance event, thereby decreasing the chance of embryo death in cold weather.

Galbraith (1988b) found that cultivation activities decreased breeding productivity by causing fewer eggs to be laid in replacement clutches with the consequent reduction in brood size at hatching. In this study, most replacement clutches were on spring sown land. Spring farming operations could not have reduced breeding productivity by affecting egg production as there was no difference in the size of first and replacement clutches. Baines (1989) studying lapwing on arable land also found no difference in the size of first and replacement clutches. The difference between the findings of this study and Galbraiths' may again be associated with crop phenology. Galbraith suggested that smaller replacement clutches were the result of incomplete first clutches being destroyed by spring cultivations (completed by mid-April) with females laying the remaining eggs in a new scrape. Klomp (1951) had reported a similar situation with lapwings breeding on spring sown land in the Netherlands. In this study later spring farming (particularly for 'vegetable' cropping) meant that spring cultivation activities destroyed completed clutches in unsown fields. Unsuccessful females were then able to acquire sufficient food to enable them to lay a replacement clutch with a similar number of eggs to their initial effort. Even though the number of eggs in replacement clutches were not diminished, spring cultivation could still reduce the brood size at hatching in re-lays due to a high incidence of embryo death/sterility.

Taking second clutches into account, at least 76% of female lapwing in this study hatched a clutch. It is possible, however, that the proportion of replacements was even higher with, perhaps, 91% of all females hatching a clutch. Nevertheless, overall the proportion of females that hatched a clutch was high indicating that nesting success was not a limiting factor for the lapwing population in this area.

Not only was nesting success high but the mean clutch size in the Altcar study area was amongst the highest reported in Europe (Table 4.3b).

Table 4.3b Summary of mean clutch sizes reported from European lapwing studies.

Locality (and habitat, if known)	**Clutch**	**Mean clutch size (n)**	**Source**
The Netherlands	First & replacement	3.88 (49)	Klomp 1951
Britain	First & replacement	3.85 (429)	Spencer 1953
Germany	First & replacement	3.69 (89)	Tillmanns 1967
Switzerland	First & replacement	3.85 (558)	Heim 1974
Finland	First & replacement	3.89 (323)	Heim 1974
S. England	First	3.85 (331)	Jackson & Jackson 1980
	Replacement	3.38 (81)	
Denmark	First	3.85 (54)	Ettrup & Bak 1985
	Replacement	3.84 (50)	
N. England (arable)	First	3.74 (53)	Baines 1989
	Replacement	3.71 (21)	
N. England (grass)	First	3.67 (462)	Baines 1989
	Replacement	3.70 (113)	
England & Wales (grass)	First & replacement	3.63 (2269)	Shrubb 1990
England & Wales (arable)	First & replacement	3.78 (844)	Shrubb 1990
Altcar, N. W. England (arable)	First	3.91 (218)	This study
	Replacement	3.86 (137)	

The high mean clutch size of both initial and replacement clutches together with the high nesting success indicates that the nesting stage of the breeding period would not have limited lapwing productivity below a population maintenance level on Altcar.

iii. Predation

It might be expected that lapwings avoid nesting in habitats where clutches experience high levels of predation preferring those where the predation risk is lower. In this study lapwings preferred to nest on spring farmed land and RSA where predation was low avoiding winter farmed cereals and silage where the predation risk was much higher. Other British studies have also found predation rates lower on arable than on grassland (*e.g.* Galbraith 1988b, Baines 1990 and Shrubb 1990). Nest predation in this study was found to be amongst the lowest of recent studies (Table 4.3c). The low levels of predation experienced by lapwing nesting on Altcar contributed to a high nesting success.

Table 4.3c Proportion (%) of nests depredated in studies of lapwing breeding on arable land.

Study	**% Nests predated**
Galbraith (1988b)	59.3
Baines (1990)	24.6
Shrubb (1990)	9.0
Blomqvist & Johansson (1995)*	19.5
Sheldon *et al.* (in litt)	25.5
Berg *et al.* (1992)**	7.2
This study	4.3

* Only data for first clutches available.

** Represent all habitats, grassland and fallow as well as arable.

As the relative importance of predation differs between grass and tilled land nesting substrate might be a factor in influencing predation rates. Klomp (1954) proposed that nest crypticity might be important in lapwing nest site choice. An unvegetated substrate could confer protection from predators by providing camouflaged concealment of unattended eggs and incubating adults. In this study lapwings preferred to nest in spring farmed land and RSA, choosing nest sites in unsown or uncultivated fields. These fields were predominantly bare when nesting commenced. This nest site choice is in agreement with the findings of Imboden (1970, 1971), Shrubb and Lack (1991) and Berg *et al* (1992) who all found a preference for nesting on spring tilled land rather than grassland. In Galbraith's study (1989b), although the preference for lapwings to nest in spring over autumn cereals was not statistically significant, most nests were in spring cereal fields. Galbraith found that incubating adults and their clutches were very difficult to locate against the bare, brown earth of spring cereal fields prior to crop emergence whereas incubating birds in autumn sown cereal and pasture were more conspicuous. Galbraith suggested that his difficulty in locating such nests would be shared by any visually hunting predator. Similarly in this study incubating adults and their eggs were much harder to see on the black (peaty) soil of RSA, unsown or recently sown spring tillage than they were in winter farmed fields or silage where a green sward had already emerged.

In contrast, Blomqvist and Johansson (1995) found no difference in lapwing nest site selection between tilled fields and pastures. They concluded that as the predation rate did not differ between the two habitats, nest predation was unlikely to influence nest site choice between arable fields and pastures. In their study in south-western Sweden 30% of nests failed with only 6% of arable nest losses attributable to farming operations. As 96.4% of arable nests were in spring cereals, cultivation activities must have finished before most laying started. It would follow that many of their nests were in fields where cereals had emerged. A young, established cereal crop may not differ significantly in appearance from pasture, *i.e.* both types of field share a dense, green sward. This might decrease the crypticity and anti-predatory advantage that bare earth or a heterogeneous substrate confers to lapwing nests. If the main predators in their study area were mammals (rather than birds) and relied upon olfactory rather than visual cues to locate food or incidental encounters with nests then differences in appearance between cereal and pasture fields may not be important.

The results of the present study indicate that egg predation within the study site may not have been primarily due to birds (or, at least corvids) but to mammals. Most egg loss was through the predation of whole clutches with no trace of egg remains. Green *et al* (1987) showed that the numbers of depredated wader nests at which there were no remains was associated with sites where mammals were the main predators. The relative influence of mammalian and avian predators might have varied, however, over the course of the nesting season (see below). In this study, lapwings preferred to nest distantly from ditches (which provided mammalian cover) where clutches suffered less predation. Also the predation risk to lapwing nests in this study did not increase with proximity to avian predator perches. This might have been the result of avoiding nesting close to trees (*i.e.* there were very few nests within 50m and a large mean distance to trees for all nests). Lapwings nesting far from trees might have been influenced by breeding adults avoiding field boundary ditches where perches for birds were also located. Another possible explanation is related to the open nature of the landscape where individual trees or small groups of trees/bushes occurred at very low density (Figure 3.1b(iii)). Excluding the two blocks of woodland, there was 1 tree or tree/bush clump for every 27 ha of the cropped area. It was, therefore, easy for lapwings to nest distantly from predator vantage points and also, perhaps, difficult for corvids to reach and utilise so few, isolated perches when such trees were surrounded by breeding lapwings. Whilst with eggs and small young lapwing are highly aggressive towards corvids and mob such potential predators until clear of nesting aggregations (Cramp and Simmons 1980; personal observation). With so few potential nesting sites for corvids it would have also been easy for gamekeepers to observe and, if they wished, destroy corvid nests. No corvid nests were found in field boundary trees or bushes during the study. The risk of predation to lapwing clutches is decreased the further the distance corvids breed from lapwing nests. Carrion crows should feed as close to their nests as possible to reduce the energy costs of foraging (Loman and Goransson 1978). Corvid density in the study area was low due to active control by gamekeepers and because corvid breeding success is lower in arable farmland than in other habitats (Gregory and Marchant 1996).

In this study lapwing breeding density was a more important factor in relation to predation rate than size of nesting group which is similar to the findings of Berg *et al* (1992) in Sweden. In contrast to that study, however, the anti-predatory effect was as effective with one as with more than five close neighbours. Berg *et al* (1992) found that 90% of the variation in mean predation risk to lapwing nests was explained by the number of nests within 100m. Galbraith (1988b and 1988d) found no evidence, however, for density dependence in hatching success for lapwings breeding on arable land and Elliot (1985a) found that the rate of predation for lapwing clutches was similar at all nesting densities. The difference between this study and that of Berg and his colleagues may be due to the type of predator taking lapwing eggs. In the Swedish study birds (particularly crows) were identified as the main nest predators. Higher densities of corvids may have existed at their site as the agriculture was more mixed (25% pasture) and the landscape was less open and more forested. In addition, there was no predator control (A. Berg, *pers. comm.*). Foxes were rare or absent due to the effect of mange in the region. Furthermore, nests are predated in proportion to the relative abundance of predators (Angelstam 1986).

Changes in the seasonal abundance of nest predators may account for the higher rate of predation early in the season. There was a large increase in predator control on the study site with the commencement of grey partridge nesting. Grey partridge stocks on the Estate were dependent on recruitment from the wild population whereas pheasant numbers relied on the buying and rearing of poults. It was important, therefore, for gamekeepers to reduce predation levels on their breeding grey partridge, especially as predator control (particularly of corvids and foxes) has been shown to be very effective at increasing population levels (Tapper *et al.* 1991, 1996). Grey partridge begin to nest at the end of April (Cramp and Simmons 1983, J. Bell[8], *pers. comm.*) and it was mainly

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[8] Mr J. Bell, the headkeeper on Altcar Estate at the time of the study, actively searched for grey partridge nests.

before this date that most lapwing nest predation occurred. The lower, late season predation rates observed in this study could, therefore, have been due to lower nest predator densities which resulted from higher levels of predator control.

5.0 Egg size, chick growth and survival

In this chapter the influence of the chick stage on the productivity of the Altcar lapwing population is examined. Galbraith (1988a) showed that on Scottish farmland lapwing chick size, mass and survival were all influenced by egg size. The survival pattern of chicks reared on arable land on Galbraith's study site, however, was largely influenced by anthropogenic factors (Galbraith 1988b, 1988c). To assess the extent of such factors on chick survival in this study the relationship between chick growth and survival and egg size needed to be established. Environmental factors influencing egg size and chick development and survival were examined to determine their effect, if any, on chick production.

5.1 Methods

5.1.1 Egg size

Egg volumes were calculated for most clutches found by measuring the length and breadth of each egg using dial callipers (to an accuracy of 0.1mm). These measurements were taken on eggs in completed clutches only, allowing the calculation of the mean egg volume of each measured clutch. Egg volumes (V) were expressed as ml and calculated using the formula: $V = K \times L \times B^2$. Where L = egg length, B = egg breadth (at maximum diameter), K = a species specific volume constant (a function of egg shape) (Hoyt 1979). In this study, 0.457 was used as an estimate of K which had been obtained from British lapwing eggs (Galbraith 1988a; Blomqvist and Johansson 1995).

Mean egg volumes were normally distributed (Ryan-Joiner *W*-test for normality:1996; $r = 0.990$, ns, n = 123 clutches; 1997; $r = 0.995$, ns, n = 148 clutches) allowing the use of parametric tests to investigate differences in egg size.

5.1.2 Chick survival and fledging success

An increased frequency of visits to nests at the end of the incubation period allowed neonates (chicks <24 hours old) to be ringed, weighed and measured (see 5.1.3). Chicks were found (mostly) in or very close to nests. Hatching was not always entirely synchronous in a clutch and on a few occasions chicks with dried down were found in nests with eggs that were still hatching. In these instances, a return visit was made to process any previously unhatched chicks. Each chick was fitted with an aluminium B.T.O ring (which allowed individual identification) in addition to a brood specific colour ring combination. Up to four plain coloured (overlapping) plastic rings (obtained from A.C. Hughes Ltd.) were fitted with a maximum of two per leg. The use of both metal and plastic rings was done under permit from the B.T.O (permit class and no. S/C/4575) with the colour-marking combination given by and registered with the Wader Study Group Colour-Marking Register. Only brood identifiable chicks were used in the investigation of chick mortality and fledging success.

Survival of chicks in study broods was monitored every 1-3 days from a vehicle with brood identification achieved using 8x30 binoculars or a 20-40× telescope. To ensure the accuracy of brood size counts when broods became older and chicks ranged further from parents (after an age of 8 days), a check was made by repeating counts until no discrepancy between counts occurred. Broods of chicks were observed until they died or fledged (over the age of 35 days; Cramp and Simmons 1983, Baines 1989; personal observation). All members of a brood were considered to have died if it disappeared from its usual rearing field and could not be relocated in any neighbouring, potential rearing field (*i.e.* fields without tall and dense crops were considered to be used for chick rearing). The locations of all potential brood rearing fields were known as they had been identified in field use surveys and were also searched over for nests. Frequent searches of suitable habitat on land peripheral to the study area were also made. Brood survival is expressed as the proportion of hatched chicks surviving until fledging, including broods from which no chicks fledged. Broods were reared on spring farmed land, RSA or pasture. The investigation of chick mortality from brood counts did not include broods that were reared in fields where, due to crop growth restricting visibility, brood identification and chick counting became too difficult.

To examine the relationship between chick survival/growth and weather daily temperature and rainfall data were obtained for 1996 and 1997.

5.1.3 Chick growth and condition

Growth rates were investigated by taking measurements of ringed nestlings (*i.e.* neonates) and by the subsequent recapture (by hand) of chicks by the author. In the nest each chick was weighed to the nearest 0.5*g* (using a 'Pesola' spring balance) and the length of head-plus-bill and tarsus length were measured to the nearest 0.1*mm*. The head-plus-bill (H+B) length was the maximum measurement from bill tip to the back of the skull. Tarsal measurements were taken from the notch on the back of the intertarsal joint to the lower edge of the last complete scale before the toes diverged. Ninth primary length of the right wing was measured once present. Linear measurements were taken with dial callipers. Chicks over 50*g* were weighed to the nearest 1*g* (using a 'Pesola' spring balance).

In a U.K. study of farmland breeding lapwing Galbraith (1988c) found that head-plus-bill length was the most accurate predictor of age during the linear phase of growth which lasts until about the 22nd day. Once growth slows Galbraith found that ninth primary length most accurately estimated age. In this study a few young chicks were captured that had not previously been ringed as nestlings. Unringed chicks ages were estimated from the following regression equation (after Galbraith 1988c);

(i) days from hatching = $1.05 \times$ H+B length (mm) $- 33.74$ (to the nearest 0.7 days).

Compared with foot, wing and bill length Galbraith also showed that H+B length was the most precise body measurement for investigating lapwing chick growth. Chick growth rates were compared, therefore, using mass and H+B lengths with the quotient (mass/H+B length) used as an index of body condition. All biometrics were taken by the same person (the author) with handling and measuring practice following Svensson (1984) and the B.T.O (Spencer 1984).

When broods are young and small, chicks stay close to parents and are frequently brooded by them. In addition young chicks tend to crouch and freeze during disturbance or when given alarm signals by parents. Such behaviour makes preliminary recapture comparatively easy. Older chicks are more difficult to catch as they are more mobile and often run from disturbance. The number of recaptures (by hand) may have been insufficient to assess chick growth and also the method did not allow chicks to be caught at targeted ages. Radio transmitters were, therefore, attached to some chicks allowing easy and age targeted recapture. Radio-marked chicks were recaptured for biometrics every two to four days until they died or fledged.

5.1.4 Radio-marking

Radio transmitters were attached to chicks in 1995, 1996 and 1997 to investigate survival and mortality. In addition, radio-marking chicks provided the only definite means by which chicks could be repeatedly recaptured. The technique, therefore, also aided the chick growth studies. In 1995 single-stage radio transmitters were used. In 1996 and 1997, the transmitters used were crystal controlled two-stage designs pulsed by a multi-vibrator. Table 5.1.4a gives details of radio transmitter dimensions and their battery life. The smallest transmitters used in 1997 were not available in previous years. Smaller tags were lighter and decreased the loading on newly hatched chicks. The reduction in size, however, was at the expense of battery life. Larger tags were also used so that if chicks survived they could be followed through to fledging at 35 + days old. Both tag models used in 1997, however, were considered of an appropriate size and weight for marking neonates (see below). A hand-held Yagi 'H' antenna was used (supplied by Biotrack Ltd.) in conjunction with a R2100 receiver (obtained from Advanced Telemetry Systems, Inc., MN, USA) with a frequency setting of between 173.000 and 174.999 MHz. Each transmitter was tuned to a different frequency within the receiver range. Licence and registration from English Nature (EN) and the B.T.O were obtained to permit radio-marking of chicks (EN licence reference no. SRB:6:95; BTO permit class and no. S/C/4575).

Table 5.1.4a Details of radio transmitters used on lapwing chicks 1995 – 1997.

Year	Weight (g)	Battery life (days)	Dimensions (mm)[a]	Supplier
1995	0.85-0.92	13-16	20x15	Biotrack Ltd., Wareham, Dorset, U.K.
1996	0.65-0.70	21-24	6x4	Holohil Systems Ltd., Ontario, Canada
1997	0.45-0.52	14-18	5x3	Holohil Systems Ltd., Ontario, Canada
	0.67-0.72	24-28	6x4	Holohil Systems Ltd., Ontario, Canada

[a] represents length by breadth. Due to the mounts, the radio packages attached to chicks were slightly larger than transmitter specifications (see text).

To enable radio attachment to chicks the transmitter body was sown to an oval piece of cotton gauze (muslin). Each piece of muslin was 30-40% larger (in length and breadth) than the transmitter body. Mounting added 0.1-0.3g to the transmitter weight. The radio and mount was attached to a central position on the back of the chick with cyanoacrilate adhesive (Loctite Superglue 3). The attachment area was first swabbed with acetone. The glued radio and mount was allowed to dry in position (which took less than 30 seconds) before permitting the chick to move. This method of adhesion was considered suitable as it has been found not to cause any damage or abnormality to the skin or feathers in the tag attachment area in other bird species. For example, Tyler *et al.* (1996) examining Corncrake (*Crex crex*) one year after tag attachment found their synsacrum to be healthy. In addition, attaching radios by other conventional methods, such as body harness, neck collar or tail mount (Kenward 1987), would have been inappropriate or impossible for small and growing chicks. The operation of radio-marking chicks (including ringing and taking biometrics) lasted approximately 5 minutes per chick.

Chicks which out-lived the battery life of their transmitter had a new tag attached. As mounts became loose (unattached from skin) with age this involved cutting off the old mount where it remained attached to down or feathers and affixing a new radio and mount following the same procedure as above. Few chicks, however, radio-marked under five days old and fitted with the smallest radio-transmitters lived long enough to need new tags. During the study period only 2 chicks (out of 74) required replacement radios. If radios became too loose there was a possibility that they may have interfered with the chicks normal behaviour or make it more visible to predators. Radios were inspected, therefore, with the regular weighing and measuring operations at least every four days to ensure they had not become too loose. The original colour (silver and white) of the transmitter and mount might have made the marked chick more conspicuous to predators. This might have been particularly true for chicks less than about 14 days old as in older chicks growing (green) feathers covered the radio packages. Each radio transmitter and mount was, therefore, camouflaged to prevent or minimize the package increasing a chick's visibility. Muslin mounts were dyed brown or dark green (depending on the age of the chick) and the dorsal surface of the transmitter was painted black and brown or dark green with permanent markers. The 100-150mm stainless steel antennae of transmitters were also rubbed with black permanent marker to remove shine. These procedures were carried out before radio packages were assembled or attached so ink could dry and chick handling time was minimized. The colouring made the radio packages very difficult to see at least for human observers using binoculars or a telescope.

Small adult birds and bats seem able to fly well with packages at 10-15% of their body weight (Graber and Wunderle 1966, Stebbings 1982, 1986), however, as chicks were being marked a 4-6% loading increase was considered more suitable in this study (Brander and Cochran 1971, Cochran 1980, Kenward 1987). As recapturing chicks by hand once they had left the nest was very difficult it was desirable to radio mark hatchlings. Capture of newly hatched chicks was straightforward as hatching dates could be estimated (see 4.1.4) and neonates stayed in the nest for up to 12 hours or more. It has been noted, however, that neonates experience a delay in mass gain for their first 2-3 days when weight loss may occur (Redfern 1983). The degree of weight loss is related to distance of post-hatching movement from natal to rearing areas and quality of feeding locations (Galbraith 1988a, 1988b). Redfern (1983), however, found neonates lost 2.2% of their hatch mass within two days but did not find any significant differences in mean mass of hatchlings and chicks of 1, 2 and 3 days old. In this study, to ensure a 6% load increase was not exceeded by radio attachment, a 10% post-hatching mass reduction was allowed for in neonates. In a Dutch study the mean mass at hatching of 1152 chicks was 17.5g ± 1.9 (Beintema and Visser 1989a). In 1995, therefore, it was considered that the size as well as the weight of the radio packages (see Table 5.1.4a) made them unsuitable for attachment to chicks less than four days old (or less than 20g). The availability of smaller, lighter transmitters in 1996 and 1997 meant that most neonates would have been heavy enough to have radios attached. In fact, the mean mass of nestlings (18.0g ± 1.5, *n* = 588) in this study was slightly heavier than in the Netherlands. Only one chick from a brood of nestlings had a radio attached at any time. The chick selected for radio attachment in a brood of hatchlings was chosen at random being the first chick to be taken out of the ringing bag.

Radio marked chick survival was assessed by obtaining at least two diurnal radio locations per day using triangulation from three to five positions up to 200m from the subject's position. A first fix was taken 1 to 4 hours after sunrise with a second one to four hours before sunset. The field type containing radio-marked chicks at each fix was recorded. If three consecutive fixes indicated an identical location and the chick could not be seen the signal was traced to source to determine if the chick had died.

Proximate causes of mortality were defined as follows:

1. Unmarked chicks that were found dead were defined as dying of poor body condition. Weight prior to death may have indicated poor weight gain. In addition, poor condition may have resulted from disease or injury or a combination of these factors. It was not possible to examine the role of disease but in several instances chicks that died from poor condition were found to have injuries. These injuries may have been

caused by escaping from a predator or by attacks from unrelated adult male lapwings. Such attacks were seen on four occasions (in three years) always occurring whilst parental birds were occupied with mobbing predators. It is likely, however, that low weight chicks were more susceptible to attack or disease.

2. Chicks were predated, either by raptors or mammals or unidentified agent. Raptorial losses were defined as such when any remains found included cleanly severed limbs (indicating the cutting action of a bill). Losses were attributed to mammals when (chewed) remains with tooth marks were found or when the chick had been cached in dense ditch-side vegetation or underground (in rabbit burrows). Complete and sudden signal loss (disappearance) was attributed to predation by unknown agent if it could not be explained by battery drain. Signal loss may have occurred for one of several reasons. It could be that the radio-marked chick had been taken out of the study area by a successful predator. Such a movement by a successful raptor was especially likely due to the dearth of trees or other perches within the study area. Signal loss may also have occurred due to a predator destroying the radio during or as a result of capture. Technical failure of the radio may also have caused signal loss. Radio failure, however, can be identified as such as it is usually indicated prior to signal loss by irregular signals. In those cases where normal signals were received up until 'disappearance' it was considered that the most likely cause of signal loss was depredation of radio-marked chicks. A similar situation was found in a study of radio-marked curlew chicks (Grant *et al.* 1999). Signal loss depredation, however, is marked as such in the analysis as it was often the case that visual contact could not be made with the radio-marked chick making it impossible to determine the exact cause of loss. It is also possible that signal loss may have occurred as a result of a radio marked chick moving away from its normal locality. Increasingly widening searches from the chick's previous radio location, however, would have revealed such cases. This is especially true as the frequency of fixes meant that the chick would not have had time to travel far since its last known location.

3. Chicks found dead in ditches were considered to have died from becoming entrapped. Chicks may have entered ditches during movements from one field to another, to feed or to seek cover from disturbance. Once in the ditch the chick presumably could not exit due to the ditches' physical dimensions. Chicks were thought to have died from exhaustion resulting from continual attempts to escape entrapment. Young chicks may also have become chilled as parents were, perhaps, less likely to brood them in such narrow and confined spaces. Chilling may have been a particularly important factor when ditches contained water and/or siblings had managed to climb out and averted parental attention from any remaining trapped offspring.

Loss of contact with radio-marked chicks also resulted from radio packages being shed. This may have been caused by improper adhesion of the mount to the back of the chick causing the package to fall off or allowing the chick to preen the radio off. It was considered highly unlikely that this was a result of predation when there was no evidence of force (*i.e.* feathers underneath the mount were not cut and feathers attached to the mount did not appear to have been pulled out of the skin) or damage to the transmitter. Shed tags were also found in the normal range of the chick and it would seem unlikely that predators would have removed only the tags, especially considering the anti-predatory behaviour of adult lapwing. In addition, loss of signal at the end of the given period of life expectancy of the radio battery was defined as battery drain.

Mortality rates for chicks were calculated using Mayfield's formula (1961, 1975) with standard errors and statistical tests taken from Johnson (1979) and Henslor and Nichols (1981) (see 4.1.5 for calculation of P (daily survival/mortality rate) and its standard error). The fledging period from hatching was taken as 35 days (see 5.1.2), thus fledging success is expressed as P^{35} ($P^{35} \times 100$).

5.2 Results

5.2.1 Egg size variation

Two causes of egg size variation are differences between clutches or females and variation within clutches. An additional source of variation in egg size may derive from differences between first and replacement clutches produced by the same female. To establish whether the main component of variation in egg volume was attributable to differences between clutches (females) or within clutches, a Model II one-way analysis of variance (Sokal & Rohlf 1981) was performed on eggs from first clutches. Replacement clutches were omitted from analysis to eliminate that source of variation.

Table 5.2.1a Variability in egg volumes of lapwings breeding in an area of intensive agriculture; the relative importance of between and within clutch variation in first clutches.

		% of total variation	
1996	Between clutches Within clutches	71.9 28.1	$F_{73,212} = 7.44$, $P < 0.001$
1997	Between clutches Within clutches	67.8 32.2	$F_{88,265} = 6.35$, $P < 0.001$

Variation between females was the main component of variation in egg volumes, accounting for 68-72% of the variation (Table 5.2.1a). Correspondingly, there was little variation in egg size within clutches in both years. This result validates the use of the mean egg volume parameter in further analysis.

5.2.2 Factors influencing egg size

i. Between years and first and replacement clutches.

There was no between year difference in the egg volumes of first clutches or replacement clutches (first clutches: $t = 0.05$, $P>0.1$, d.f. = 160; replacements: $t = 1.93$, $P>0.05$, d.f. = 82). First clutches were slightly larger than replacement clutches in both years, although this difference was significant only in 1996 (Table 5.2.2a).

Table 5.2.2a Volumes of lapwing eggs (ml) in 1996 and 1997. n = number of clutches measured.

	1996			**1997**		
	n	**mean**	**se**	**n**	**mean**	**se**
First clutches	74	23.80	0.14	99	23.79	0.13
Replacement clutches	40	22.93	0.22	45	23.56	0.24
t-test between clutches	$t = 3.33$; $P<0.01$; d.f.=72			$t = 0.84$; $P>0.1$; d.f.=69		

ii. Habitat.

There was no significant difference in mean egg volumes of first clutches between habitats (Table 5.2.2b). This suggests that females were obtaining food to build up reserves for egg production in the same localities or in sites that did not differ in prey quality or quantity.

Table 5.2.2b Mean egg volumes (ml) of first clutches of lapwings breeding in unsown and sown habitats in intensive lowland farmland (1996 & 1997 combined). n = number of clutches measured.

Habitat	**n**	**mean**	**se**
Sown	94	23.86	0.11
Unsown	77	23.73	0.16
t-test between habitats	$t = 0.69$; $P>0.1$; d.f.=142		

Sown represents nests of winter farmed and spring sown fields;

Unsown includes nests in RSA and unsown spring farmed fields.

iii. Laying date

To test the effect of season on egg size, mean egg volumes were correlated with first egg dates. The first egg dates for each clutch were numbered according to the number of days after the first egg date of the first nest found in each year. In 1996 there was a significant negative correlation for mean egg volumes with first egg dates ($r = -0.227$, d.f. = 121, $P<0.05$). In 1997 the negative correlation was not significant for mean egg volumes and first egg dates ($r = -0.11$, d.f. = 146, $P>0.05$). Mean egg volumes for first and replacement clutches in 1996, however, showed no significant correlation with first egg dates ($r = 0.17$, d.f. = 72, $P>0.05$; $r = 0.11$, d.f. = 38, $P>0.1$; for first and replacement clutches respectively). There was a significant reduction, however, in mean egg volume between first and replacement clutches in 1996 (Table 5.2.2a). This indicates that the apparent seasonal reduction in egg volumes in 1996 is actually due to the higher proportion of replacement clutches.

5.2.3 The relationship between egg volume, hatchling size and chick survival

In both years, the hatchling mass of a brood was highly and positively correlated with the mean egg volume of the corresponding clutch (r = 0.91, $P<0.001$ in 1996; r = 0.72, $P<0.005$ in 1997; Figures 5.2.3a and b). Hatchling head + bill length was also positively and significantly correlated with mean egg volume (r = 0.64, $P<0.005$, n = 18 in 1996; r = 0.56, P = 0.02, n = 17).

Part of the variation in neonate body mass is, therefore, explained by structural size, heavier eggs producing heavier chicks which are also larger. Another component explaining variability in hatchling body mass might be the yolk reserve. Large eggs produce chicks with greater reserves of protein, lipid, carbohydrate and water. Such hatchlings might be expected to have a better chance of survival, particularly in their first few days of life when they have to learn to feed. Chick survival in relation to egg size was investigated by separating clutches into three categories according to their mean egg volumes. The fates of the resulting chicks from each category were compared by Chi-square tests (for association with Yates' correction) on three different fledging periods. These periods were hatching to 10 days old, 10 days old to fledging and from hatching to fledging at 35 days. Chicks had to survive to any part of each period to be included in any particular age category. Three categories of egg volume were examined in order to reduce the possibility of artificially significant results that might have been caused by using only two arbitrarily chosen egg size categories (Table 5.2.3a).

Figure 5.2.3a Relationship between mean mass of lapwing chicks at hatching and mean egg volume of the corresponding clutches, in 1996.

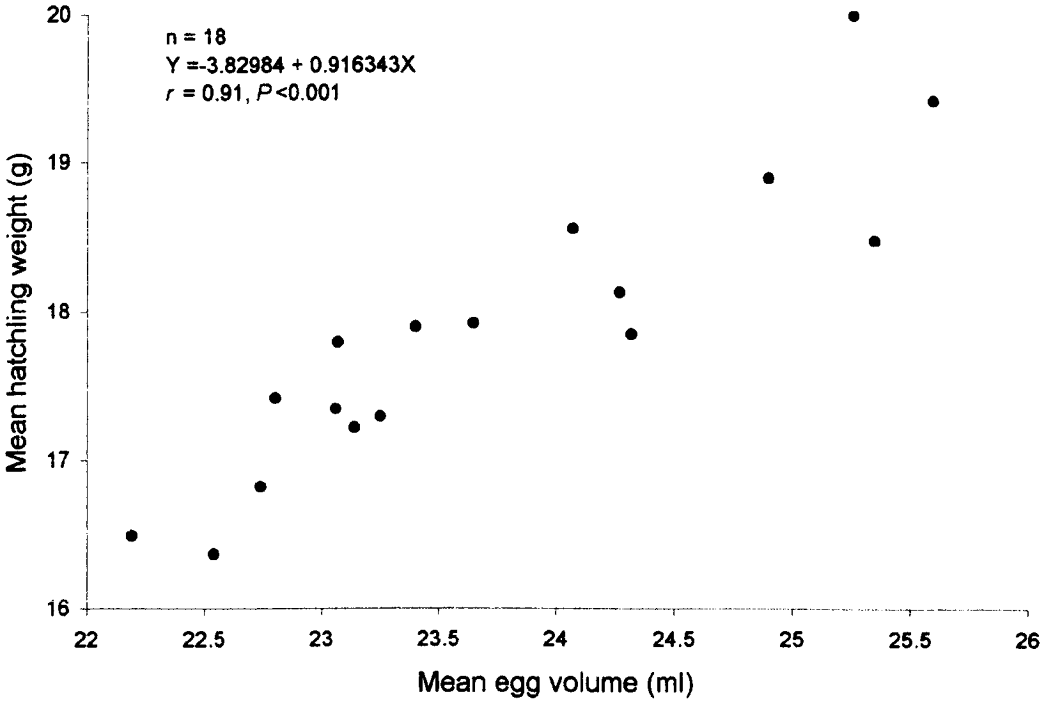


Figure 5.2.3b Relationship between mean mass of lapwing chicks at hatching and mean egg volume of the corresponding clutches, in 1997.

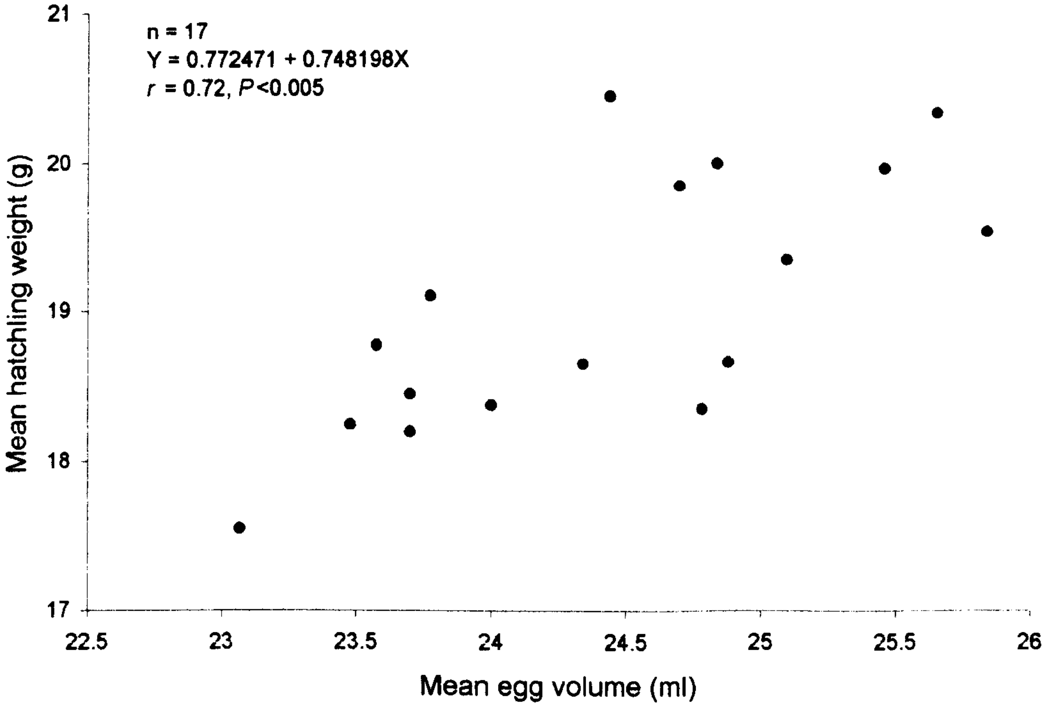


Table 5.2.3a Relationship between lapwing chick survival and mean egg volume for clutches from intensively cultivated farmland. The numbers of chicks which died or survived examined for different stages in the fledging period, categorized according to the mean egg volumes of the clutches from which they hatched. (i) = 1996, (ii) = 1997.

(i)

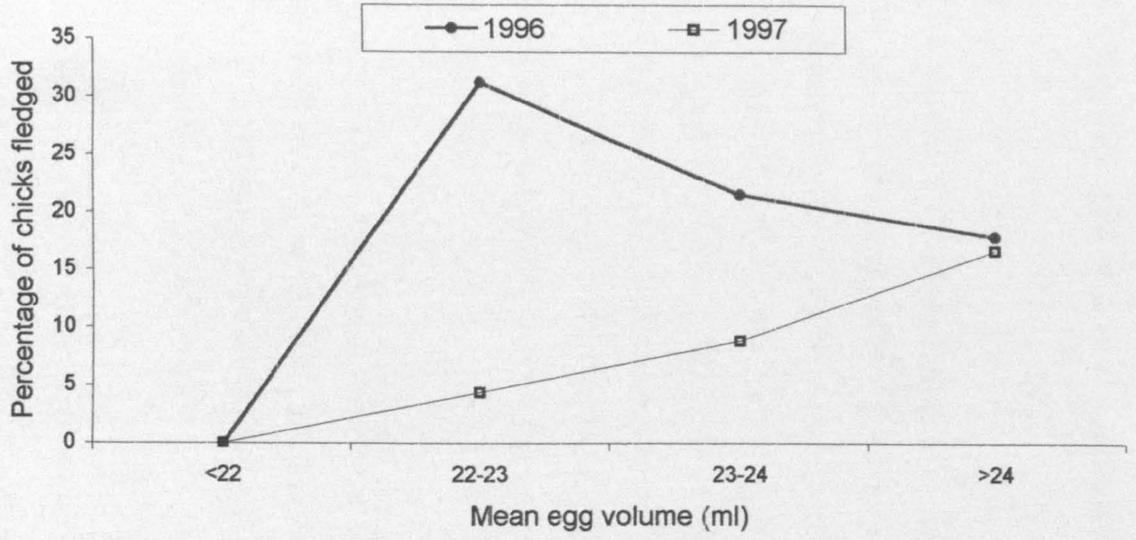
Fledging stage (days)	Mean egg volume categories (ml)					
0 - 10	<23.0>		<23.5>		<24.0>	
Died	18	76	37	57	47	47
Survived	4	26	11	19	16	14
	$X^2 = 0.172$, ns		$X^2 = 0.125$, ns		$X^2 = 0.15$, ns	
0 - 35						
Died	19	81	39	61	50	50
Survived	3	21	9	15	13	11
	$X^2 = 0.84$, ns		$X^2 = 0.084$, ns		$X^2 = 0.189$, ns	
10 - 35						
Died	1	5	2	4	3	3
Survived	3	21	9	15	13	11
	$X^2 = 0.36$, ns		$X^2 = 0.29$, ns		$X^2 = 0.24$, ns	

(ii)

Fledging stage (days)	Mean egg volume categories (ml)					
0 - 10	<23.0>		<23.5>		<24.0>	
Died	36	118	64	90	89	65
Survived	3	44	10	37	16	31
	$X^2 = 7.06$, $P<0.01$		$X^2 = 6.53$, $P<0.05$		$X^2 = 8.15$, $P<0.01$	
0 - 35						
Died	38	141	69	110	98	81
Survived	1	21	5	17	7	15
	$X^2 = 4.08$, $P<0.05$		$X^2 = 2.25$, ns		$X^2 = 4.16$, $P<0.05$	
10 - 35						
Died	2	23	5	20	9	16
Survived	1	21	5	17	7	15
	$X^2 = 0.62$, ns		$X^2 = 0.17$, ns		$X^2 = 0.19$, ns	

There was no relationship between the survival of chicks and egg size in 1996. In 1997 significantly better survival to fledging was exhibited by chicks hatching from larger eggs (Figure 5.2.3c, Table 5.2.3a). These results indicate that in 1996 chick mortality independent of egg size or hatchling mass, whereas, in 1997 increasing egg size

Figure 5.2.3c Fledging success of lapwings on intensively cultivated farmland in relation to the mean egg volumes of the clutches from which they hatched.



The number of chicks hatched for each egg volume category was as follows;
1996: <22 = 10, 22-23 = 16, 23-24 = 37, >24 = 61;
1997: <22 = 12, 22-23 = 45, 23-24 = 56, >24 = 88.

increased fledging success by enhancing chick survival in the first 10 days. After 10 days, egg size did not significantly affect survival.

5.2.4 Environmental factors affecting chick survival

i. Rearing field type and brood movements

Field use by broods differed between years (Figures 5.2.4a and 5.2.4b). In 1996 broods hatched in winter farmed and RSA fields moved quickly into spring cultivated and permanent pasture fields. Similar proportions of broods were reared in spring cultivated and pasture fields (Figure 5.2.4a). In 1997 broods behaved similarly in moving out of winter farmed and RSA fields but fewer chicks were reared in pasture and a larger proportion remained in their natal spring sown fields (Figure 5.2.4b). Although there was a similar proportion of nests in winter farmed fields in each year, significantly fewer nests hatched in winter crops in 1997 due to destruction from different timing of farm operations (4.2.3. ii.).

The proximity of pasture to nests significantly benefited survival with 14 (or 28%) of 50 chicks hatched from clutches in fields adjacent to pasture fledging, although only 33 (or 12%) of 275 chicks fledged from clutches that were more distant (*i.e.* had to cross at least one field) to pasture ($\chi^2_1 = 8.14$, $P<0.01$).

Of those broods using spring farmed land there was also a between year difference in the types of crop used. In 1996 chicks reared on spring cultivated land used cereal fields with most remaining until fledging (Figure 5.2.4c). Late sowing in 1996 delayed crop growth which allowed spring cereals to be used for chick rearing. However, some chicks moved into vegetable fields towards the end of the fledging period as cereal density and height increased. Earlier sowing in 1997 meant cereal fields were unsuitable earlier causing

Figure 5.2.4a Field types used by lapwing broods in intensively cultivated farmland in 1996

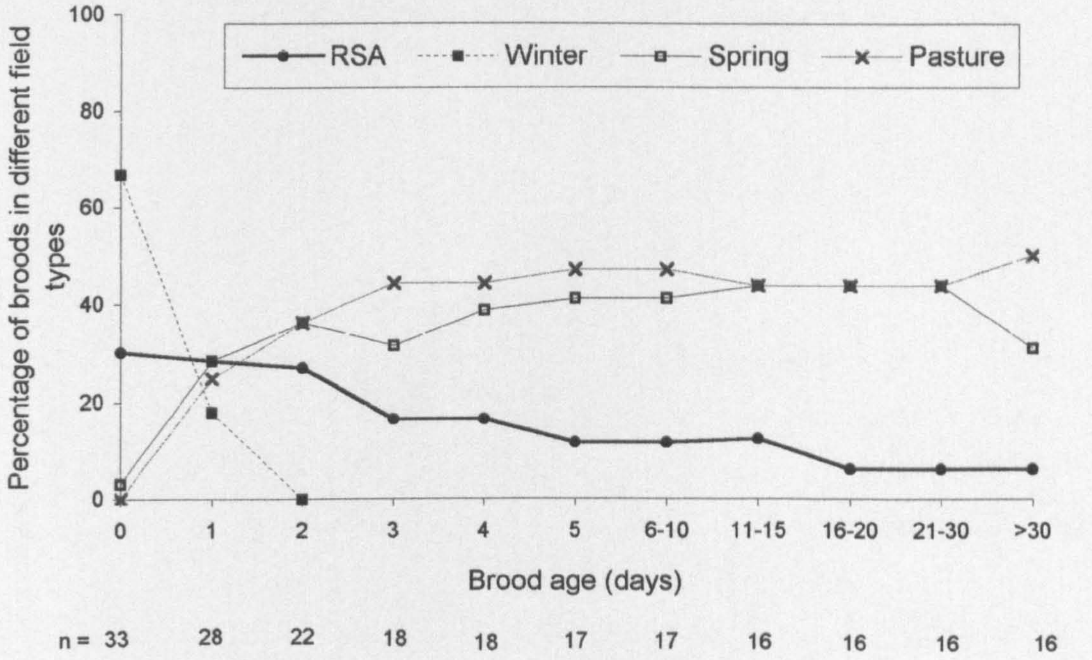


Figure 5.2.4b Field types used by lapwing broods in intensively cultivated farmland in 1997.

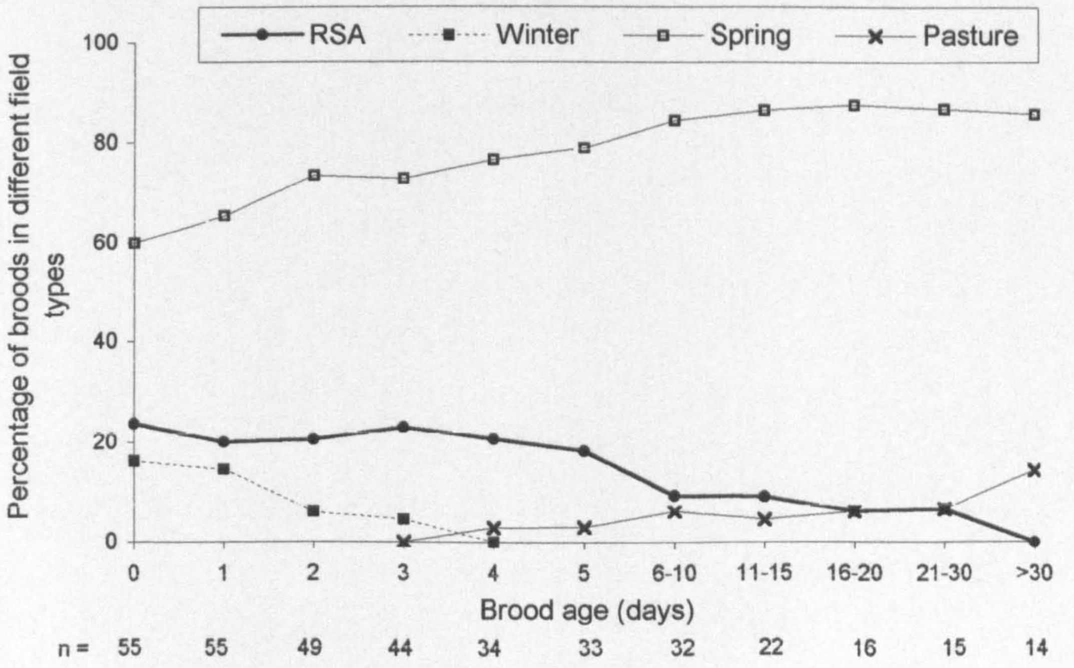


Figure 5.2.4c Proportions of lapwing broods reared on intensive spring farmed land using cereal or vegetable fields

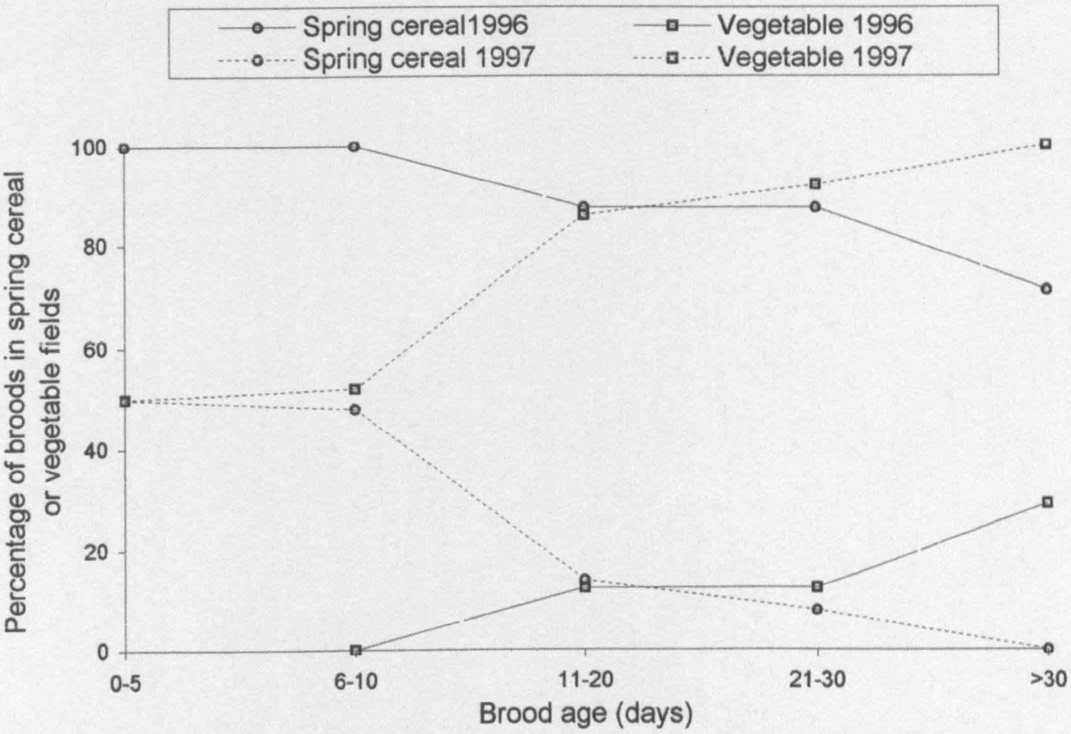
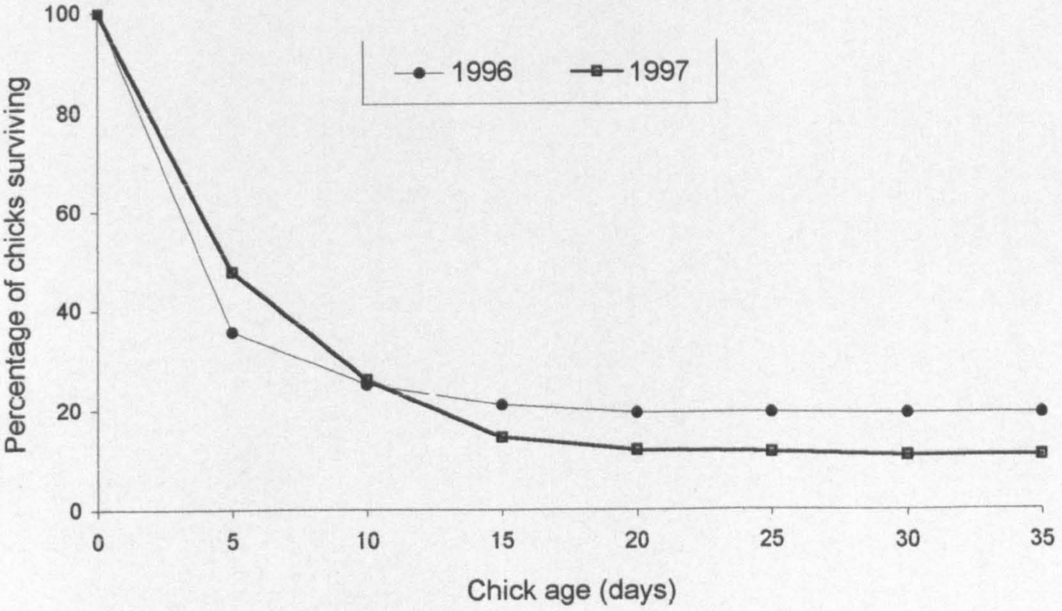


Figure 5.2.4d The survival of lapwing chicks in intensively cultivated farmland.



Initial sample sizes were 124 (1996) and 201 (1997) chicks to leave and move into vegetable fields from their second week with all 'spring farmed' chicks fledging in vegetable crops.

The between year differences in brood movements influenced the mortality patterns of chicks, although the survival rates of chicks increased with age in both years (Figure 5.2.4d; Table 5.2.4a).

Table 5.2.4a The mortality rate (percentage of chicks dying/day) for stages in the fledging period of lapwing chicks reared in intensively cultivated farmland. *n* = the number of chicks alive at the beginning of each period

	1996		1997	
Age (days)	*n*	%	*n*	%
0-4	124	12.9	201	10.5
5-9	44	5.9	96	9.2
10-14	31	3.2	52	8.8
15-19	26	1.5	29	3.5
20-24	24	0	24	0.83
25-30	24	0	23	0.87
30-35	24	0	22	0.9

The most severe mortality occurred immediately post-hatching in both years. However, in 1997 a significantly higher proportion of chicks survived to four days old than in 1996 (28% and 35.5% respectively; $\chi^2_1 = 4.71$, $P<0.05$). There was no significant between year difference in the proportions of chicks surviving between 5 and 9 days old ($\chi^2_1 = 3.32$, $P>0.05$). Chick survival was significantly higher in 1996 between the age of 10 days and fledging at 35 days at 77.4% than in 1997 when it was 42.3% ($\chi^2_1 = 9.69$, $P<0.01$). From 0 to 35 days old fledging success was significantly higher in 1996 with 19.4% surviving to this age, whereas in 1997 only 11% of chicks survived to fledge ($\chi^2_1 = 4.46$, $P<0.05$). Expressed in terms of productivity (mean number of chicks fledged) per pair, this was 0.72 (24/33) in 1996 and 0.40 (22/55) in 1997. This difference between years was not only attributable to more chicks being reared on pasture in 1996 as survival in the 10-35 day fledging stage for chicks reared in crops (*i.e.* excluding pasture reared broods) was significantly higher in 1996 than in 1997 ($\chi^2_1 = 5.15$, $P<0.05$). The differences in survival and production between the two years was, therefore, caused by the lower rate of survival of the 10-35 day age class in 1997. Chick survival would, therefore, appear to be partly related to brood movements. In 1996, the greater mortality in the 0-4 day fledging stage was associated with brood movements out of natal fields and into pasture or spring cereals. In 1997, chick survival in their first few days was greater as broods remained, initially in their natal fields. More advanced crop growth in 1997 caused broods to seek more suitable rearing locations after about their tenth day. Again this period was associated with increased mortality.

ii. Field boundaries - ditch entrapment

Broods that had to move might have suffered higher mortality for several reasons. Brood movements could have been associated with a decrease in body condition resulting from less time spent feeding, a decrease in prey availability due to traversing poor quality feeding areas and/or increased energy expenditure. Predation risk might also have been increased and chicks might have encountered physical obstruction or barriers. Physical impediment to chick movement in the study area may have been provided by the ditches that formed many of the field boundaries (Plate III). Whether ditch boundaries had an effect on chick survival was investigated by chi-square tests of association comparing the proportions of fledged chicks from broods categorized by whether natal fields were separated from the nearest rearing field by a ditch. As broods from clutches in winter crops and RSA moved out of natal fields to be reared, the analysis was carried out on clutches from these field types. Ditches were defined as being >1.0m deep (field surface to water surface or ditch bottom).

Plate III. Field boundary ditch

Table 5.2.4b Fates of recently hatched chicks from winter farmed and RSA fields categorized by whether natal fields were separated from the nearest rearing field by a deep ditch.

	Chicks died	Chicks fledge	Percentage fledging success
1996 Ditch	51	3	5.6
No ditch	44	23	34.3
1997 Ditch	39	4	9.3
No ditch	33	9	21.4

The chance of survival was greater for chicks that did not have to cross a deep ditch in order to access a rearing area from their natal field (Table 5.2.4b). In 1996 the proportion of chicks that fledged that had not encountered a ditch in their post-hatching movement was significantly greater than that of chicks where natal localities were separated from rearing fields by ditches ($X^2_1 = 14.78$, $P<0.001$). The mortality caused by ditch entrapment might be expected to act randomly with respect to hatchling mass. This might explain why in 1996, with more broods undergoing immediate post-hatching movements (see above), there was no relationship between hatchling mass and fledging success (Table 5.2.3a (i)). In 1997 there was no significant difference between the proportions of chicks fledging according to whether ditches separated natal and rearing fields ($X^2_1 = 2.5$, $P>0.05$). This could be explained by the fact that recently hatched broods remained in natal fields.

iii. Weather

Chick mortality was highest in the first few days after hatching (see 5.2.4 and 5.2.7.ii (d)). To examine any effect weather may have had on the immediate post-hatching period, the relationship between the percentages of broods that survived five days after hatching and the mean daily temperature and rainfall for that five day period was investigated. Due to anthropogenic mortality factors (see 5.2.4.ii.) only broods reared in their natal fields or fields adjacent to their natal locations were included in the analysis.

Linear regression on the arcsine transformations of the percentages of broods (from 1996 and 1997) that survived the five days after hatching against the independent variables of mean daily temperature and rainfall for that period did not reveal any significant relationship ($r = 0.01$, $P > 0.1$ for mean daily temperature and $r = -0.23$, $P > 0.1$ for mean daily rainfall; n = 15). The results must be considered with caution as the causes of death of chicks under five days old was not known. Young chicks may have been predated or have become entrapped in field boundary ditches. The exact day of death was also unknown. Also, the structure of vegetation (or lack of it) may influence the micro-climate of brood rearing fields. The risk to a chick of getting wet and becoming chilled increases as vegetation becomes taller and denser. The density of plants and the height of vegetation may also affect the temperature at chick level (*i.e.* below 10cm). The analysis included broods reared in a variety of different stages of vegetation development as it involved hatches occurring between April 16 and June 5. In addition, the analysis is based on a small sample size.

5.2.5. Effect of laying date on chick survival

To investigate any effect that hatch date might have on survival chicks were separated into three categories according to the first egg dates of the clutches from which they hatched and their fates were compared (Table 5.2.5a). As the relationship between egg size and fledging success was only established for chicks hatched in 1997, data from 1996, when anthropogenic factors affected chick survival, were excluded from the analysis.

Table 5.2.5a Fate of lapwing chicks on intensive farmland in 1997 according to the first-egg dates of the clutches from which they hatched.

	First-egg date		
	<16/04	16/04 – 30/04	>01/05
Chicks fledge (%)	17 (14.3)	4 (14.3)	1 (2)
Chicks died (%)	102 (85.7)	24 (85.7)	53 (98)
	$\chi^2_3 = 6.26$, $P<0.05$*		

*Chi-square value calculated by assuming the proportions of chicks dying or fledging were unaffected by laying date.

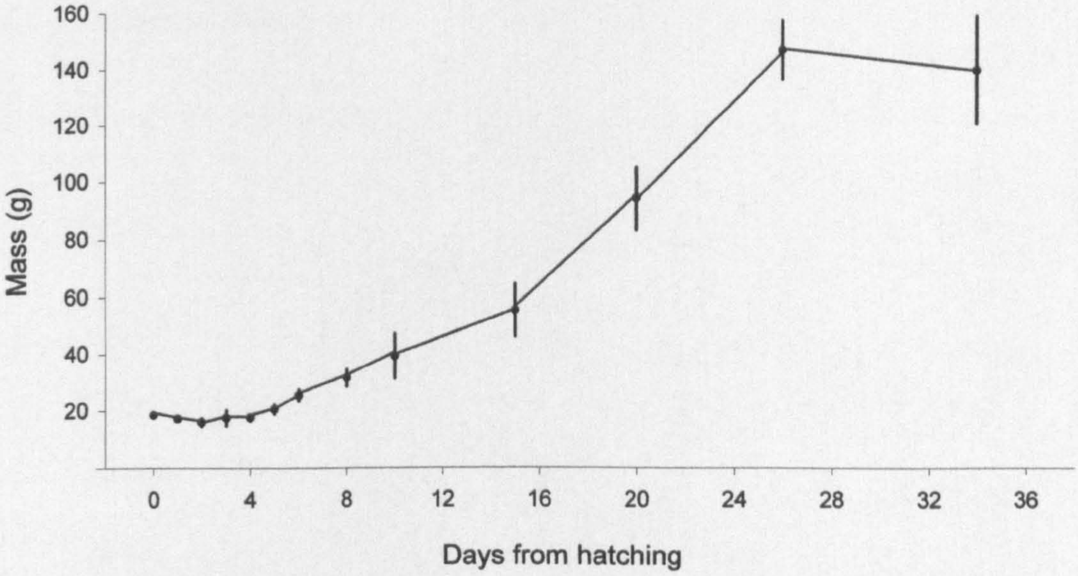
Survival for chicks in the first two date categories was similar but was lower for chicks from clutches laid later in the season. Chicks hatched in April and May, therefore, had a better chance of survival than chicks hatched in June and July.

5.2.6 Factors affecting chick growth

i. Differences between years

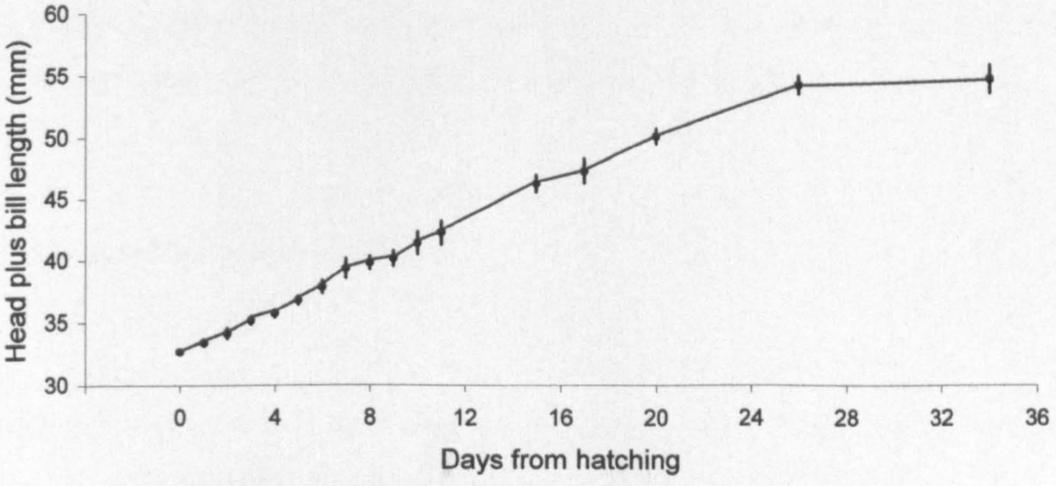
Between year chick growth rates, using body size (denoted by head plus bill length) and mass, were investigated with t-tests (Table 5.2.6a). These two parameters did not grow linearly (Figures 5.2.6a and 5.2.6b) as was also found by Galbraith (1988c). Two phases of growth were, therefore, examined; 0-5 and >5 days from hatching for mass, and 0-20 and >20 days from hatching for head plus bill length. Growth rates were taken from chicks re-trapped within these age classes. Growth was examined according to whether or not chicks had been reared on pasture, as it has been established that survival significantly differed for these two categories of broods (see 5.2.4).

Figure 5.2.6a Mean mass relative to age for lapwing chicks reared in intensively cultivated farmland (data from all rearing habitats and from 1996 and 1997 combined). Error bars represent 95% confidence intervals.



The number of chicks weighed at each age were as follows; 0 = 113, 1 = 36, 2 = 9, 3 = 13, 4 = 32, 5 = 32, 6 = 23, 7 = 20, 8 = 22, 9 = 18, 10 = 12, 11 = 16, 15 = 8, 17 = 12, 20 = 13, 26 = 7, 34 = 8.

Figure 5.2.6b Mean head plus bill length relative to age for lapwing chicks reared in intensively cultivated farmland (data from all rearing habitats from 1996 and 1997 combined). Error bars represent 95% confidence intervals.



For the sample sizes at each age see Figure 5.2.6a.

Table 5.2.6a Growth rates of chicks in 1996 and 1997 according to rearing field type in an area of intensive farming. n = number of chicks from which growth rates taken, (sd) represents standard deviation.

Non-pasture reared						
	0-5 days from hatching			>5 days from hatching		
Chick mass (g)	n	Mean (sd)	t-test	n	Mean (sd)	t-test
1996	9	-0.3 (0.88)	t = -0.06, *P*>0.5	14	4.4 (1.40)	t = -0.75, *P*>0.4
1997	14	-0.3 (0.71)		15	4.7 (1.34)	
Head+bill (mm)	0-20 days from hatching			>20 days from hatching		
1996	17	0.9 (0.11)	t = -1.02, *P*>0.3	7	0.5 (0.08)	t = -0.11, *P*>0.5
1997	22	0.9 (0.12)		8	0.5 (0.13)	
Pasture reared						
	0-5 days from hatching			>5 days from hatching		
Chick mass (g)	n	Mean (sd)	t-test	n	Mean (sd)	t-test
1996	7	1.1 (0.71)	t = 0.29, *P*>0.5	12	4.4 (0.99)	t = -0.97, *P*>0.3
1997	5	1.0 (0.30)		6	5.1 (1.60)	
Head+bill (mm)	0-20 days from hatching			>20 days from hatching		
1996	28	0.9 (0.03)	t = -0.08, *P*>0.5	5	0.4 (0.05)	t = -1.14, *P*>0.2
1997	7	0.9 (0.06)		4	0.4 (0.05)	

There were no significant between year differences in chick growth rates between the age classes in either of the rearing field type categories. The similarity in growth rates permitted data from both years to be combined for further analysis.

ii. Differences between field types

Three field types were used for chick rearing. All chicks were hatched in crop or RSA fields, although most broods were reared in spring cultivated fields (Figures 5.2.4a and 5.2.4b). Some chicks remained in natal RSA fields and some chicks, immediately after hatching, moved to pasture. Spring cultivated rearing fields were either the natal locations of broods or fields directly adjacent to nest sites. Most chicks tended to remain in their rearing field type until fledging.

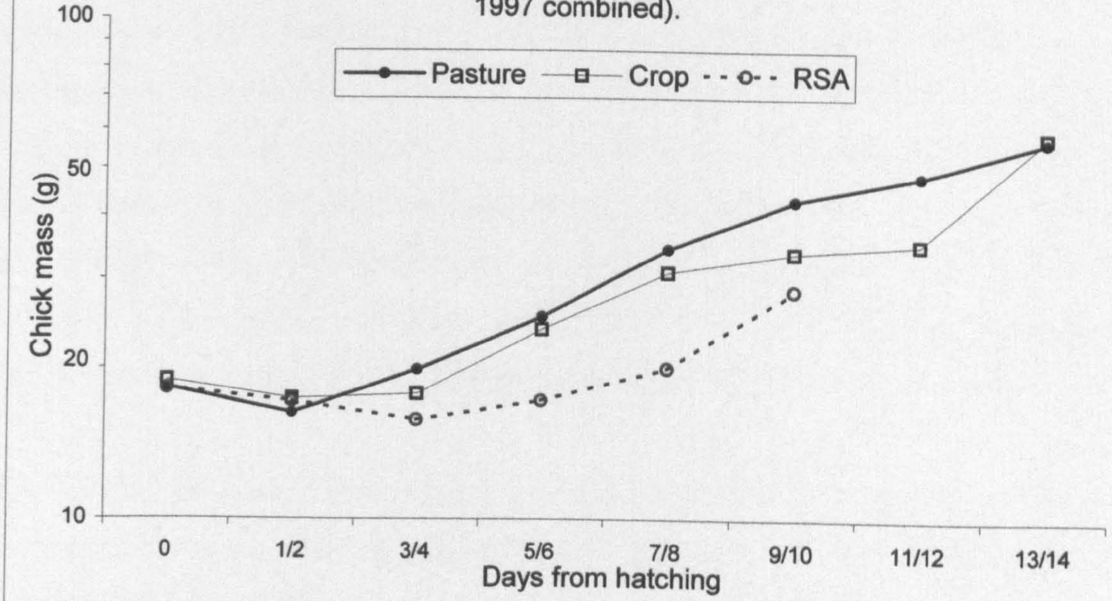
Chicks in all field types suffered mass loss immediately post-hatching, this being most notable for those chicks that moved to pasture (Figure 5.2.6c). Mass gain after the first few days post-hatching was greatest for chicks feeding in pasture resulting in this category of chicks being significantly heavier by the time they were 9-10 days old than chicks of the same age reared elsewhere (Mann-Whitney tests: $W = 190$, $n = 12/12$, $P<0.05$; $W = 146$, $n = 12/6$, $P<0.01$; for crop and RSA field reared chicks respectively). At this age crop (*i.e.* spring cultivated field) reared chicks were 22% lighter than those feeding in pasture, with 'pasture' chicks being 31% heavier at 11-12 days after hatching than their crop reared contemporaries. The faster mass gain of pasture reared chicks was not sustained as by 13/14 days after hatching crop reared chicks were a similar mass to chicks of the same age that had been feeding in pasture fields (Mann-Whitney tests: $W = 66$, $n = 9/9$, ns).

Chicks reared in RSA were significantly lighter than chicks reared in spring crop fields 3-4 days after hatching (Mann-Whitney test: $W = 550$, $n = 24/13$, $P<0.01$). Chicks reared in RSA fields remained significantly lighter than contemporaries until 9-10 days after hatching when there was no significant difference in mass between RSA and spring crop field reared chicks (Mann-Whitney test: $W = 348$, n = 19/9, $P<0.01$; $W = 127$, $n = 12/6$, ns; tests at 7-8 and 9-10 days after hatching respectively).

A number of chicks re-trapped in RSA were covered in a sticky (plant) exudate which had covered their down. As this might have interfered with the chicks thermo-regulatory capacity, increasing heat and mass loss, the mass of crop chicks was tested against those of RSA excluding 'sticky chicks'(31% of RSA chicks at 3-4 days and 33% of RSA chicks at 5-6 and 7-8 days old). The differences between the two categories remained for chicks between the ages of 3-4 and 7-8 days after hatching (Mann-Whitney test: $W = 461.5$, n = 24/9, $P<0.05$; $W = 407$, n = 21/10, $P<0.01$; $W = 291$, 19/6, $P<0.01$; tests between RSA and crop chicks for 3-4, 5-6, and 7-8 days after hatching respectively).

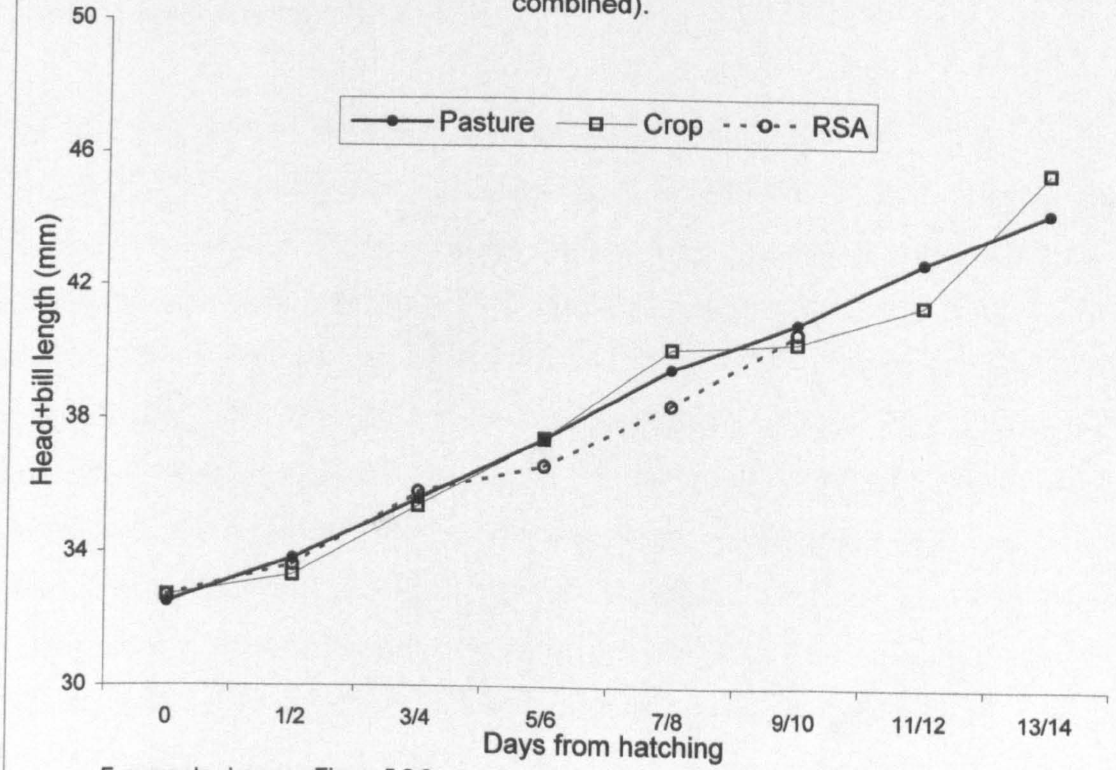
Although significant differences were found between the mass of chicks reared in pasture and crop fields, chick sizes were similar for these two categories at least up to 9-10 days

Figure 5.2.6c Mean mass (plotted on a log scale) relative to age for lapwing chicks reared in pasture, spring crop and RSA fields (1996 and 1997 combined).



	0	1/2	3/4	5/6	7/8	9/10	11/12	13/14
n pasture	22	15	8	19	14	12	9	9
n spring crop	63	19	24	21	19	12	16	9
n RSA	28	11	13	15	9	6	0	0

Figure 5.2.6d Mean head + bill length relative to age for lapwing chicks reared in pasture, spring crop and RSA fields (1996 and 1997 combined).



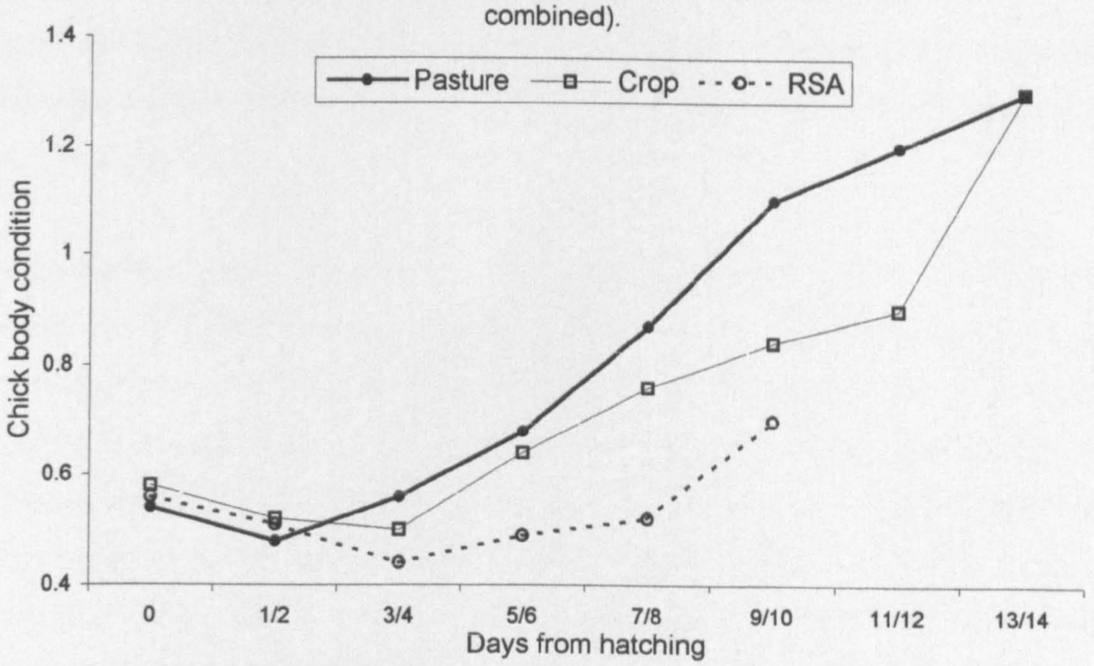
For sample sizes see Figure 5.2.6c.

after hatching (Figure 5.2.6d). There were no significant differences in head-plus-bill lengths between pasture and crop reared chicks for any age between 1 and 10 days after hatching (Mann-Whitney tests: $W = 314.5$, $n = 15/19$; $W = 390$, $n = 19/21$; $W = 168$, $n = 12/12$, ns in all cases; tests on 1-2, 5-6 and 9-10 days after hatching respectively). Although pasture reared chicks were significantly larger than 'crop' chicks at 11/12 days after hatching (Mann-Whitney test on head-plus-bill length: $W = 184.5$, $n = 12/12$, $P<0.01$) by 13/14 days after hatching, as with chick mass, there was no difference in size between these two categories of chicks (Mann-Whitney test: $W = 66$, $n = 9/9$, ns).

Chicks reared in RSA fields were significantly smaller than their contemporaries elsewhere by 5-6 days after hatching (Mann-Whitney test on head-plus-bill length: $W = 455.5$, $n = 21/15$; $W = 390.5$, $n = 19/15$, $P<0.05$ in both cases; for crop and pasture reared chicks respectively). By the time they were 9-10 days old RSA reared chicks were a similar size to both crop field and pasture reared chicks (Mann-Whitney test on head-plus-bill length: $W = 110.5$, $n = 12/6$; $W = 122$, $n = 12/6$, ns in both cases; tests for crop and pasture categories respectively).

In the first five days of life chick size increases irrespective of loss of mass (Figures 5.2.6c and d). By moving into pasture the body condition of recently hatched chicks temporarily deteriorates (Figure 5.2.6e), chicks from this rearing category having a significantly lower body condition at 1-2 days after hatching than those reared in spring crop fields (Mann-Whitney test: $W = 194$, $n = 15/19$, $P<0.02$). After this age the mass gain enjoyed by chicks on pasture resulted in chicks reared in both crop and pasture fields having similar body condition. The decrease in mass gain of chicks reared on spring cultivated land from 7-8 days after hatching, whilst increasing in size, resulted in a decline of body condition. The slower rate of mass gain in chicks reared in RSA whilst increasing in size resulted in poor body condition until 9-10 days after hatching. At this age 'RSA chicks' did not differ in body condition from chicks reared in crop fields (Mann-Whitney test: $W = 130$, $n = 12/6$, ns). By 9-10 days after hatching pasture reared chicks, however, were in significantly better condition than contemporaries reared elsewhere (Mann-Whitney test: $W = 190$, $n = 12/12$, $P<0.05$; $W = 146$, $n = 12/6$, $P<0.01$;

Figure 5.2.6e Mean body condition relative to age for lapwing chicks reared in pasture, spring crop and RSA fields (1996 and 1997 combined).



For sample sizes see Figure 5.2.6c.

tests for crop and RSA reared categories respectively). After this age, however, with the increase in chick mass feeding in spring cultivated fields, crop reared chicks achieved a similar body condition to those chicks foraging in pasture fields (Mann-Whitney test: *W* = 81, n = 9/9, ns).

The convergence in growth parameters of pasture and crop reared chicks is unlikely to be due to accelerated growth rates of crop reared chicks as there was no difference in the mean growth rate of chicks older than five days reared in pasture and those reared elsewhere in both years (1996: t = -0.97, ns; 1997: t = 0.46, ns; see Table 5.2.6a for means and sample sizes). It is possible that smaller, lighter crop reared chicks experience higher mortality with most dying before they are ten days old (chicks with poor body condition may also be easier to re-trap and represent a bias in the sample). After this age the only chicks remaining in crop fields are the heavier, fitter chicks. Data are too few to examine this hypothesis but different growth patterns for crop reared chicks might be explained by differences in crop field rearing quality (*e.g.* food availability and height/density of the crop). There would seem to be differences, at least, in some arable habitats, *e.g.* for chicks reared in spring crops and RSA (see above).

iii. Hatching date - the effect of season

As survival of chicks from late season clutches was lower than those hatched earlier (Table 5.2.5a), the effect of season on growth rates was examined to determine if mortality differences were accompanied by growth differences. Due to the influence that post-hatching movements and rearing field type has on growth, chicks reared in pasture were excluded from the analysis. Chicks reared close to their natal location were separated into early-, middle- and late-hatched categories (representing the hatch periods of before 7 May, 7 to 31 May and after 31 May respectively). Chicks within these categories were allocated to four separate age classes with t-tests used on the growth parameter means of each class to investigate any differences (Table 5.2.6b (i) & (ii)).

Table 5.2.6b (i) Mean mass (*g*) and (ii) head-plus-bill length (*mm*) for lapwing chicks hatched in different periods and reared on intensively cultivated spring farmed land. Early-, middle- and late hatch seasons represent chicks hatched <7 May, 7 May to 31 May and >31 May respectively. Data from 1996 and 1997 combined.

(i) Mass

Age class	Hatch season	*n*	Mean (sd)	t-test
0 days	Early	51	19.0 (1.3)	Early/late: t = 1.98, ns
	Middle	22	18.6 (1.2)	Early/mid: t = 1.24, ns
	Late	18	18.4 (1.2)	Mid/late: t = 0.32, ns
1-3 days	Early	14	17.9 (1.4)	Early/late: t = 1.05, ns
	Middle	19	17.6 (1.1)	Early/mid: t = 1.86, ns
	Late	8	17.2 (1.6)	Mid/late: t = -0.2, ns
4-7 days	Early	44	20.5 (5.9)	Early/late: t = 1.21, ns
	Middle	22	21.1 (5.3)	Early/mid: t = -0.4, ns
	Late	14	18.6 (4.9)	Mid/late: t = 1.46, ns
8-9 days	Early	11	31.5 (6.2)	Early/late: t = 0.8, ns
	Middle	8	29.2 (8.1)	Early/mid: t = 0.7, ns
	Late	5	29.2 (5.1)	Mid/late: t = -0.1, ns

(ii) Head + bill

Age class	Hatch season	*n*	Mean (sd)	t-test
0 days	Early	51	32.7 (0.7)	Early/late: t = 0.6, ns
	Middle	22	32.7 (0.6)	Early/mid: t = 0.3, ns
	Late	18	32.6 (0.6)	Mid/late: t = 0.2, ns
1-3 days	Early	14	34.5 (0.9)	Early/late: t = 1.39, ns
	Middle	19	33.8 (0.9)	Early/mid: t = 1.9, ns
	Late	8	33.7 (1.2)	Mid/late: t = 0.1, ns
4-7 days	Early	44	37.1 (1.6)	Early/late: t = 0.64, ns
	Middle	22	36.9 (1.8)	Early/mid: t = 0.6, ns
	Late	14	36.8 (1.7)	Mid/late: t = 0.1, ns
8-9 days	Early	11	39.9 (1.3)	Early/late: t = 0.8, ns
	Middle	8	39.4 (1.7)	Early/mid: t = 0.7, ns
	Late	5	39.3 (1.5)	Mid/late: t = 0.1, ns

Chicks hatched late in the season tended to be lighter and smaller than those hatched earlier, at least until 9 days after hatching. There were, however, no seasonally statistically significant differences in these growth parameters for any of the age classes. Late-and early hatched chicks appear to hatch and grow, therefore, to similar sizes and at similar rates. These results indicate that the increased mortality of chicks hatched late in the season is not associated with retarded growth and a deterioration in body condition.

iv. Weather

As chick growth in the first few days after hatching may be dependant upon the size of yolk reserves (see 5.2.3), the effect of weather on growth was examined for chicks between 5 and 10 days old. In addition, the distance traveled to feeding areas may also influence growth (see 5.2.6. ii.), therefore, analysis was confined to chicks reared in their natal crop or RSA field or fields immediately adjacent to their natal location. To study the relationship between weather and chick growth, mean daily temperature and rainfall over the 5 days preceding weighing were linearly regressed as independent variables against the mass of 48 chicks weighed in 1996 and 1997. Mean daily temperature over the five day period previous to weighing was only weakly positively correlated with chick mass ($r = 0.357$, $P < 0.01$). The effect of mean daily rainfall on chick mass over this period was not significant ($r = 0.13$, $P > 0.1$).

5.2.7 Radio-marked chick mortality

i. Age of radio attachment

Radio transmitters were mainly attached to recently hatched chicks with 62% of transmitters affixed to chicks of less than five days old (Table 5.2.7a). The different weights of radios used each year, however, resulted in chicks from different age cohorts being marked. In 1995 no chicks under 6 days old were marked, with most radios being attached to chicks older than 10 days. In 1996 almost half (45%) the chicks tagged were less than 5 days old, and in 1997, 73% of chicks had radios attached as nestlings.

Table 5.2.7a Distribution of ages for attachment of radio transmitters to lapwing chicks. The age cohort 0 refers to nestlings. Mean represents the mean age (in days) of radio attachment with its standard deviation in parenthesis.

	Age cohort (days)							
Year	0	1-5	6-10	11-15	16-20	21-25	Total	Mean (sd)
1995	0	0	2	3	4	1	10	15.4 (4.0)
1996	2	7	2	7	0	2	20	8.6 (7.4)
1997	32	5	2	2	3	0	44	2.5 (5.5)
Total	34	12	6	12	7	3	74	5.9 (7.4)
Percentage	*46.0*	*16.0*	*8.1*	*16.2*	*9.5*	*4.1*		

ii. The fate of radio-marked chicks

(a) Causes of mortality

Over the three years it was possible to determine the fate of over 90% (68 of 74) of the radio-marked chicks with the proportion of chicks with unknown fate (through radio failure or loss) decreasing annually (Table 5.2.7b).

Table 5.2.7b The outcome of radio-marking 74 lapwing chicks in an area of intensive agriculture. Percentages are of total known fate except where marked with an asterisk where they are of the total number of radio-marked chicks.

	1995		1996		1997		Total	
	n	*%*	*n*	*%*	*n*	*%*	*n*	*%*
Fledged	1	*16.7*	3	*15.8*	6	*14.0*	10	*14.7*
Died	5	*83.3*	16	*84.2*	37	*86.0*	58	*85.3*
Total known fate*	**6**	***60.0***	**19**	***95.0***	**43**	***97.7***	**68**	***90.5***
Battery drain/failure	1		1		1		3	
Radio shed	3		0		0		3	
Total unknown fate*	**4**	***40.0***	**1**	***5.0***	**1**	***2.3***	**6**	***8.1***

Of those radio-marked chicks whose fate was known most (85%) died (Table 5.2.7b). Most deaths (52%) were likely to have been the result of predation with 22.4% of chicks lost definitely being depredated. Nearly one third (31%) of tagged chick loss was through poor body condition with 17% of chicks lost dying in ditches (Table 5.2.7c).

Table 5.2.7c Proximate causes of mortality of radio-marked lapwing chicks in an area of intensive agriculture. Percentages are of total losses except those marked with an asterix where they are of total numbers predated. See 5.1.4 for definitions of losses.

	1995		1996		1997		Total	
Losses to:	*n*	%	*n*	%	*n*	%	*n*	%
Raptors*	0	0	3	*37.5*	2	*11.8*	5	*16.7*
Mammals*	0	0	1	*12.5*	4	*23.5*	5	*16.7*
Unknown predator*	2	*40*	0	*0*	1	*5.90*	3	*10.0*
Unknown predator; signal loss*	3	*60*	4	*50.0*	10	*58.8*	17	*56.7*
Predation (total)	5	*100*	8	*50.0*	17	*46.0*	30	*51.7*
Poor condition	0	*0*	6	*37.5*	12	*32.4*	18	*31.0*
Ditches	0	*0*	2	*12.5*	8	*21.6*	10	*17.3*
Total losses	5		16		37		58	
No. radio-marked	10		20		44		74	

Three out of the five (60%) losses to raptors occurred between the two diurnal fixes. Three out the five (60%) losses attributed to mammals were between days (*i.e.* between the last fix of one day the first fix of the next). Most chicks that were predated involved signal loss. Most (59%) of these 'disappearances' occurred during the day (*i.e.* between the two diurnal fixes). It cannot necessarily be inferred that in those instances where disappearance occurred between days that predation was nocturnal as there were several hours of daylight before and after fixes.

(b) Between year and seasonal differences in survival

Survival of all tagged chicks over the three years was 1.9% and there was no significant difference in between year mortality rates (z = 0.61, 0.14 and 0.74 for 1995 and 1996, 1995 and 1997 and 1996 and 1997 respectively; $P > 0.1$ in all cases; Table 5.2.7d).

Seasonal differences in survival were investigated by comparing the mortality rates of tagged chicks that hatched before each year's median hatch date to those hatched on or after that date.

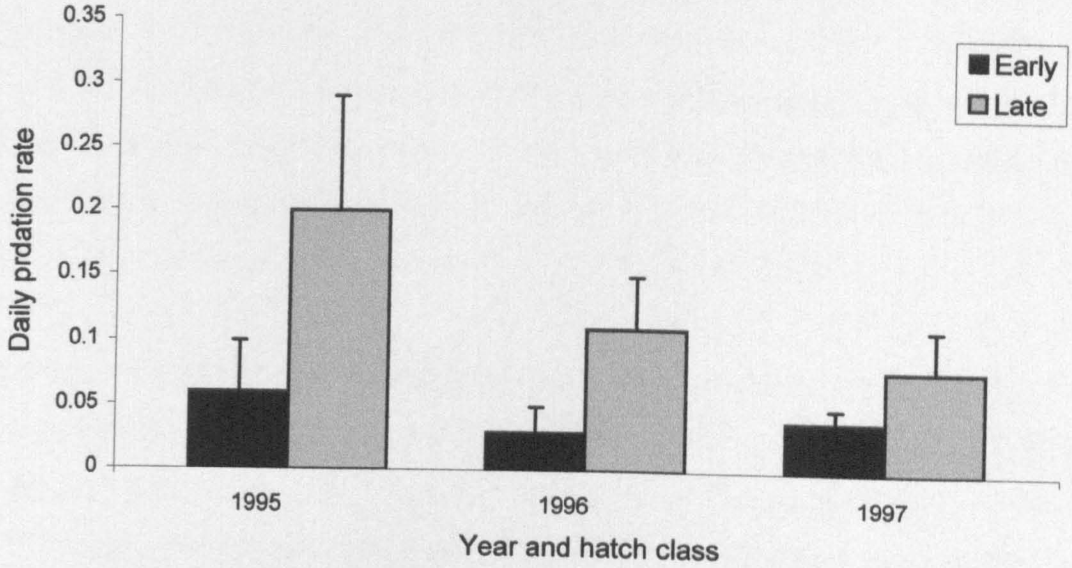
Table 5.2.7d Survival of radio-marked lapwing chicks from hatching to fledging in an area of intensive agriculture. One chick-day represents one marked chick tracked for one day (24 hrs). Percentage survival is the probability of a chick surviving until 35 days after hatching ($P^{35} \times 100$).

Year	Hatch class[a]	No. of chicks	No. lost	No. chick days	Mortality rate/ day ± se	Mortality rate test	Percentage survival
1995	Early	5	2	34	0.0590 ± 0.04	$z = 1.15$; NS	12.0
	Late	5	3	18	0.170 ± 0.088		0.2
	All	10	5	52	0.096 ± 0.041		2.9
1996	Early	8	5	70	0.071 ± 0.031	$z = 2.04$; $P<0.05$	7.6
	Late	12	11	56	0.196 ± 0.053		0.1
	All	20	16	126	0.127 ± 0.030		0.9
1997	Early	30	24	286	0.084 ± 0.0164	$z = 1.90$; NS	4.6
	Late	14	13	76	0.171 ± 0.0432		0.14
	All	44	37	362	0.102 ± 0.0160		2.3
1995-97	Early	43	31	390	0.080 ± 0.0137	$z = 2.93$; $P< 0.01$	5.5
	Late	31	27	150	0.180 ± 0.0314		0.1
	All	74	58	540	0.110 ± 0.0133		1.9

[a] Early chicks hatched before the median hatch date; late chicks hatched on or after the median hatch date. The median hatch dates were 24/05/96 and 18/05/97. The median hatch date for 1995 could not be estimated due to a small sample size of clutches with known first egg dates. The 17/05 was apportioned as the division between early and late hatched chicks which divided the range of hatch dates for the tagged chicks (02/05 – 02/06/95) equally. Excluding 1995 data from the overall calculations of mortality rate and percentage survival does not alter the daily mortality rate for overall hatch classes but does decrease the percentage survival of 'early' hatched and 'all' chicks to 5.1 and 1.8 respectively (from 5.5% and 1.9% respectively).

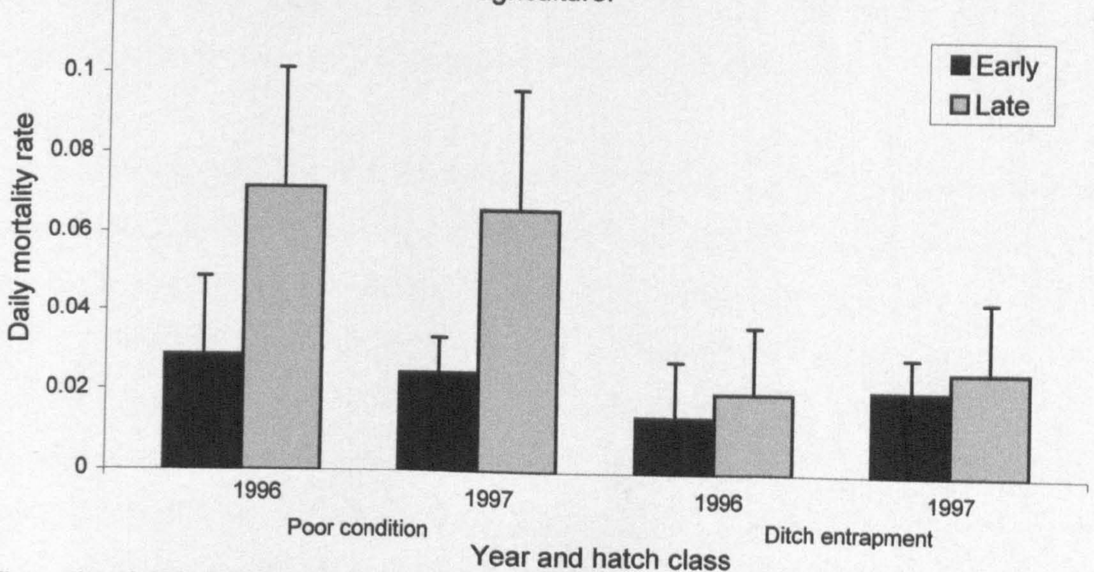
Losses from all three causes of mortality (predation, poor body condition and ditch entrapment) were higher for late hatched chicks in each year (Figures 5.2.7a and 5.2.7b) and consequently late hatched chicks suffered higher daily mortality rates than early hatched chicks with this difference being significant in 1996 (Table 5.2.7d). As there

Figure 5.2.7a Daily predation probability of early- and late-hatched radio-marked chicks in an area of intensive agriculture.



The numbers of chicks, chicks predated and chick days were as follows: 1995: Early; 5, 2 and 34; Late; 5, 3 and 18; 1996: Early; 8, 2 and 70; Late; 12, 6 and 56; 1997: Early; 30, 11 and 286; Late; 14, 6 and 76. There were no significant differences between hatch classes in each year.

Figure 5.2.7b Daily probability of dying from two causes for early- and late-hatched radio-marked lapwing chicks in an area of intensive agriculture.



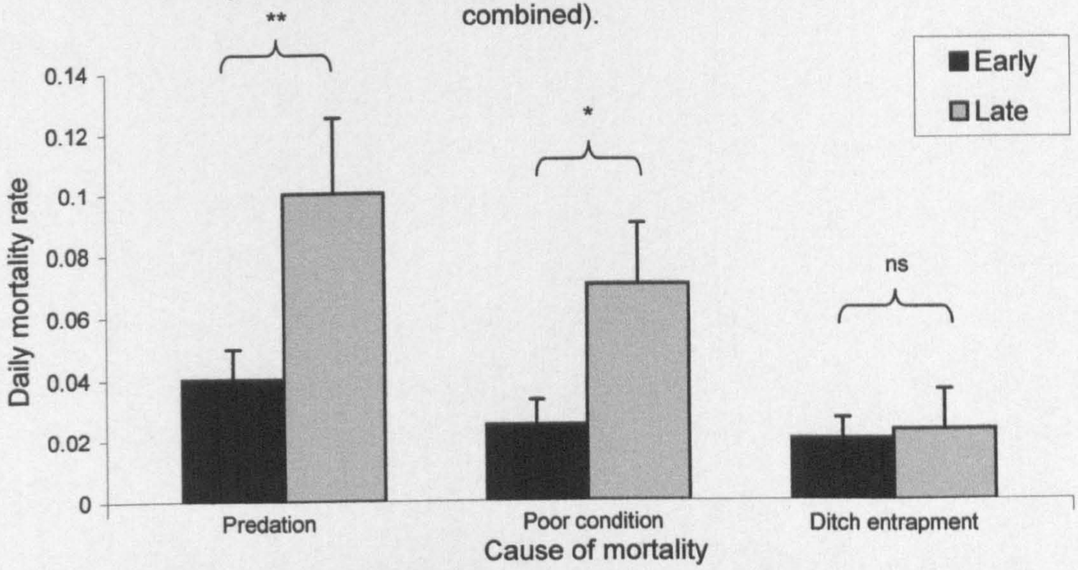
The number of chicks lost were as follows: from poor condition; Early = 2 and 7; Late = 4 and 5: from ditch entrapment; Early = 1 and 6; Late = 1 and 2; for 1996 and 1997 respectively. For the number of chicks and chick days see Figure 5.2.7a. In 1995 all radio-marked chick mortality was from predation. There were no significant differences between hatch classes in each year for either cause of mortality.

were no significant differences in chick survival for early and late hatch classes between years (between 1995 and 1996, 1995 and 1997 and 1996 and 1997, z = 0.24, 0.58 and 0.40; z = 0.25, 0.01 and 0.40 for early hatches and late hatches respectively; P >0.1 in all cases) data from hatch class from each year were combined. Overall daily mortality rates were significantly higher for late hatched chicks, with 0.1% survival, than for chicks hatched earlier in the season when survival was 5.5% (Table 5.2.7d).

Even though the predation rate was higher for late-hatched chicks (Figure 5.2.7a) there was no significant difference in the probability of predation between the hatch classes in each year (z = 1.12, 1.71, 1.23; for 1995, 1996 and 1997 respectively; P >0.05 in all cases). Predation rates for each hatch class did not differ significantly between years (for early-hatched chicks z = 0.7, 0.5, 0.4; for late-hatched chicks z = 0.6, 0.9, 0.6; P>0.1 in all cases; in tests between 1995 and 1996, 1995 and 1997 and 1996 and 1997 respectively for each hatch class) and data were pooled. The combined hatch class data showed that overall late–hatched chicks suffered significantly higher predation than chicks hatching earlier (z = 2.33, P <0.02; Figure 5.2.7c). Overall, the daily predation rate of late-hatched chicks was 2.5x higher than the predation rate of early-hatched chicks.

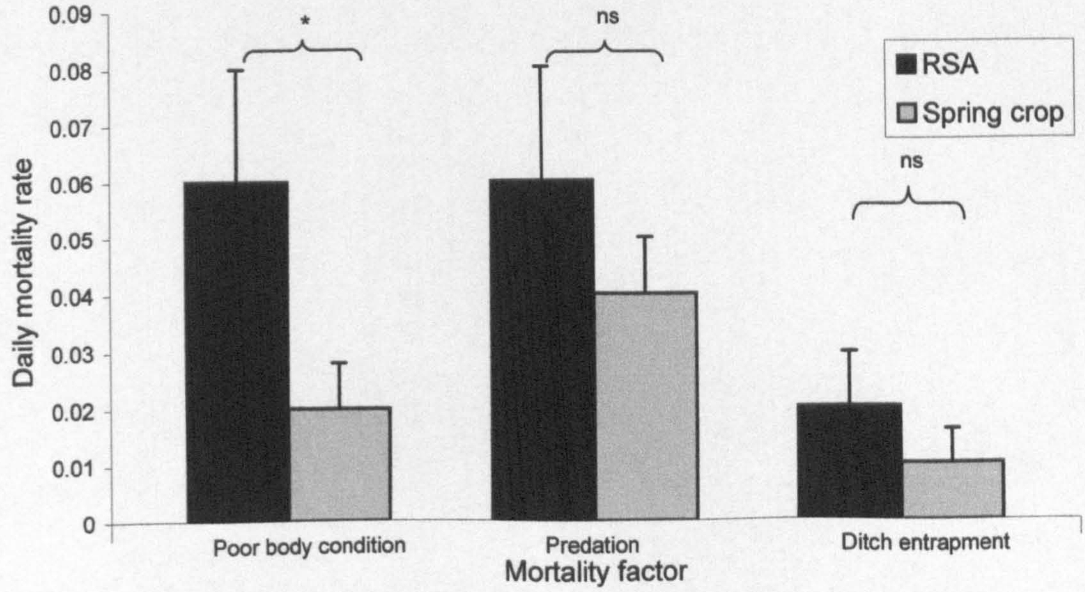
It was not possible to compare data from the other mortality causes for all three years as there were no radio-marked chick deaths from poor body condition or ditch entrapment in 1995. This was probably due to chicks having radios attached at an older age in 1995 (Table 5.2.7a). Investigation of mortality from poor condition and ditch entrapment was possible combining 1996 and 1997 data as mortality rates did not differ significantly between hatch classes between years (for poor body condition; z = 0.20 and 0.13; for ditch deaths; z = 0.40 and 0.30; for early- and late-hatched chicks respectively; P >0.1 in all cases). Overall, the risk of mortality from these two causes did not differ significantly between the hatch classes (z = 1.83 and 0.2 for poor body condition and ditch entrapment respectively; P >0.05 in both cases; Figure 5.2.7c)).

Figure 5.2.7c The probability of mortality from three different causes for early-and late-hatched radio-marked chicks (1995-1997 data combined).



The number of chicks, chicks lost and chick days were as follows: for predation; 43, 15 and 390 for early chicks; 31, 15 and 150 for late-hatched chicks; for poor condition; 38, 9 and 356 for early chicks and 26, 9 and 132 for late chicks; for ditch deaths; 38, 7 and 356 for early chicks and 26, 3 and 132 for late-hatched chicks. Poor condition and ditch death figures include data from 1996 and 1997 only as in 1995 all radio-marked chick mortality was through predation. Asterisks indicate significance levels: * = $P > 0.05$, ** = $P < 0.01$, ns = not significant.

Figure 5.2.7d Probability of dying from three different causes for radio-marked lapwing chicks reared in two intensively farmed field types (1996 and 1997 data combined).



The numbers of chicks and chicks lost were as follows: for poor condition; 26 and 11 for rsa reared; 33 and 6 for spring crop reared; for predation; 14 and 5 for rsa reared; 22 and 11 for spring crop reared; for ditch deaths; 26 and 3 for rsa reared; 30 and 4 for spring crop reared. There were 180 and 296 chick days for rsa and spring crop fields respectively. Level of significance: * = $P < 0.05$, ns = not significant.

(c) Differences in survival between rearing field type

The effect of rearing field type on chick survival was investigated by comparing the mortality rates of chicks reared in the two main rearing field types (RSA and spring cultivated fields). Chicks reared in RSA fields were defined as chicks that hatched and remained in RSA until dying or fledging (no chicks hatched elsewhere moved into RSA fields). Spring crop reared chicks hatched and remained in natal spring farmed fields or hatched elsewhere and then moved (usually within one to three days) to a spring crop field. Data from 1995 were excluded from this analysis as the average chick age for radio attachment was 15.4 days and the rearing field type of chicks before tagging was unknown. Five chicks from 1996 and 1997 that hatched in autumn or winter sown crops and died before reaching rearing fields were also excluded.

There was no significant difference in survival for chicks reared in either RSA or spring crop field types (Table 5.2.7e). As there was no significant difference in the risk of mortality between years for either field type ($z = 0.52$ and 0.41 for RSA and spring crop fields respectively; $P > 0.1$ in both cases) data were combined. Overall, there was not a significantly higher chance of survival between chicks reared in spring cultivated fields and RSA (Table 5.2.7e).

Table 5.2.7e Mortality of radio-marked lapwing chicks according to rearing field type in an area of intensive agriculture. Chicks not reared in RSA or spring cultivated fields (n = 5) and those from 1995 (n = 10) are excluded.

Year	Field type	No. chicks	Chicks lost	Chick days	Mortality rate/ day ± se	Mortality rate test
1996	RSA	12	11	74	0.150 ± 0.041	$z = 0.93$, ns
	Spring crop	8	5	52	0.096 ± 0.041	
1997	RSA	14	13	106	0.123 ± 0.032	$z = 1.20$, ns
	Spring crop	25	19	244	0.078 ± 0.017	
1996+1997[a]	RSA	26	24	180	0.133 ± 0.025	$z = 1.75$, ns
	Spring crop	33	24	296	0.081 ± 0.016	

[a] The mean age (in days) of radio attachment was 4.64 (s.d. = 5.5) and 5.0 (s.d. = 7.85) for RSA and spring crop reared chicks respectively.

Overall, predation accounted for most (50%) chick losses and the risk of predation did not differ significantly for chicks reared in either field type (z = 1.13, P >0.1; Figure 5.2.7d). The probability of chicks dying in ditches was also not significantly different between rearing field types (z = 0.57, P >0.1). Poor body condition was the second largest mortality factor causing the death of 35% of the radio-marked chicks from the two field types. Despite overall mortality rates not differing significantly between rearing habitats, however, chicks reared in RSA had a significantly greater chance of dying through poor body condition than those reared in spring crop fields (z = 2.1, P <0.05; Figure 5.2.7d). The age at which a chick is tagged might influence the mortality rate from poor body condition as such deaths might be more prevalent in young chicks. There was no significant difference, however, in the age at which chicks from the two field types were tagged (t-test on mean age of radio attachment; t = - 0.22, P >0.7, d.f. = 56; Table 5.2.7e).

(d) The effect of chick age on mortality

The risk of dying might be expected to decrease with age for a lapwing chick. Older chicks become more experienced at feeding and finding cover. They are also larger, stronger and faster than younger chicks, all of which may aid survival. The age of mortality was examined for the radio-marked chicks by comparing the mortality rates for different age cohorts.

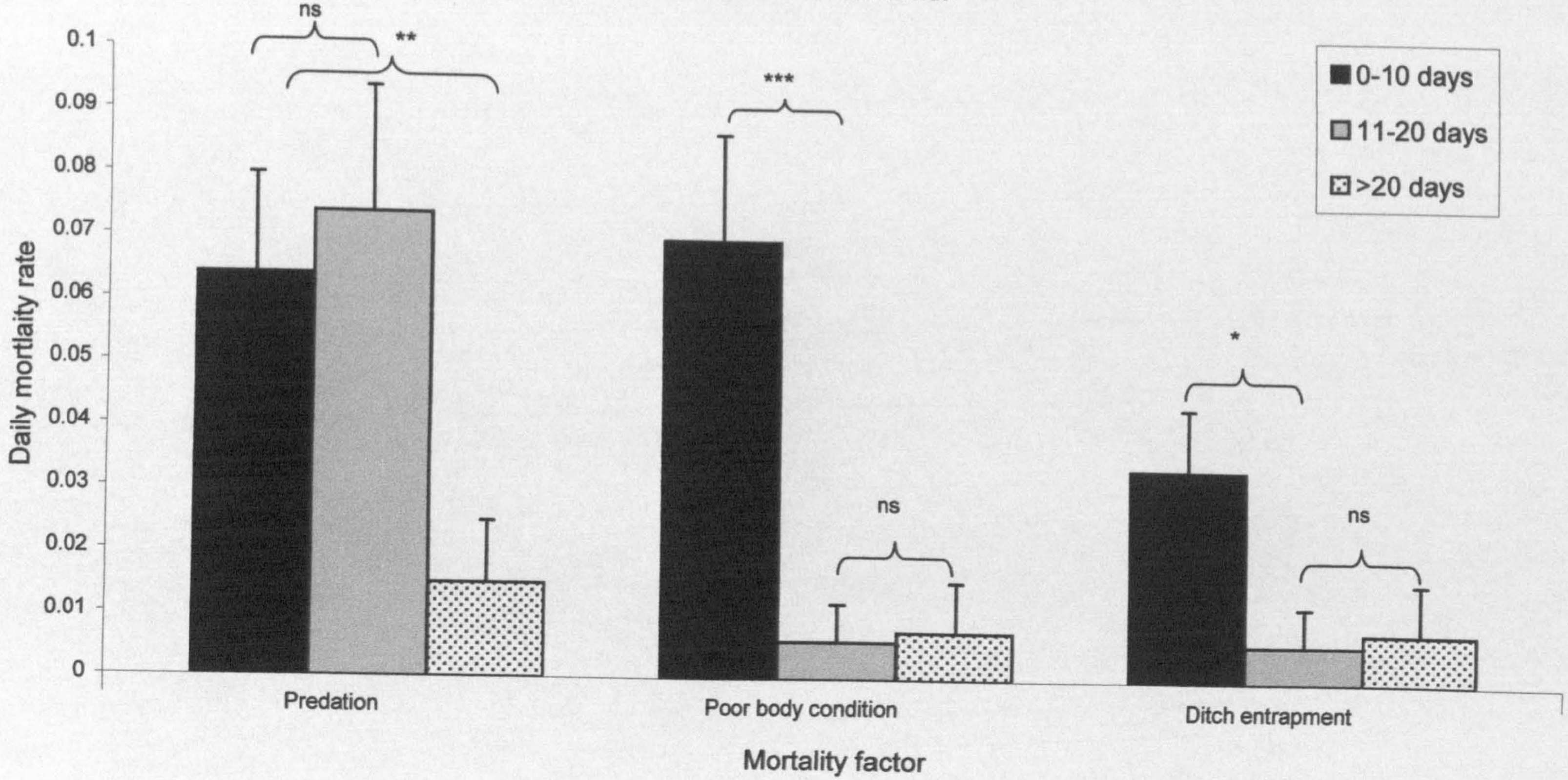
Table 5.2.7f The probability of dying at a particular age for 58 lapwing chicks reared in an area of intensive agriculture. The number of chicks represents the number of chicks alive for at least one day in each cohort.

Age cohort (days)	No. chicks	Chicks lost	Chick days	Mortality rate/ day ± se
0-10	49	39	234	0.167 ± 0.024
11-20	23	15	175	0.086 ± 0.021
>20	8	4	131	0.031 ± 0.015

The probability of dying was greatest for the youngest chicks and least for the oldest (Table 5.2.7f). The mortality rate for chicks in the 0-10 days old cohort was significantly greater than those aged between 11-20 ($z = 2.5$, $P<0.02$). The probability of dying for chicks older than 20 days was significantly lower than chicks aged 11-20 days old ($z = 2.14$, $P<0.005$). Thus, considering all mortality factors together, chick survival increased with age.

The risk of dying from each of the three mortality factors was examined to determine if the same pattern of significantly decreased mortality with age class was followed. The risk of dying from poor body condition and ditch entrapment was highest for the youngest age cohort of chicks (Figure 5.2.7e). These factors exerted a significantly lower risk to chicks that were 11-20 days old than to those 0-10 days old ($z = 3.6$, $P < 0.001$ for poor condition; $z = 2.1$, $P < 0.05$ for ditch entrapment). The risk of ditch death decreased about six times from the first to second age cohorts. A degree of risk was maintained through to fledging, however, as there was no significant difference in mortality between the second and third cohort ($z = 0.21$, $P >0.1$). In fact, 8/10 chicks that died in ditches were less than 5 days old with the two older chicks possibly dying for different reasons. These older chicks (19 and 29 days old) were found in prone positions on the water surface of ditches close to the level of the field surface and appeared large enough to have been able to escape entrapment. This suggests they may have died from trauma (as opposed to entrapment) as they had not drowned. They may have entered ditches to escape disturbance (*e.g.* from farm machinery working their rearing field) or a predator. Excluding these two individuals as dying from actual entrapment indicates that ditches present problems to only very young chicks. The risk of dying from poor body condition decreased 12 times from the first to second age cohort. With no significant difference in mortality probability between the second and third cohorts ($z = 0.2$, $P >0.1$), this factor continued to operate at a low level until fledging. In contrast to the other two mortality factors, the risk of predation was similar for 0-10 and 11-20 day old chicks with no significant difference between the two age cohorts ($z = 0.4$, $P >0.1$; Figure 5.2.7e). The predation risk to chicks only decreased significantly for chicks older than 20 days ($z = 3.2$, $P <0.002$ between chicks 0-20 and >20 days old).

Figure 5.2.7e Mortality probability at different ages of three different factors from 58 radio-marked lapwing chicks in intensive farmland.



The number of chicks lost for the 0-10, 11-20 and >20 age cohorts were as follows: for predation; 15, 13 and 2: for poor condition; 16, 1 and 1: for ditch entrapment; 8, 1 and 1. The number of chicks and chick days were 66 and 234; 48 and 175; 17 and 131 for cohorts 0-10, 11-20 and >20 respectively. Asterisk indicates level of significance: * = P<0.05, ** = P<0.01, *** = P <0.001, ns = not significant.

5.3 Discussion

i. Chick survival

Most Holarctic waders lay determinant clutches of four eggs (Lack 1947). In this study, almost 88% of lapwing clutches comprised four eggs which was a similar proportion to that found in Scottish lapwings (Galbraith 1988a) and nine other European studies (see Ettrup and Bak (1985) for a summary). The adaptive significance of a fixed clutch size remains unresolved (Arnold 1999), but for determinant layers, differences in habitat and parental quality are more likely to be expressed in egg size and quality than clutch size (Galbraith 1988a). In some wader species however, egg size has been shown to be largely controlled by inheritance (*e.g.* Grant 1991). In contrast, egg size in lapwing has been shown to be determined by female body condition and the quality of foraging location prior to laying (Galbraith 1988a, Blomqvist and Johansson 1995). In this study lapwing chicks from large eggs were bigger and heavier at hatching and, in one year (1997), survived better than those from smaller eggs. The effect of egg size on chick survival was detectable up until ten days after hatching. This might have been expected as it has been found elsewhere in lapwing (*e.g.* Galbraith 1998a, Blomqvist *et al.* 1997) and in other wader species (*e.g.* Grant 1991). In the current study, the relationship between egg size and chick survival appears associated with brood movements. In 1996 when no such relationship could be established broods made post-hatching movements out of natal fields which increased their mortality. Such chicks may have died from poor body condition through the exhaustion of yolk reserves and/or a lack of food. Mortality may have also resulted from chicks becoming entrapped in ditches situated between fields. Brood movements, as well as poor body condition and ditch entrapment, may have made chicks more vulnerable to predation. These mortality factors would possibly act irrespective of egg size or hatchling mass. In 1997 chick survival in the post-hatching period was better as chicks remained in their natal fields. The between year differences in brood movements were determined by the different starting date of spring farming operations in relation to the timing of lapwing breeding and the distribution of crops. Chicks hatched from nests in RSA and winter farmed fields in 1996 moved into pasture and spring cereal fields. In 1997 nests in fields near pasture were destroyed by earlier cultivation (rolling) activities than in 1996. As the majority of these fields were winter cereals, failed adults had to re-nest elsewhere (in spring farmed fields) as initial locations were no longer suitable for nesting with, consequently, fewer brood movements due to less chick production in winter cereals.

Mortality in both years was most severe in the first five days after hatching but less so in 1997 as few chicks were produced in winter cereals with chicks hatched elsewhere remaining in natal fields. As winter cereals have a well developed crop stand by the time chicks hatch, broods, on hatching, are moved to more favourable rearing locations. Galbraith (1988b) found that chick survival was enhanced by chicks hatching in nests in arable fields close to pasture. Galbraith (1988a) showed that chicks from nests far from pasture foraging locations lost body condition and suffered high mortality in gaining access to pasture. In Galbraiths' study weight loss and mortality were not so severe for chicks in nests close to pasture. In this study chick survival was also enhanced by proximity to pasture. Loss of chick mass and body condition, however, may not have been the only factors responsible for an increase in chick mortality. In 1996, when more chicks undertook post-hatching movements, there was a significant difference in survival between chicks that had natal fields separated from rearing fields by ditches and those that did not have to cross ditches. Radio-tracking showed all chicks that died from becoming entrapped in ditches were under 5 days old, *i.e.* broods undertaking post-hatching movements. The closer nests were to pasture and the fewer fields they had to cross significantly benefited chick survival, therefore, as there was less chance of chicks becoming entrapped in a ditch. Previously, obstacles, such as ditches, have not been thought to present problems for young lapwing broods. It was thought their parents could coax them around or even transport chicks over such features by holding them between their legs as they flew across (Cramp and Simmons 1983 and references therein, W. Hale, pers. comm.). There may have been recent changes to ditch engineering in the study site (increasing ditch depth) due to peat shrinkage resulting from modern drainage lowering the local water table.

Despite these between year mortality differences in young chicks, fledging success was significantly higher in 1996 than in 1997. Higher mortality in chicks over ten days old in 1997 decreased fledging success that year. In 1997 brood movements were associated with chicks of this age as crop growth in their natal fields forced them to new rearing locations. Additionally, a greater proportion of chicks were reared in pasture in 1996 which may have conferred a survival advantage (see 5.3 iii). Similar anthropogenic factors causing lapwing brood movements and associated with high chick mortality were also found in arable farmland in Scotland (Galbraith 1988a, 1988b).

ii. Chick growth

Chicks that moved to pasture experienced greater mass loss than those that stayed in natal fields. A loss of body condition was associated with the mass loss to which an increase in body size (even in the absence of additional nutrients) contributed. Pasture chicks soon increased their mass and body condition above that of chicks reared in spring crop fields and RSA suggesting that feeding conditions were better in pasture than elsewhere. More sub-surface chick prey might be expected as earthworm and Tipulid densities are lower in cultivated soils than grassland (see 6.2.2, Edwards and Lofty 1977, Galbraith 1988b). The soil of the study area, however, was peat and such soils are faunistically poor containing few earthworms (Edwards and Lofty 1977). Furthermore, as young chicks are short billed (mean bill length at hatching ± SD; 10.6mm ± 0.7, n = 1769; data from Beintema and Visser 1989) their capacity for taking advantage of soil dwelling prey must be limited. In The Netherlands lapwing chicks reared in pasture have been found to feed largely on fauna (mainly Dipteran larvae) associated with cow dung (Beintema *et al.* 1991). Lapwing chicks feeding on sheep pastures can, perhaps, similarly take advantage of sheep dung fauna. Furthermore, the switch from grazing cattle to sheep has only occurred at Altcar in the last few years (J. Bell, pers. comm.) and lapwings may not yet have responded to such changes by altering chick rearing field types.

Pasture reared chicks were considerably heavier and in better condition by nine to ten days after hatching than chicks reared in arable habitats. This is similar to the situation found by Galbraith (1988b). In contrast to that study, however, the advantage of being reared in pasture for chicks in the current study was short lived. By 13 to 14 days after hatching chicks reared in spring crop fields were of a similar mass, size and, consequently, body condition than those reared in pasture. It would appear, therefore, that some crop fields provide rearing conditions of similar quality to that provided by pasture. Galbraith (1988b) also found that arable fields could provide adequate conditions for successfully rearing lapwing broods. The highest fledging success in his study was in one year when adverse weather retarded crop growth and chicks remained in their natal cereal fields. In two other years, when chicks hatched in spring cereals had moved to pasture, fledging success had been significantly lower.

Chick growth and development in RSA was lower than chicks reared in crop fields until nine to ten days after hatching. The reasons for this are not known. Additionally, post-hatching mortality, due to poor body condition, was higher in radio-marked chicks from RSA nests than in those hatched in spring crops. RSA was not generally used as a brood rearing habitat with most broods leaving RSA nest sites very soon after hatching. These fields, therefore, had a quality that was not conducive to the successful rearing of lapwing chicks. This may have been due to areas of tall and dense natural regeneration impeding parental vigilance for predators. This would not explain, however, poor chick growth. It is unlikely that slow chick development was due to low food abundance (see 6.2.2.i). A possible reason is that the nature of natural regeneration makes it harder for chicks to catch prey. In this study lapwing chicks were reared in pasture where the sward was kept short by high stocking rates or in spring farmed fields. Spring cereal fields were used until crop development pushed chicks into vegetable fields where plant stem density was low (compared to cereal and RSA) and larger areas of bare ground existed. Even in flowering (*i.e.* mature) potato and bean fields the ground is largely bare. The main components of chick diet in this study were cursorial, epigeal arthropods such as adult coleoptera (see 6.2.1). In RSA common plants (*e.g. Matricaria* spp, *Veronica* spp. and *Viola* spp.) grew in dense stands and formed mats of vegetation. In such a habitat chicks may have found beetle prey harder to see and catch, even though prey densities were not dissimilar to cultivated fields. Chicks may feed more successfully on bare ground and a short grazed sward as surface-active prey may be easier to see and catch. The few adults that nested and attempted to rear chicks in RSA may have been inexperienced (young) parents. Blomqvist *et al* (1997) found a significant difference in fledging success between first-time and experienced breeders. They suggested that foraging ability and the selection of foraging sites may differ between experienced and less experienced breeding lapwings. The quality of RSA, in terms of chick rearing, and the natural regeneration in RSA may, however, vary between fields and locations depending on several factors, such as previous management and cropping history, the 'arable weed' seed bank, soil type, etc.

iii. Radio-marked chick mortality

Most of the radio-marked chicks that died were probably predated. In many cases the predator could not be identified. Mammals were responsible for a proportion of the chicks taken but it is possible that the major predators of lapwing chicks in this study were avian, particularly raptors. In 23 observed predator attacks on lapwing chicks over three years (and 4200+ hours) at the study site, 21 (91%) were by kestrels and two were by stoats. The kestrels were successful on 15 (71%) of occasions and stoats on one. In addition, Marsh Harriers were observed to hunt over ditches possibly searching for any trapped potential prey. Predation was a significant mortality factor for chicks until at least 20 days after hatching. Observations of kestrel predation included attacks on chicks aged between 10 and 25 days old. Predation was unlike the mortality caused through ditch entrapment or poor body condition which mainly affected very young chicks.

Many of the predated chicks disappeared during the day which may mean that predation was not due to foxes which tend to be nocturnal (*e.g.* Baines 1990). Indeed, foxes might be expected to more strictly nocturnal in areas where they are persecuted due to game interests. Other mammalian predators, however, may hunt diurnally, *e.g.* both observed stoat incidents occurred during the late morning. Nevertheless, mammalian predators in the study area could be expected to occur at low densities due to predator control practised by the gamekeepers (*e.g.* see Reynolds 1999, Tapper *et al.* 1996). Also, if foxes were responsible for chick predation, nest predation might have also increased during the chick rearing period (*i.e.* mid-April –July). Egg predation, however, was lower after mid-April than it was earlier in the season.

Mortality of radio-marked chicks was higher for chicks hatched late in the season (after mid-May). In addition, chicks that hatched earlier in the season had significantly higher fledging success than those that hatched later. The increased mortality of chicks that hatched late in the season was not due to retarded growth rate and deterioration in body condition. Also, there was no seasonal decrease in the main food (beetles) of chicks (see chapter 6). For the radio-marked chicks, significantly higher predation (rather than poor body condition or ditch entrapment) caused the difference between early and late season survival. Kestrels might be expected to increase their provisioning of nests from mid-May as this is when their chicks hatch (Cramp and Simmons 1980). The higher predation of lapwing chicks late in the season might, therefore, be associated with an increase in predation effort by their main predator. Long-billed curlew (*Numenius americanus*) chicks hatched after the median hatch date have been found to have significantly higher mortality than chicks hatched earlier (Redmond and Jenni 1986). The higher mortality of late season chicks was shown to be the result of more intense raptor predation.

Kestrel predation of lapwing chicks is not unknown. At a local RSPB nature reserve (Marshside, Southport), consisting of coastal grazing meadows, lapwing chick production has been depressed most years due to chick predation by kestrels. In the current year, there was no kestrel predation of chicks (as no kestrels nested near the reserve) and fledging success was the highest since the meadows gained nature reserve status in 1995 (T. Baker, Marshside warden, Pers. comm.).

In the current study, fledging success was significantly higher in 1996 than in 1997. A greater proportion of chicks were reared on pasture in 1996 than in 1997 and high fledging success has been associated with the presence of pasture in arable areas (*e.g.*

Galbraith 1988b, Shrubb and Lack 1991). In this study, however, growth data showed that some arable fields provided rearing areas of comparable quality to that provided by pasture. Better feeding conditions in pasture fields might not, therefore, completely explain the lower fledging success of 1997. If kestrels were mainly responsible for the chick predation at the study site, the distribution of crops and pasture might have influenced the predation rates of particular field types. During the breeding season kestrels mainly hunt within 1km from their nest (Korpimaki *et al* 1994, Valkama *et al* 1995). Most of the pasture at the study site was centrally positioned and spring crop rearing fields more peripheral. As there were no kestrel nests within the study site (pers. obs), the chance of a lapwing chick being taken by a kestrel was higher for chicks reared in crop fields. All of the observed attacks by kestrels occurred against chicks in spring crop rearing fields.

It is possible that kestrels were not the only bird of prey responsible for taking young lapwing. One pair of Long-eared owls successfully bred within the study site. This species can be a significant predator of other birds during the breeding season even if their main prey (*Microtus* voles) are available (Nilsson 1981, in Cramp 1985). The targeting of avian prey by raptors and owls may be more pronounced in a landscape dominated by intensive cultivation where vole and other small mammal densities may be low.

To conclude, most mortality (52% of deaths) was probably the result of depredation with chicks being susceptible to predators throughout the fledging period, although chicks under 20 days old were most likely to have been depredated. Almost a third (31%) of chick deaths were the result of poor body condition and 17% of chick losses were the result of chicks becoming entrapped in ditches. The latter two mortality factors operated almost exclusively on very young chicks soon after hatching.

6.0 Chick diet and food abundance

This chapter investigates the abundance of lapwing chick prey in different rearing habitats and examines the diet of chicks feeding in those habitats.

6.1 Methods

6.1.1 Dietary (Faecal) Analysis

Chick diet was examined by the analysis of chick faeces obtained from 1995 to 1997. Faecal analysis was considered a reliable indicator of diet as it has previously been used to investigate the diet of lapwing chicks (Galbraith 1989a, Beintema *et al.* 1991) as well as the diet of birds in several other studies (*e.g.* Green 1978 and 1984, Hill 1985, Yalden 1986, Bowden and Smith 1997). Faeces were collected during the regular measuring operations for growth studies from chicks captured in the main rearing field types (RSA, pasture and spring cultivated fields). To negate any effect of individual specialization in prey type only one faecal sample per chick was analysed. Individual chicks could be recognised by their BTO ring number. Faeces were stored in 70% alcohol. Collected faeces were teased apart in a petri dish and the fragments counted and identified to family level under a binocular microscope with 10-45x magnification. Identification of invertebrate fragments was facilitated by reference to a collection of arthropods obtained from the pitfall traps of each field type (see 6.1.2.i.).

In order to relate the numbers of fragments of the common invertebrate taxa found in the chick faeces to the number of animals originally eaten the correction factors obtained by Galbraith (1989a) were used (Table 6.1.1a).

Table 6.1.1a The major fragments of 7 beetles, 4 beetle larvae, 4 spiders and 8 leatherjackets fed to a captive lapwing chick and recovered in the resulting faeces. *k* = a conversion factor relating the number of component parts eaten to the numbers obtained, *e.g.* $k_{\text{beetle mandibles}}$ = 14/11 (from Galbraith 1989a).

	Number fed	Number in faeces	*k*
Beetle mandibles	14	11	1.3
Beetle femora	42	35	1.2
Beetle tibiae	42	38	1.1
Beetle larvae-mandibles	8	7	1.1
Spider fangs	8	8	1.0
Leatherjacket mandibles	16	13	1.2

The result of the conversion with *k* was divided by the number of parts per animal to obtain the numbers of whole animals eaten. Fragments of taxa that occurred less commonly (*e.g.* Formicidae and Orthoptera) were identified using other component parts (*e.g.* heads, antennae). Minimum numbers of whole animals eaten for less frequent taxa were estimated by dividing the number of fragments found by the number of component parts per animal.

Galbraith's captive chick yielded 438 setae/earthworm eaten from which he obtained an estimate of the number of earthworms eaten from the faeces of wild chicks. In this study, however, the number of setae in faecal samples were few (with a maximum of 15 in one faecal sample). It is possible setae were overlooked although this seems unlikely as a similar method, using less powerful magnification, has been used by other workers *e.g.* Galbraith (1989a). The presence of setae or undigested earthworm segments were used, therefore, as an indication that one earthworm had been eaten.

Beintema *et al.* (1991), in digestion experiments on captive reared lapwing chicks, found that peak occurrence of insect fragments in the faeces was three to five hours after feeding. Galbraith (1989a) found that most taxa were represented in the faeces of a captive reared chick within 60 minutes of feeding. It was considered, therefore, that collected faeces represented a sample originating from the fauna of the locality (field) where the chick had been captured.

The estimated frequencies of prey items found in faeces were converted to approximate biomass by oven-drying to a constant weight 10 (or in the case of Aranae and Formicidae, 30) medium-sized representatives of each of the taxa. This allowed calculation of the mean dry-weight of individuals and the numbers of each item eaten could be multiplied accordingly.

Results of faecal analysis are presented as the estimated proportions and dry weights of the different invertebrate taxa in the diet of chicks reared in the three main brood rearing field types. Chi-square tests for association (with Yates correction applied) were used to investigate if the proportions of surface living arthropods and soil fauna differed between chicks that had fed in the different brood rearing habitats.

6.1.2 Food Abundance (Invertebrate sampling)

To assess the abundance of chick animal prey in different field types both surface-active and soil-living invertebrates were sampled using different methods. All results are from sampling carried out in 1997, however, familiarity with both methods and invertebrate identification was obtained by sampling in 1995 and 1996.

i. Surface-active prey

Surface-active invertebrates were sampled using pitfall traps. These were circular, plastic beakers 10.5cm deep with a neck diameter of 7.5cm. The beakers were buried to their rims in soil so the tops of the beakers were level with the field surface. Traps were filled to about one-third of their depth with an aqueous solution of tri-sodium orthophosphate ($Na_3PO_4.12H_20$; at 80g/*l*) used as a preservative (Sunderland *et al.* 1976) plus a few drops of detergent (reducing surface tension and, thus, escape potential). Traps were placed in parallel rows of five, with the first trap 1m from the field edge and subsequent traps 10m apart. Tramlines were avoided for trap placement so that farm machinery did not damage the beakers during cultivation activities. The first row of traps was placed 50m from a field corner (selected randomly by throwing a die) and the second row 50m from the first. All traps were placed, *i.e.* buried (with lids and without preservative) four days before operation to reduce 'digging-in effects' (Joose 1965 and Greenslade 1973). On activation lids were removed and preservative added. Traps were emptied fortnightly but checks were made at more regular intervals (at least every five days). These were done to ensure sufficient preservative remained in each beaker (especially during dry weather) or that beakers did not contain too much liquid (after heavy rain) possibly allowing animals to escape or diluting the preservative. Invertebrates were identified to the family level, counted and oven dried to a constant weight at 60°C. Keys used in the identification of invertebrates were (for all groups) Paviour-Smith & Whittaker (1968), Chinery (1973), Tilling (1987), for Arachnida, Jones (1984) and, for Coleoptera, Unwin (1988).

As traps were designed to capture cursorial, epigeal fauna, flying insects, such as adult Hymenoptera (*e.g. Bombus spp.*) and diptera (*e.g.* Calliphorids and Muscids), were excluded from sorting. The 1 mm mesh gauge of the (tea-strainer) sieve used for emptying traps was found to be too large to restrain all Collembola that had been captured and these were also excluded from sorting. This was considered reasonable as micro-arthropods have never been found to be a constituent of lapwing diet (*e.g.* Galbraith 1989a, Cramp & Simmons 1983).

Invertebrates were sampled in spring crop and RSA fields from the end of April to the end of June, thus measuring food availability during the main chick rearing period (Table 6.1.2a). Food availability was sampled in fields used for brood rearing. Disturbance of the substrate of spring farmed fields from cultivation meant that sampling earlier in the season was not possible. Spring cultivated land was sampled using both cereal and 'vegetable' (field bean) fields. Sampling in cereal was undertaken until crop development made it unsuitable for chick rearing (the beginning of June). Sampling after this date continued in fields containing field beans only. From 30/04 to 10/06 two crop fields (one spring cereal and one field bean field) were sampled. From 10 to 24/06 traps were operated in two fields containing field beans. Sampling in potato fields was attempted but unsuccessful due to the nature of cultivation of this crop type making the method ineffective (*e.g.* soil from the drills continually fell into traps, especially during 'earthing-up' operations). Due to the high stocking rates during the period of study (more than 28 sheep per hectare) pitfall trapping in pasture was not permitted due to the danger of injury to animals. Suction sampling could have been used as an alternative to pitfall traps but this method is considered unsuitable for recording carabid beetles (Aebischer 1991). Carabids have been identified as a major component in the diet of lapwing chicks in previous studies (*e.g.* Cramp & Simmons 1983, Galbraith 1989a, Baines 1990, Beintema *et al.* 1991).

As the number of arthropods caught in pitfall traps is based not only on the abundance of a particular species but also its activity, trap catches have been referred to as measures of 'activity-density' (Thiele 1977). Thus, the more active an animal the greater the probability of it being caught in a pitfall trap. Using pitfall traps was considered an appropriate method of measuring epigeal invertebrate availability because lapwings use visual cues for feeding and are, therefore, more likely to take active prey.

To remove weather as a potential source of variation in trap catch (Southwood 1978), all traps were operated contemporaneously and, thus, exposed to the same weather conditions.

The abundance and biomass (dry weight) of animals caught in pitfalls were expressed as means per trap-day, one trap-day representing one pitfall trap in operation for 24 hours. As two fields per field type (spring farmed and RSA) were sampled each fortnight there were 280 trap-days for each field type and sampling period.

Table 6.1.2a Details of pitfall trapping for surface active arthropods in lapwing brood rearing field types in 1997. Traps were emptied every fortnight.

Field type	No. fields sampled	No. of traps	Dates operated
RSA	2	20	30/04 – 24/06
Spring cereal	1	10	30/04 – 10/06
Field bean	1	10	30/04 – 24/06
Field bean	1	10	10/06 – 24/06

ii. Soil-living prey

Sub-surface invertebrates were sampled using a soil corer, 10 cm deep and 11 cm in diameter. Ten cores were taken from each of three crop fields (a potato field plus the two fields with pitfall placements), three RSA fields (including the two with pitfall placements) and two pasture fields (Table 6.1.2b). Sampling design was the same as for pitfall traps, except in those fields with pitfalls where it mirrored the surface invertebrate sampling (*i.e.* core lines were started from the opposite field edge to the pitfall placements). Time constraints meant that it was not possible to take all eighty soil cores on the same day. In order to even out possible variation from different weather conditions, half the samples from each field type (*i.e.* five from each field) were taken on 14/05 with the remainder obtained the next day. Each sample was placed in a sealed plastic bag and frozen for up to three months. After thawing, samples were placed in a 200mm diameter, 1mm mesh gauge sieve and shaken to remove soil particles. Any remaining soil was removed by gentle agitation of the sieve in a sink filled with water. Material that remained after this process was emptied into a shallow white tray half-filled with water and hand-sorted. Soil fauna were divided into Lumbricids, tipulid larvae or other larvae (which included other Dipteran and Coleopteran larvae) and oven-dried at 60°C to a constant weight.

The efficiency of hand-sorting in providing absolute population estimates varies for invertebrate groups, earthworm species and between soil types, the method being less efficient for heavier soils (Raw 1960, Edwards & Lofty 1977). For the fine-grained, light soils of the study area, however, it was considered to provide a reliable index of abundance for the comparative purposes of the invertebrate groups concerned.

Table 6.1.2b Details of soil core sampling for sub-surface fauna in lapwing brood rearing field types in 1997. Half the samples from each field were taken on the 14/05 with the remainder the following day.

Field type	No. fields sampled	No. of samples/field
RSA	3	10
Pasture	2	10
Spring cereal	1	10
Field bean	1	10
Potato	1	10

Data resulting from both pitfall traps and soil cores were not normally distributed, therefore, distribution free techniques were used for analysis. For pitfall trap data non-parametric Mann-Whitney tests were used to investigate differences in abundance and biomass of different taxa between field types for each sampling period and for investigation of seasonal differences between invertebrate groups. Mann-Whitney tests were also used on soil core data to investigate differences in invertebrate groups between different rearing field types.

It was not possible to use extraction techniques (using formaldehyde and salt) for sampling sub-surface prey availability as these were considered inappropriate by a number of farmers due to the nature of the sampling area.

6.2 Results

6.2.1 Chick diet

Faeces were collected from 54 chicks reared in RSA, pasture and spring cultivated fields. The results of the faecal analysis of the 54 chicks are shown in Table 6.2.1a.

Table 6.2.1a Estimated proportions and dry weights (*mg*) of invertebrate prey in the diet of 54 lapwing chicks reared in an area of intensive agriculture between 1995 and 1997.

Taxon	Individuals of each taxa *n*	% of total *n*	Individual mean dry weight	Total dry weight	% of total dry weight
Carabidaeae	299	*38.5*	1.6	478.4	*46.6*
Staphylinidae	138	*17.8*	1	138	*13.4*
Curculionidae	232	*29.9*	0.7	162.4	*15.8*
Histeridae	16	*2.1*	0.6	9.6	*0.9*
Chrysomelidae	2	*0.3*	0.7	1.4	*0.14*
Total adult Coleoptera	**687**	***88.5***		**789.8**	***76.9***
Formicidae	35	*4.5*	0.27	9.5	*0.9*
Aranae	15	*1.9*	0.5	7.5	*0.7*
Orthoptera	1	*0.13*	1.8	1.8	*0.2*
Total surface-living invertebrates	**738**	***95.1***		**808.6**	***78.7***
Lumbricidae	9	*1.2*	20.2	181.8	*17.7*
Coleopteran larvae	12	*1.6*	0.85	10.2	*1*
Tipulid larvae	5	*0.6*	3.3	16.5	*1.6*
Other Dipteran larvae	12	*1.6*	0.85	10.2	*1*
Total sub-surface invertebrates	**38**	***4.9***		**218.7**	***21.3***
Total	**776**			**1027.3**	

The most important constituent of chick diet, in terms of both abundance and biomass, was surface active invertebrates, particularly adult Coleoptera (mainly Carabid beetles). Soil living prey were also taken by chicks with larger, heavier taxa (*e.g.* Lumbricids and

Tipulid larvae) accounting for a proportionately greater part of the prey biomass. Separating the 54 chicks into categories according to rearing field type (*i.e.* field of capture) showed that this pattern remained with surface active prey forming the bulk of the diets in the RSA, spring crop and pasture reared chicks (Table 6.2.1b). Chicks reared in RSA and spring crop fields had similar diets. Even though the frequencies of prey taxa differed, the proportions (by dry weight) of surface active and soil living prey did not differ significantly between the two field types ($X^2_1 = 1.3$, $P > 0.2$). Surface living prey accounted for 90% of the dietary biomass and 98% of the total prey items of the RSA and crop reared chicks. The diet of chicks reared on permanent pasture, however, showed a greater prevalence of sub-surface invertebrates. These prey items accounted for a significantly greater part of the dietary biomass of the pasture reared chicks than of chicks reared elsewhere ($X^2_1 = 155.1$, $P < 0.001$). Specific identification of larval prey was not attempted so it could not be established if these organisms were associated with sheep dung. Lapwing chicks are known to feed on Dipteran larvae associated with cow dung (Beintema *et al.* 1991).

6.2.2 Prey abundance

i. Surface-living invertebrates

(a) Differences between field types

The percentage composition in terms of numbers and biomass of different invertebrate taxa caught in pitfall traps placed in spring farmed and RSA fields used for chick rearing are shown in Table 6.2.2a. The most abundant group in both field types was Coleoptera (mainly adult Carabid beetles) which accounted for 96% of the biomass of crop samples and 73% of those from RSA. The principal difference between the two field types was the greater abundance of spiders in RSA throughout the trapping period of 30/4 to 24/6

Table 6.2.1b Estimated proportions and dry weights (*mg*) of different invertebrate taxa in the diet of lapwing chicks reared in different field types in intensively cultivated farmland.

Taxon	Individuals of each taxa *n*	% of total *n*	Individual mean dry weight	Total dry weight	% of total dry weight
RSA *n* =16 chicks					
Carabidae	70	*46.4*	1.6	112	*57*
Staphylinidae	39	*25.8*	1	39	*19.8*
Curculionidae	16	*10.6*	0.7	11.2	*5.7*
Histeridae	4	*2.7*	0.6	2.4	*1.2*
Chrysomelidae	1	*0.7*	0.5	0.5	*0.3*
Total adult Coleoptera	**130**	***86.1***		**165.1**	***84***
Formicidae	14	*9.3*	0.27	3.8	*1.9*
Aranae	3	*2*	0.5	1.5	*0.8*
Orthoptera	1	*0.7*	1.8	1.8	*0.9*
Lumbricidae	1	*0.7*	20.2	20.2	*10.3*
Coleopteran larvae	1	*0.7*	0.85	0.85	*0.4*
Tipulid larvae	1	*0.7*	3.3	3.3	*1.2*
Total sub-surface invertebrates	**3**	***2***	**0.7**	**24.4**	***12.4***
Totals	**151**			**196.6**	
Spring crop *n* =28 chicks					
Carabidae	189	*47*	1.6	302.4	*61*
Staphylinidae	41	*10.2*	1	41	*8.3*
Curculionidae	138	*34.2*	0.7	96.6	*19.5*
Histeridae	4	*1*	0.6	2.4	*0.5*
Chrysomelidae	1	*0.3*	0.5	0.5	*0.1*
Total adult Coleoptera	**373**	***92.6***		**442.9**	***89.4***
Formicidae	17	*4.2*	0.27	4.6	*0.93*
Aranae	4	*1*	0.5	2	*0.4*
Lumbricidae	2	*0.5*	20.2	40.2	*8.1*
Coleopteran larvae	3	*0.74*	0.85	2.6	*0.5*
Dipteran larvae*	4	*1*	0.85	3.4	*0.7*
Total sub-surface invertebrates	**9**	***2.2***		**46.2**	***9.3***
Totals	**403**			**495.7**	
Pasture *n* =10 chicks					
Carabidae	40	*18*	1.6	64	*19*
Staphylinidae	58	*26.1*	1	58	*17.3*
Curculionidae	78	*35*	0.7	54.6	*16.3*
Histeridae	8	*3.6*	0.6	4.8	*1.4*
Chrysomelidae	0	*0*	0.5	0	*0*
Total adult Coleoptera	**184**	***82.9***		**181.4**	***54.2***
Formicidae	4	*1.8*	0.27	1.1	*0.3*
Aranae	8	*3.6*	0.5	4	*1.2*
Lumbricidae	6	*2.7*	20.2	121.2	*36.2*
Coleopteran larvae	8	*3.6*	0.85	6.8	*2*
Tipulid larvae	4	*1.8*	3.3	13.2	*4*
Dipteran larvae	8	*3.6*	0.85	6.8	*2*
Total sub-surface invertebrates	**26**	***11.7***		**148**	***44.2***
Totals	**222**			**334.5**	

* = Tipulid larvae absent

Table 6.2.2a Percentage composition (by numbers and biomass) of arthropods caught in pitfall traps in spring crop and rsa fields during lapwing chick rearing in an area of intensive cultivation.

			CROP					**RSA**		
Percentage numbers	30/4-13/5	13-27/5	27/5-10/6	10-24/6	**TOTAL**	30/4-13/5	13-27/5	27/5-10/6	10-24/6	**TOTAL**
Small Carabidae	85.8	76	47.2	63.5	**63**	40.8	31.9	39.2	29	**34.4**
Large Carabidae	1.2	2.6	31.1	20.1	**18.2**	0.6	2	4.7	5.9	**4**
Total Carabidae	87	78.6	78.3	83.6	**81.2**	41.4	33.9	43.9	34.9	**38.4**
Staphylinidae	5.7	7.4	4.5	8.4	**6.2**	4.3	11.1	11.2	8.7	**9.2**
Curculionidae	1.6	2.6	2.4	0.8	**1.9**	2	1.4	0.7	0.2	**0.9**
Histeridae & Chrysomelidae	0.3	0.4	0.4	0	**0.3**	3.4	0.9	0.4	0.3	**0.9**
Other Coleoptera	0	0.4	2.3	1.7	**1.5**	0	0.07	0.2	0.3	**0.2**
Total adult coleoptera	**94.5**	**89.4**	**87.9**	**94.5**	**91.1**	**51.1**	**47.4**	**56.4**	**44.4**	**49.6**
Aranae	4.4	8.1	8	4	**6.3**	38.3	45.5	38	53	**44.9**
Formicidae	0.4	0.9	3.5	1.5	**2**	3.7	5.3	4	1.9	**3.4**
Other	0.7	1.6	0.6	0	**0.6**	6.9	1.8	1.6	0.7	**2.1**
Total other	**5.5**	**10.6**	**12.1**	**5.5**	**8.9**	**48.9**	**52.6**	**43.6**	**55.6**	**50.4**
TOTAL NUMBERS	768	766	1773	1194	**4501**	1158	1374	2488	2994	**8014**
Percentage dry weight										
Small Carabidae	89.8	78.6	34.2	56.3	**54**	58.7	45.1	48.7	42.1	**47.1**
Large Carabidae	2.4	5.6	51.8	38.8	**35**	1.8	5.5	12.7	18.5	**12.1**
Total Carabidae	92.2	84.2	86	95.1	**89**	60.5	50.6	61.4	60.6	**59.2**
Staphylinidae	3.4	5.6	2	2.4	**2.8**	5	10.2	8.5	8.3	**8.3**
Curculionidae	0.8	1.3	0.9	0.3	**0.8**	1.3	1.1	0.3	0.1	**0.5**
Histeridae & Chrysomelidae	0.01	0.6	0.5	0	**0.3**	6.9	2.2	0.7	0.4	**1.7**
Other Coleoptera	0	0.5	6.5	0.4	**3.2**	0	0.1	3.5	5.9	**3.3**
Total adult coleoptera	**96.4**	**92.2**	**95.9**	**98.2**	**96.1**	**73.7**	**64.2**	**74.4**	**75.3**	**73**
Aranae	1.3	5.1	2.1	1.6	**2.3**	19.9	30.6	21.5	22.2	**23**
Formicidae	0.003	0.1	0.4	0.2	**0.2**	0.8	1.3	1.7	0.4	**1**
Other	2.3	2.6	1.6	0	**1.4**	5.6	3.9	2.4	2.1	**3**
Total other	**3.6**	**7.8**	**4.1**	**1.8**	**3.9**	**26.3**	**35.8**	**25.6**	**24.7**	**27**
TOTAL DRY-WEIGHT (mg)	1174	1109	3726	2167	**8176**	1244	1515	3224	3317	**9300**

Small Carabidae =<10mm in length; large Carabidae = >10mm in length.

Other Coleoptera' includes Cantharidae, Coccinelidae, Elateridae, Endomychidae, Lathridiidae, Scarabaeidae and Silphidae.

Other' includes Chilopoda, Diplopoda, Dermaptera, Hemiptera, Isopoda, Lepidoptera and Coleoptera (mainly Coccinelidae) larvae.

(Mann-Whitney test $_{numbers}$: $W_{80,80}$ = 3347, P<0.001). Despite non-Coleopteran invertebrates contributing a greater proportion of both quantity and biomass in RSA fields, the numbers of surface living invertebrates was significantly higher in RSA fields only for the periods 30/4 to 13/5 (Mann-Whitney test $_{numbers}$: $W_{20,20}$ = 296, P<0.01) and 13/5 to 27/5 (Mann-Whitney test $_{numbers}$: $W_{20,20}$ = 308, P<0.01; Table 6.2.2b). The mean dry weight of trapped invertebrates for these periods, however, did not differ significantly for these two periods between field type (Mann-Whitney test $_{dry\ weight}$: $W_{20,20}$ = 369 and $W_{20,20}$ = 355 for 30/4-13/5 and 13/5-27/5 respectively). In May, therefore, the more numerous (but small) Aranae in RSA did not significantly add to the overall biomass and in June the more numerous larger Carabids of crops compensated for the lack of biomass of non-Coleopteran taxa.

Table 6.2.2b Mean numbers and dry weights (*mg*) per trap-day of surface-living invertebrates caught in pitfall traps placed in spring crop and RSA fields in intensively cultivated farmland. Figures in parentheses represent standard error. The number of trap-days for each period and each field type was 280.

	Dates and periods of placement of traps			
	30/4-13/5	13/5-27/5	27/5-10/6	10/6-24/6
Mean numbers/trap-day				
Crop	2.7 (0.39)	2.7 (0.23)	6.3 (0.66)	4.3 (0.36)
RSA	4.1 (0.33)**	4.9 (0.53)**	8.9 (1.08)	10.7 (2.18)
Mean dry weight/trap-day				
Crop	4.2 (0.63)	4.1 (0.42)	13.3 (1.81)	7.7 (0.74)
RSA	4.4 (0.44)	5.4 (0.66)	11.5 (1.43)	11.8 (2.57)

** = P<0.01, probability value of Mann-Whitney tests between field types. One trap-day = one pitfall trap operating for 24 hours.

If just the main Coleopteran prey taxa (Carabid, Staphylinid and Curculionid beetles) found in chick faeces are considered there were no significant differences in numbers between crop and RSA fields (Mann-Whitney tests: $W_{20,20}$ = 452, 457, 456, 467 for periods 30/4-13/5, 13-27/5, 27/5-10/6, 10-24/6 respectively; Table 6.2.2c). Biomass similarly did not differ significantly between field types (Mann-Whitney tests: $W_{20,20}$ = 452, 447, 457 for periods 30/4-13/5, 13-27/5, 10-24/6 respectively) except for the period

27/5 to 10/6 (Table 6.2.2c). In this period the large (>10 mm in length), heavier Carabid beetles in crop fields accounted for 52% of the total sample biomass whereas in RSA they constituted 13% (Table 6.2.2a). When the dry weight of the more numerous small Carabidae (<10 mm in length) plus that of Staphylinidae and Curculionidae is considered there is no significant difference in biomass in this period between field types (Mann-Whitney test: $W_{20,20}$= 385).

Table 6.2.2c Mean numbers and dry weights (*mg*) per trap-day of Carabid, Staphylinid and Curculionid beetles caught in pitfall traps in spring crop and RSA fields in intensively cultivated farmland. Figures in parentheses represent standard error. The number of trap-days for each period and each field type was 280.

	Dates and periods of placement of traps			
	30/4-13/5	13/5-27/5	27/5-10/6	10/6-24/6
Mean numbers/trap-day				
Crop	2.6 (0.39)	2.4 (0.20)	5.4 (0.53)	4.0 (0.36)
RSA	2.0 (0.27)	2.1 (0.31)	5.0 (0.77)	4.7 (1.18)
Mean dry weight/trap-day				
Crop	4.0 (0.62)	3.8 (0.33)	12.1 (1.63)	7.5 (0.75)
RSA	3.1 (0.43)	3.4 (0.49)	8.1 (1.11)*	8.2 (1.96)

* = $P<0.05$, probability value for Mann-Whitney test between field types ($W_{20,20}$ = 490).

(b) Seasonal differences in prey abundance

The effect of season on surface living prey abundance and biomass was investigated for spring crop fields (the main rearing field type). As it was found that chick growth rate was not affected by hatch date (5.2.6. iii) it might be expected that prey availability was also unaffected by season. The numbers and biomass of carabid, staphylinid plus curculionid beetles caught in traps between 30/4-13/5 and 10-24/6 were compared. These prey items occurred in significantly greater numbers and weight later in the chick-rearing season (Mann-Whitney test: $W_{20,20}$ = 310, $P<0.01$ $W_{20,20}$ = 288, $P<0.01$; for numbers and dry weight respectively; Table 6.2.2c).

Chicks might be expected to take small to medium sized surface living prey as such items might be easier to catch if they are more abundant (see 6.2.2c) and are not as fast moving as larger beetles. Prey that is <10mm in length might be easier to swallow. In the trap period 30/4-13/5, 97.4% of Carabids were classified as small (10 mm or less in length), whereas between 10-24/6, 41% of the Carabidae caught consisted of large beetles (>10 mm in length; Table 6.2.2a). Seasonal differences were, therefore, examined excluding large beetles (Table 6.2.2d).

Table 6.2.2d Mean numbers and dry weights (*mg*) per trap-day (with standard error in parenthesis) of small (10 mm or less in length) Carabid, Staphylinid and Curculionid beetles caught in pitfall traps in intensively cultivated spring sown crops.

	Number of trap-days	Mean numbers/ trap-day	Mean dry weight/ trap-day
30/4-13/5	280	2.6 (0.39)	2.5 (0.39)
10-24/6	280	3.1 (0.37)	2.9 (0.38)

No significant differences between numbers or biomass of small beetles were evident between the two periods (Mann-Whitney tests; $W_{nWmbers20,20} = 310$, $P>0.2$; $W_{dry\ weight\ 20,20} = 384$, $P>0.4$). This indicates that there is no seasonal change in the availability of small and medium sized coleopteran prey for chicks.

(c) Chick diet in relation to rearing field arthropod abundance

In both crop and RSA fields lapwing chick diet consisted of the most abundant arthropods. In general, the commoner the taxa the more prevalent it was in chick diet (Table 6.2.2e). This suggests chicks fed opportunistically. Carabid beetles were the single most abundant taxa and composed the greatest part of the diet in chicks reared in both crop and RSA fields. Staphylinid beetles were significantly commoner in RSA than in crop fields after mid-May (Mann-Whitney tests: for 30/4-24/6; $W_{80,80} = 5960$, $P>0.05$; for 13/5-24/6; $W_{60,60} = 3236$, $P<0.05$), and were significantly more common in the diet of RSA than crop reared chicks ($X^2_1 = 21.8$, $P<0.001$). Curculionid beetles were significantly more abundant as prey items in the diet of crop reared chicks than in those reared in RSA fields ($X^2_1 = 30.6$, $P < 0.001$). These taxa were significantly more abundant in crop fields than in RSA after mid-May (Mann-Whitney tests: for 30/4-24/6; $W_{80,80} = 6771$, $P > 0.1$, for 13/5-24/6; $W_{60,60} = 4022$, $P < 0.05$). Histerid and Chrysomelid beetles were significantly more abundant in RSA fields than in crop fields (Mann-Whitney test: $W_{80,80} = 5389$, $P < 0.001$). Although the difference between the field types was not significant ($X^2_1 = 2.7$, $P > 0.1$), these beetles were also 2.8 times more abundant in the diet of RSA than in crop reared chicks.

Table 6.2.2e Numerical percentage composition of the surface-living arthropod component in the diet of lapwing chicks compared to that of pitfall traps from the same field types.

	Crop		RSA	
	Pitfall	Diet	Pitfall	Diet
Carabidae	81.2	47	38.4	46.4
Staphylinidae	6.2	10.2	9.2	25.8
Curculionidae	1.9	34.2	0.9	10.6
Histeridae & Chrysomelidae	0.3	1.3	0.9	3.4
Other	10.4	5.2	50.6	12

'Other' is mainly Aranae and Formicidae. The remainder of the diet was composed of soil living invertebrates.

The only taxa well represented in pitfall traps but not in chick faeces were the Aranae. These were seven times more abundant in the RSA samples than those from crop fields and contributed ten times more of the overall biomass of RSA traps (Table 6.2.2a). Although spiders were twice as abundant in the RSA chick faeces than the crop reared sample, they only contributed 2% of the total prey items. The majority of the spiders in the RSA pitfall samples were very small (body length <2mm). It is likely, therefore, that any Aranid remains (*e.g.* fangs and legs) in the faeces were too small or fragmented to be recognised and counted. No remains of similarly small arthropods, such as those from Collembola, were found in faeces either. It may also be that with larger prey (*e.g.* ground and rove beetles), perhaps in surfeit, very small prey items were not taken.

ii. Soil living prey

The number and dry weights of sub-surface invertebrates in 950.5 cm^3 soil cores taken in spring crop, RSA and pasture fields are shown in Table 6.2.2f. Similar numbers of earthworms and arthropod larvae were found in spring crop and RSA fields (Mann-Whitney tests: $W_{30,30} = 960, 987, 978$, in each case $P>0.2$; for earthworms, Tipulids and other larvae respectively). Not surprisingly the biomass of these three invertebrate groups also did not differ significantly between the two field types (Mann-Whitney tests: $W_{30,30} = 987, 996$ and 969 for earthworms, Tipulid larvae and other larvae respectively). As there were no significant differences in either numbers or biomass of soil invertebrates from RSA and crop fields, samples from these field types were combined for comparison with pasture fields. Numbers and biomass of each of the invertebrate groups were significantly higher in samples from pasture fields than in those from RSA and crop fields combined (Mann-Whitney tests: $W_{numbers\ 60,20} = 1893, 2096$ and 2028, $P<0.001$ in each case; for earthworms, Tipulid larvae and other larvae respectively; $W_{dry\ \mathrm{weight}\ 60,20} = 1899, 2095$ and 2034, $P<0.001$ in each case; for earthworms, Tipulid larvae and other larvae respectively). The main soil living prey of lapwing chicks were, therefore, more abundant in pasture fields than elsewhere.

This difference between field types in soil invertebrates is reflected in chick diet (Table 6.2.1b). Compared to chicks reared in RSA and crop fields, soil living invertebrates were 5.3 times more abundant in the faeces of pasture reared chicks and contributed 4.8 times more of the invertebrate biomass.

Table 6.2.2f Mean numbers and dry weights (*mg*) of soil living invertebrates in 950.5 cm^3 (10cm deep and 11cm in diameter) soil cores from three different field types in intensively cultivated farmland. Standard error in parenthesis.

		Lumbricidae	Tipulid larvae	Other larvae
	Samples *n*	Mean *n*/sample	Mean *n*/sample	Mean *n*/sample
Crop	30	0.73 (0.14)	0.63 (0.16)	0.50 (0.15)
RSA	30	0.97 (0.19)	0.87 (0.20)	0.73 (0.17)
Pasture	20	3.20 (0.23)	1.80 (0.23)	2.70 (0.40)
		Mean dry weight/ sample	Mean dry weight/ sample	Mean dry weight/ sample
Crop	30	12.6 (2.63)	1.98 (0.49)	0.45 (0.14)
RSA	30	19.6 (3.91)	2.50 (0.50)	0.62 (0.15)
Pasture	20	67.5 (7.13)	5.80 (0.74)	2.30 (0.31)

'Other larvae' represent other Dipteran and Coleopteran larvae.

6.3 Discussion

The diet of lapwing chicks in this study was composed largely of adult beetles (Coleoptera) which is similar to the findings of other studies (*e.g.* Matter 1982, Galbraith 1989a, Baines 1990 and Beintema *et al.* 1991). As beetles were commoner than other types of prey chicks appeared to feed opportunistically rather than selectively. Differences between studies tend to be in the differing proportions of sub-surface and surface active prey in the diet of chicks. In contrast to this study and others, Galbraith (1989a) found that earthworms were the most important constituent (in terms of mass) of chick diet in both arable and rough grazing habitats. This may partly reflect the fact that Galbraiths' 'arable' habitat included faecal samples taken from chicks reared in pasture as opposed to cultivated fields. Nevertheless, in this study, even chicks reared in pasture relied mainly on beetles for food. Pasture reared chicks did, however, take more earthworms and fly and beetle larvae than chicks reared in crops and RSA. This reflects an opportunism as these groups were more abundant in pasture than elsewhere. It is possible that higher levels of larval prey (especially Dipteran) reflect chicks taking advantage of sheep dung as has been found elsewhere where cow dung is available (Beintema *et al.* 1991). Baines (1990), examining chick diet from stomach contents for lapwings breeding in upland grasslands found no earthworm remains. The commonest animals eaten were adult Coleopterans which, similarly to this study, formed 80% of chick diet. Baines thought that lapwings switched their dietary emphasis from soil living organisms to surface active prey as the season progressed. He based this conclusion, however, on the comparison of stomach contents of adults that had died before the 1 May with those of adults and chicks that had died after 1 May. His conclusion may only pertain to adult lapwing as experience and, particularly, the different bill lengths of adults and chicks may cause dietary differences, particularly with sub-surface prey. In Dutch agricultural grasslands, however, earthworms, as well as beetles, were found to be common dietary elements of lapwing chicks (Beintema *et al.* 1991).

There was no seasonal affect on chick growth rates in this study (see 5.2.6.iii) and in accordance with this finding there was no seasonal decrease of their main arthropod prey (see 6.2.2.i). In fact, the numbers and the biomass of the main prey items actually increased through the season. Conversely, Galbraith (1988b, 1988c) found late hatched chicks grew less well than earlier hatched chicks in rough grazing sites. Galbraith thought that this was probably due to a deterioration in chick food supply as earthworms had burrowed to deep to be obtainable and leatherjacket larvae had metamorphosed into adults. In Beintema *et al.*'s (1991) study on Dutch farmland, chicks showed retarded growth before a peak in arthropod abundance. They proposed that lapwing chicks cannot mature on small insect food alone and that they need to switch to more profitable (*i.e.* larger) prey, such as earthworms, to develop. Slower chick growth rates from mid-May are, therefore, the result of earthworms or large prey items being less available later in the season. The unaffected seasonal growth rates of chicks in this study might be due to differences between arable and grassland habitats in the availability and profitability of arthropod prey. Surface-active invertebrates in arable have been found to be larger and more abundant than in pasture (*e.g.* Galbraith 1988b). In the current study, large beetles were common in samples in May and, particularly, June. As the same method was used for measuring surface-active prey abundance comparison can be made between this and the Dutch and Scottish studies. The trap size of pitfall traps used by Beintema *et al* (1991) is unknown although the neck diameter of traps in this study (7.5cm) was similar to that used by Galbraith (7.0cm). Surface-active invertebrates were up to 32 times more abundant in spring crops in this study than in spring cereal fields sampled by Galbraith (1988b) and seven times more abundant than in the Dutch agricultural grasslands sampled by Beintema *et al.* (1991). Such comparisons must be treated with caution as, although sampling dates were similar, weather differences may affect arthropod population sizes and the activity (and, therefore, the catch rate) of invertebrate species. It would appear, though, that the crop rearing fields of this study had high surface-active invertebrate populations. Furthermore, chicks may find surface-active prey easier to see and catch in arable, where there is much bare ground, than in grassland habitats, where the surface is covered in vegetation. Alternatively, late season chicks may have fed more in field boundary ditches where, closer to the water table, earthworms were easier to obtain.

There was no difference between RSA and spring crop fields in the measured abundance and biomass of the main chick prey. The reason that RSA was not generally used to rear chicks was presumably due to some reason other than chick food abundance (see 5.3). In fact, it is possible that coleopteran prey were less common in spring crop fields than RSA but more active, which may have made them more available to lapwings which hunt visually. Regulations set by MAFF governing the management of RSA prohibited the use of insecticides (see 1.4.2). Chiverton (1984) has suggested that the use of pesticides in a crop depletes the prey of coleoptera, increasing the activity of carabids (thereby increasing their catching rate in pitfall traps) as they become hungry. This antiexenosis would not have been apparent in carabids in RSA as pesticides were not used.

As lapwing are visual hunters prey abundance (as measured by the sampling methods used in this study) in a particular field may not reflect food availability. Lapwing may be less successful at capturing prey in fields where there is a complex sward as prey items may be hidden even though occurring in high densities. A direct measure of the prey available to lapwing could be obtained from observations of foraging adults and chicks.

A comparison of success rates and, perhaps, even prey sizes, could be then made between different arable field types to provide an assessment of what prey is available to lapwing adults and chicks.

7.0 General discussion and overall conclusions

7.1 Breeding ecology

On the Altcar Estate in south-west Lancashire lapwings preferred to nest in unsown fields where nest loss from farming operations (the main cause of nest destruction) was highest. There was, however, a high replacement rate of lost clutches. Lapwings chose such nest sites as the extensive first clutch losses were compensated for by the high hatching success of replacement clutches laid in sown fields. This is similar to the situation that was found in central Sweden where lapwing were also breeding in an area with much spring tillage (Berg *et al.* 1992). Including replacement clutches, at least 76% of the female lapwings in this study were estimated to have hatched a clutch. This is comparable to the hatching figure of 69% on unimproved grassland in northern England reported by Baines (1989). It is also higher than the 51.5% of successful females reported by Berg *et al.* (1992) in Sweden as in the Altcar study more females hatched first clutches in unsown fields and RSA. The significantly higher success of nests in unsown fields in this study (23% versus 9% in the Swedish study, $z = 3.84$, $P<0.001$) is either due to differences in the timing of laying or, more probably, the timing of spring cultivation which continued until mid-May at Altcar. The timing of cultivation activities are not known for the Swedish study. In Sweden, however, farm operations were, presumably, significantly earlier considering the low hatching success of first clutches (in unsown fields) and the fact that spring crops only included cereals and not later sown crops, such as potatoes. There was no set-aside in the Swedish study although a similar field category, fallow, differed to RSA in that it received considerable management over the nesting period which reduced hatching success to 31% (compared to 88% in RSA). This emphasises the benign nature of RSA and the importance of prohibiting farming operations during the nesting period for high nesting success. Similarly to Berg *et al.* (1992) it can be concluded that in cultivated fields at Altcar the influence of intensive cultivation on successful nesting was smaller than could have been expected. The important factor was the crop phenology, the cultivation of spring crops causing some destruction of first clutches but allowing the high success of replacements. As a result overall nesting success was high. There was a difference, however, between RSA and spring farmed land in the higher success (100%) of first clutches in RSA. This feature of RSA had advantages for productivity due to the lower depredation and consequent higher survival of early hatched chicks (see below and chapter 8).

It is possible that some of the nests classified as replacements at Altcar actually represented initial breeding attempts with a proportion of the population adopting a strategy of late nesting to avoid early season failure. This was impossible to determine in this study as the adult population was unmarked. Such a strategy may be unlikely as the majority (62%) of females hatched a first clutch and most unsuccessful first attempts were replaced with a successful second clutch. As replacements were of the same size as initial clutches, delaying breeding would not have conferred advantage. In addition, rapid crop growth later in the breeding season reduces the area available for nesting and chick rearing increasing interspecific competition. Furthermore, no evidence of a late or delayed breeding strategy has been found in any study of breeding lapwing where the adult population has been marked (*e.g.* Galbraith 1988b, Thompson *et al.* 1994, Hegyi and Sasvari 1998). The high proportion replacements in this study may be a result of the prolonged cultivation period. This may have allowed females (possibly from outside the study area) unsuccessful in first and second attempts to nest later in the season as nesting habitat became available through late cultivation.

The nesting phase of lapwings, therefore, appears to be well adapted to spring tilled farmland, allowing high success despite heavy losses to farming operations. Indeed, the preference for choosing unsown fields for nesting emphasises the importance of spring farming to lapwing as a requirement for successful nesting on tilled land.

Egg predation was low (only 7.25% of all clutches were recorded as having had one egg or more depredated) and was reduced by behavioural adaptations. Lapwings preferred to nest far from ditches where their hatching success was higher. Perches for avian egg predators were scarce and their proximity to nests did not influence egg predation risk.

Predation was also reduced by lapwings preferring to breed in dense aggregations, hatching success being lower only for pairs without any close neighbours. It would appear, therefore, that some egg predation is the result of predators that can be deterred by the group nest defence behaviour of breeding adults. The number of lapwing involved in attacks against predators, such as foxes, has been shown not to be related to the size of lapwing aggregations (Elliot 1985b). Elliot thought that this was because foxes present a danger to adult lapwing. Smaller mammals may not present such a high degree of danger to lapwing. A stronger relationship may be expected, then, between the size of groups of lapwing attacking smaller mammals, such as hedgehogs, rats and stoats, and the size of the breeding aggregation. Berg (1996) illustrated the advantage to be gained from lapwing breeding in aggregations through experiments with artificial nests. Berg showed that solitary lapwing nests had higher predation rates than those nests within aggregations. In comparison, artificial nests without defending adults had the highest rates of predation.

Predation was further reduced by lapwing choosing spring farmed land for nesting where fewer eggs were depredated than from nests on winter farmed land. Predation from winter farmed nests was, however, low with only 13.6% of nests losing one or more eggs to predators. Overall, low egg predation rates were experienced by the Altcar lapwing population which may indicate that pressures other than predation were operating on nest site selection. Such a pressure could be food availability to females prior to breeding for egg formation. The bare substrates of unsown fields could provide females with a more available food source as prey items could be harder to detect in those fields with a dense, emergent sward. As over a third of the Altar study area was spring farmed females nesting in winter farmed fields would not have had to have made long (energetically expensive) journeys to reach a spring farmed feeding location. It has been found, however, that that in the week before laying foraging journeys of female lapwing are mostly restricted to within 170m of the nest site (Blomqvist and Johansson 1995). Furthermore, during the early incubation period it has been found that breeding female lapwing tend to forage mostly within 100m of the nest this distance increasing but remaining less than 200m during the latter half of incubation (Hegyi and Sasvari 1998). If a similar situation existed for female lapwing breeding at Altcar the majority of females would forage in their nesting field prior to egg laying and during incubation. Where there are low predation rates the choice of unsown fields for nesting may reflect the pressure exerted by the need for the increased condition of breeding females as opposed to that exerted by predation. Females may improve their breeding condition by a reduction in energy expenditure and increasing food intake by nesting in areas with greater prey availability. A similar situation would exist for chicks on hatching as areas of bare ground and high prey availability may remain. An additional pressure on young chicks is that they must avoid their down becoming wetted by moving through vegetation. This would also select for nesting sites in or near areas with bare ground or very short vegetation (*e.g.* Galbraith 1988b).

The intensity of predator control and the consequent intensity of predation varied during the nesting season. The risk of egg predation was greatest early in the nesting season when predator control was least. It would appear, therefore, that predator control may also be an important factor in the low egg predation reported in this study. Even though lapwing reduced predation risk by breeding in dense aggregations in spring farmed fields, avoiding sites near ditches and nesting far from trees, this only deterred predators against which lapwing can mount effective attacks. As Berg *et al* (1992) noted if foxes are the commonest nest predator it would be expected that nesting in dense aggregations would be disadvantageous. Tinbergen *et al* (1967) used artificial nests to show the degree of predation was positively related to nesting density, due to predators showing 'area restricted searching' after a successful find. This finding has been corroborated from studies on natural nests (*e.g.* Dunn 1977). In this study as 98% of lapwings nested in aggregations and 85% of nests had close neighbours, predation levels may have been low due to the low densities of foxes which was, probably due to predator control by gamekeepers. If predator control ceased on Altcar fox density may increase with a possible detrimental effect on the lapwing population. As lapwings on Altcar nest in aggregations the chance of foxes finding nests through area restricted searches would be high unless lapwings modified their breeding behaviour and nested less densely. Such a change would increase the risk of predation to nests from birds and small mammals. This study found that the present management of Altcar is beneficial to nesting lapwings as egg production (a high mean clutch size for first and replacement clutches) and high hatching success are not factors that would limit breeding productivity.

In contrast to eggs, chick predation appeared high. Amongst radio-marked chicks, the proximate cause of most (52%) losses was depredation. Identification of the predator species involved was partly speculative, however, raptors, particularly kestrels, appeared to be mainly responsible. It was not known, however, how many kestrels were involved, if this was the main species taking chicks. In contrast to other lapwing chick predators (*e.g.* foxes, stoats and crows), raptor densities were not affected by predator control as all raptor species are legally protected. There was no evidence of the law being broken in this respect at Altcar during the study period.

Declining lapwing chick production in intensively farmed arable areas has been connected to the decline in permanent pasture with a concomitant increase in the area of tilled land (Shrubb and Lack 1991). Lapwing chicks that hatch on arable land move to the better rearing conditions provided by pasture with the result that chick survival is influenced by the distance from the nest to pasture (Galbraith 1988b). Previously it has been thought that chick prey was more abundant in pasture than in cultivated fields and that (short-legged) chicks are better adapted to the short grazed sward provided by pasture (Hudson *et al.* 1994). This study has shown that lapwing chicks reared in arable can grow as well and maintain a similar body condition to those that are reared in pasture. Furthermore, pasture only represented about 2% of the cropped land area in the current study and surface-active food prey was abundant in spring farmed fields. The presence of pasture may not, therefore, be so important where chicks have access to arable fields which provide suitable rearing conditions. The mix of crops and the crop phenology at the study site, with sowing until mid-May, meant brood use of many arable fields was not truncated by crop growth. The presence of row and other vegetable crops allowed chicks to move into bean, potato or carrot fields once spring cereals became dense and tall.

It would, therefore, appear that the most important influence on lapwing breeding ecology at the Altcar study site was the crop phenology. Cultivation occurred from the late winter through to late spring. This provided ideal nesting requirements for lapwing and the opportunity to replace any clutches lost from cultivation activities. Consequently most females hatched clutches and mean clutch size and hatching success was high. The hatching success of first clutches was increased by late spring sowing which allowed many nests on unsown land to hatch before cultivation commenced. First clutch hatching success was also increased by the introduction of RSA into the cropping regime (where no farm operations were permitted) and the avoidance of nests by some farmers during cultivation. As there were game interests within the study area predator control probably had an affect on reducing predation by keeping predators, particularly foxes and corvids, at low density. Behavioural adaptations of lapwing (*e.g.* nesting in dense colonies and far from ditches) and, perhaps, the nature of the landscape reduced nest predation from smaller mammalian predators and birds. Chick predation was a significant mortality factor and seemed to be mainly due to kestrels. Chick predation was lower earlier in the chick rearing season and, therefore, the high hatching success of first clutches in RSA and elsewhere may have benefited productivity at the site. All first clutches on RSA at Altcar were successful and accounted for 13.25% of all first clutches. If these clutches had been on unsown land only 22.6% of these would have hatched (as opposed to 100%). Only an estimated 13.6% of the females failing in the original attempt would have hatched a replacement clutch. In the absence of RSA (assuming the average clutch size for both first and replacement clutches; see 4.2.4.ii), therefore, it can be estimated that 116.7 fewer chicks would have been produced (the number of chicks produced from the successful first clutches in RSA minus the number of chicks hatched from the successful 22.6% first clutches in unsown fields plus those hatched from the successful replacements). In addition, the 12% of the chicks hatched in the absence of RSA would be from the replacement clutches later in the season and would be exposed to a significantly higher risk of predation than the first clutch chicks from RSA nests.

Post-hatching movements of chicks out of natal fields seemed to be related to the stage of crop development or, in RSA, vegetation height. RSA was a preferred nesting field type but was not generally used for rearing chicks. Broods moved into fields where crops were not tall and dense, thus, brood movements were related to the sowing date, crop type and distribution. Fledging success was related to brood movements which may have resulted in chicks starving, becoming entrapped in ditches and being more vulnerable to predators. The cultivation of vegetable crops extended the breeding season as there were still arable fields suitable for chick rearing in July. Chicks could feed in vegetable fields with mature crops but were forced out of spring cereals once the crop was established. In spring farmed areas with little pasture and little or no vegetable cultivation the breeding season of lapwings may be less prolonged (*e.g.* Galbraith 1988b).

This study has established that through high egg production and high hatching success the Altcar lapwing population had a sufficient brood size at hatching not to limit productivity. Fledgling production for the two years, however, was below that which is required to maintain the population. Peach *et al.* (1994) have shown that lapwing breeding productivity needs to be 0.83–0.97 fledglings per pair, depending on the proportion of first year recruitment into the breeding population, in order for a population to replace adult losses. At Altcar productivity (0.73 in 1996 and 0.40 in 1997; 5.2.4.i.) was insufficient in both years for population maintenance. A similar situation was found by Galbraith (1988b) in Scotland and Baines (1989) in northern England. Their productivity (mean number of young fledged per pair) estimates for arable breeding lapwing were 0.5 and 0.6 for the Scottish and English studies respectively. These figures are not too dissimilar to the overall productivity figure of 0.57 fledglings per pair for this study. With such low production the population at Altcar was in decline unless supported by immigration from elsewhere. Over the two years of the study, therefore, productivity ranged from 41-88% of what was needed to maintain numbers. Hence, in some years declines may exceed those estimated for the North of England (see 1.2.1).

As nest success was high the productivity deficit was due to poor chick survival. In order to achieve a productivity of 0.9 (the mean value of 0.83 and 0.97) fledglings per pair an additional 6 chicks would have needed to have fledged in 1996 with an additional 28 chicks in 1997 (see 5.2.4, Table 5.2.4a). Using radio-marked chick survival data (5.2.7ii) this would have represented a reduction in predation of 13.5% and 30% in 1996 and 1997 respectively. Whilst these calculations are very approximate they indicate the levels needed to produce a stable population.

7.2 Status

The mix of spring farmed crops at the study site provided lapwing with an environment suitable for both nesting and chick rearing. It may be difficult to obtain a reliable population trend for the study area, however, due to the nature of arable farmland. Crops are rotated and the proportions of different crop types change. As the study site was surrounded by an area of similar farmland, which also held breeding lapwing, there may have been some immigration/emigration as once suitable breeding areas became unsuitable due to cropping changes. For example, lapwing did not use oilseed rape fields, the commonest single crop type in the study area. Cropping changes might, therefore, cause a redistribution of breeding birds. Nevertheless, the breeding density of lapwing in the study area may reflect the suitability of the site as breeding habitat. Calculating the number of pairs from the number of nests classified as first clutches in each year gives a breeding density of 13.5 pairs 100 ha^{-1} in 1996 and 13.0 pairs 100 ha^{-1} in 1997. This is more than twice the density of 5.8 pairs 100 ha^{-1} found recently on 23km^2 of agricultural land in the Forest of Bowland by the RSPB (Babbs 1998). This indicates that the intensively farmed land at Altcar is better for breeding lapwing than the agricultural land in the Pennines. In addition, the RSPB survey showed that there had been a decline of 33% in the number of lapwing pairs since 1993. The Forest of Bowland forms part of the Pennine area that the 1987 BTO lapwing survey showed to hold some of the highest densities in England and Wales (Shrubb and Lack 1991). In lowland grassland (including both farmland and nature reserves) in England and Wales lapwing densities have declined so that by 1989 there were only 1.05 pairs 100 ha^{-1} (O'Brien and Smith 1992). With national as well as local declines it would seem unlikely that the lapwing population of the Altcar study site has increased as a result of recruiting surplus lapwings originating from outside the Amounderness plain.

There have been no previous censuses of lapwings in the survey area and it is, therefore, difficult to ascertain if the population has diminished. The recent national lapwing survey (Wilson *et al.* in press), however, has shown the population of the north of England to have declined by 42-60% since 1987 (see 1.2.1). Comment on the status of the study site population may be inferred from examination of agricultural change in the area. This study has shown that it is the spring tillage in the area that provides lapwing with all of their breeding requirements. Changes in the area of spring tilled land are, therefore, likely to have detrimental effects on the size of the lapwing population. It is not possible to obtain agricultural data for specific parishes but statistics are published by MAFF for parish groups. The study site included much of the parish of Altcar and data for this parish and three adjoining parishes were obtained to examine any changes in cropping. Over the ten years from 1988 to 1998 there was a 23% decrease in the spring farmed area, mainly due to a decrease in spring cereals (rather than vegetables) and a large increase in the area autumn sown (Table 7.0a). There was a 2% increase in permanent pasture over the period but sheep numbers more than doubled from 1,710 in 1988 to 4,237 in 1998, an increase of 60%. Cattle numbers also increased by 20%, rising from 898 to 1,122 over the same period. Furthermore, within the four parishes there was a 13.5% decrease in the total area of agricultural land.

The increase in the area of pasture may benefit chicks, particularly if it abuts spring tillage. The large increase in stocking densities, however, would increase trampling pressure on nests. The increase in the area of autumn sown crops and the decrease in the spring tilled area would make the area less suitable for lapwing. This change would represent a reduction in the area available for nesting and chick rearing. The change in the ratio of land suitable for nesting and land suitable for chick rearing might result in an increase in the distance of the post-hatching movements of broods as it would make it more difficult for adults to find suitable nest sites close to suitable rearing areas. As noted above brood movements are associated with an increase in chick mortality and a reduction in fledging success.

Table 7.0a Table showing cropping as a proportion (%) of tilled land in 1988 and 1998 in part of the Amounderness Plain, Lancashire[a].

	1988	1998	% change
Winter cereal	31.6	58	+26.4
Spring cereal	26.3	5.6	-20.7
Vegetables[b]	33.5	31.6	-1.90
Spring tilled area	59.8	37.2	-22.6
NRSA and RSA	0	5.30	+5.30
Temporary grassland[c]	4.10	7.00	+2.90
Permanent pasture[c]	3.30	5.30	+2.00

[a] These figures are derived from the 'Small Area Statistics' collected by MAFF in the agricultural and horticultural census carried out annually in June. Statistics are only available for groups of parishes. The information shown here represents data collected from the adjoining parishes of Altcar, Downholland, Halsall and Great Altcar (Agricultural District 12, Parish Group 1).

[b] This category includes horticultural crops grown under glass which are not separated from crops grown out in the open.

[c] Represents proportion (%) of total agricultural land.

The removal of spring tilled land from Altcar could result in the direct reduction in the number of pairs nesting there. The number of pairs or females nesting on spring farmed land on Altcar can be estimated from (i) the number of pairs/females nesting on unsown land (all first clutches); (ii) the number of pairs/females with first clutches on spring sown land; (iii) the number of females/pairs that fail initially on winter farmed land and re-lay on spring tillage. From this it can be calculated that overall 66.6% of pairs/females at Altcar nested on spring tilled land. A 2.3% reduction in this figure would represent a loss of 4.6 pairs year $^{-1}$, equivalent to 23 pairs over 5 years. As a caveat, however, the use of spring tilled fields for nesting is not uniform as it depends on the fields previous cropping history, its size and the presence of trees or other predator vantage points on boundaries. This could exaggerate the affect on nesting of any reduction in the area spring tilled. The maximum density of lapwing nesting aggregations is not known. A reduction in the area spring tilled might have the effect of increasing lapwing nest density on the remaining spring tilled land. It is possible that an increased nest density might further reduce egg predation (5.2.6vi). Less spring farmed land, however, may also increase competition between broods for food.

If the agricultural trend continues, further decline can be expected in lapwings. Prescriptions affecting local agricultural practice are, therefore, needed to halt or reverse any downward trend in the lapwing population, especially as the spring farmed area of south-west Lancashire appears to hold some of the highest lapwing densities in England.

8.0 Recommendations

To improve breeding conditions for lapwing at Altcar management should focus on three issues: (i) habitat loss - lapwing at Altcar prefer to nest and rear chicks on spring farmed land which is declining - attempts should be made to reduce, prevent or reverse the decrease in spring tillage; (ii) protection of nesting birds from farming operations; (iii) the enhancement of chick survival.

i. Reducing habitat loss

The most important element in the agricultural landscape for lapwings is spring tillage. It is apparent (see chapter 7) that the spring farmed area is decreasing. This trend needs to be halted or reversed. There is an evident financial advantage for the growing of winter cereals as farmers appear to favour autumn sowing rather than spring farming. Any attempt to redress the balance between autumn and spring sowing would, of course, need to compensate farmers for any financial penalty incurred from so doing. Encouragement of spring farming would, therefore, have to be carried out under agricultural policy using the Agri-environment Regulation (see 1.4.1). This provides a financial aid scheme to encourage farmers to introduce or continue farming practices that are compatible with the protection of the environment (Appleby 1994). The growing of vegetables, such as potatoes and carrots, is presumably more market orientated than that of cereals (due to intervention) and, therefore, fluctuations in the area of such crops might vary accordingly. A mix of spring farmed crops (cereals and vegetables) is needed to maintain the lapwing population and this would need inclusion in any aid scheme promoting spring farming. Crop distribution is important and any agri-environment scheme targeting lapwings would have to try and ensure that suitable nesting sites, such as RSA, are adjacent to suitable rearing sites, such as field beans, potatoes or pasture.

At present agri-environment schemes seek to decrease agricultural production or reduce cropping. Such schemes may have multiple environmental benefits. At Altcar, however, lapwing production may be sufficient if the right type of farming (mixed spring) is combined with other management measures to reduce chick predation (see below). It might be easier, cheaper (for the taxpayer) and more acceptable to farmers to alter cropping practices rather than to compensate them for not farming. Temporarily uncultivated land could, however, be beneficial to nesting lapwings if managed correctly as has been shown by RSA in this study.

ii. Protecting nesting birds from farming operations

The management rules in place for RSA during the period of the study provided good nesting habitat for lapwing. Unchecked natural regeneration, however, meant that broods were taken out of RSA to be reared elsewhere. To avoid broods having to make these dangerous movements the suppression of vegetation growth in RSA should be considered. This might be expected to make RSA more suitable for brood rearing. Restraining or prohibiting natural regeneration could be achieved by the application of a non-selective herbicide such as glyphosphate ('Round-up'), preferably in late April/early May before plant growth accelerates. Other methods such as mowing or harrowing would destroy nests and should be avoided. The impact of the late use of herbicides on the ground fauna would need to investigated. RSA could be made less suitable for rearing if herbicide use resulted in a decrease in beetle numbers. Such decreases might only be short-lived, however, as beetles dispersed back into RSA from adjoining land. Breeding lapwing would benefit by maintaining set-aside (managed as suggested above) as a form of land use. The Agenda 2000 (Commission of the European Communities 1997) proposals for reform of the CAP, however, include elimination of set-aside as set-aside functions as a supply control measure (see 1.4.1 and 1.4.2) and is not intended for environmental purposes. Set-aside managed for lapwings could, therefore, be considered as a specific scheme under the Agri-environment Regulation. Option 1B of the pilot Arable Stewardship (administered by MAFF) would appear a suitable form of arable management for lapwings. This allows overwintered stubble followed by a spring/summer fallow which would provide a benign nesting habitat to lapwing if nesting period management is prohibited. At present, however, this scheme is under evaluation and restricted to two pilot areas (in the west Midlands and East Anglia) and it is not known if or when it will become a national scheme. The Amounderness Plain was included as a target area for new Countryside Stewardship objectives by MAFF (MAFF 2000). Unfortunately none of the objectives are suitable for breeding lapwing.

Nest avoidance by farmers should be encouraged. Such nests survive well (see also Berg *et al.* 1994). Early hatching may aid productivity as chick predation is low compared to later in the season and a more diverse chick prey is available. Avoided nests also hatch into recently spring sown fields and, therefore, it is unnecessary for these broods to make dangerous post-hatching movements. The practice of avoiding nests during rolling (as opposed to sowing) could also be encouraged. Lapwing nests in crops about to be rolled may be harder to see than those in unsown fields. It may be better to delay such activities, especially as the precise timing of rolling is not usually agronomically critical (Pearson and Stoate 1994). If rolling had been delayed in winter sown crops by 10-14 days in 1997 nest losses in that crop category would have been decreased by 68% and overall losses through farming operations by 21%. In 1996 the exact first egg dates of all nests in unsown fields was not known, however, a delay of one week in sowing or drilling (after the median sowing date) would have increased nest success from 39.7% to between 57.5-64.4%. Between year differences in first egg dates mean that such a strategy may vary annually in its efficacy. For example in 1997, if spring sowing of vegetable crops had been delayed by one week hatching success would have only increased from 37% to 41.4% with little further effect if a delay of ten days had been allowed. Furthermore, there may be some intransigence over sowing/drilling dates as they are weather dependent activities.

Nest avoidance and RSA both served as measures which reduced the impact of intensive farming on nesting lapwing. Nest success (expressed as the percentage of successful nests) was 89% for nests deliberately avoided and 91.5% for RSA was, therefore, similar for both measures. However, the majority of 'avoided' nests were on the holding of one tenant farmer and only two other farmers practised this measure. Two of the three tenants had comparatively smallholdings. The practise was, therefore, not widespread and it may be difficult to encourage less sympathetic farmers (who farm large areas) to adopt this practice, especially as nests can be difficult to see and avoidance results in a decrease in the area sown. In addition, as many cultivation activities are done under contract it could be difficult to repeat avoidance before nests had a chance to hatch. The nature of RSA, in contrast, meant that this field type was adopted by each farmer and, therefore, widespread. Also, no actions had to be taken by the farmer in order for it to provide a benign nesting environment for lapwing. Even though implementation of RSA as a nest protection measure could be more efficient than nest avoidance, both practices should be adopted where possible.

iii. Enhancing chick survival

In this study three chick mortality factors were identified. Losses to predators were thought to be the most important chick mortality factor. Poor body condition and, to a lesser extent, entrapment in ditches were also responsible for chick deaths. The last two factors combined were less significant than that of predation and are, perhaps, more difficult to decrease as they impact upon very young chicks and may be related to parental age and breeding experience or weather. Reducing predation may be the most practicable way of enhancing lapwing chick survival.

At Altcar Kestrels were suspected of being the chief chick predator. If this is proves to be true, it would not be possible to remove kestrels directly by killing or culling them as the kestrel is fully protected under UK law (Wildlife and Countryside Act 1981). Even if removing kestrels was permissible it may not be efficacious as culled individuals or pairs may be replaced by others. The legal status of kestrels may also prevent any investigation into taking direct action as a means of removing them from lapwing breeding areas. In any event, considering the persecution of raptors in the past (and present) it may be difficult for conservation agencies to get public acceptance for such a measure. If one or two individuals of a single, unthreatened species were responsible for the majority of depredated chicks, however, their removal might be a way of increasing lapwing productivity at Altcar to sustainable levels. Relatively small reductions in predation would have been needed each year for chick production to reach population maintenance levels (see chapter 7). Indirect measures could be taken to try and reduce kestrel densities or from nesting near chick rearing sites. For example, the use of kestrel/owl nest boxes within or near to the study area could be discouraged as it is known that kestrels do not hunt far (<1km) from nest sites (see 5.3 iii).

Maintenance of game interests would allow the continuation of predator control. This may not only help reduce predation on lapwing eggs and chicks but may also increase small mammal populations through the reduction in the number of mustelids. Higher densities of small mammals may help reduce the predation pressure on lapwing chicks by providing an alternative food supply for kestrels or other birds of prey. Methods, such as substitute feeding of raptors, which have been tried elsewhere (see Scottish Natural Heritage 1999), may not be practical in this case, unless taken on by conservation agencies. There are no provisions for such action in agri-environment schemes.

The open character of the landscape should be maintained. There should be no attempts to plant boundary hedges or trees as these might provide cover and vantage points or potential nest sites for predators. Recently planted hedging should be removed. Beetle (chick food) populations could be encouraged by the use of conservation headlands (unsprayed crop margins) and beetle banks (grass 'islands' within crops, *e.g.* Thomas *et al.* 1992). Improving habitats for passerines may also help provide an alternative prey source for kestrels feeding young as newly fledged passerines are often fed exclusively to chicks (Cramp and Simmons 1980). Common passerine species at the study site, however, included skylark and corn and reed buntings (*Emberiza schoeniclus*), which considering national declines in their populations (see 1.4.3) are perhaps not appropriate prey alternatives to lapwing chicks.

Changes to ditch engineering practice are needed to try to reduce the danger ditches present to young, small chicks when moving from natal to rearing areas. The steepness or angle of the slope needs to be reduced so that chicks have a better chance of climbing out once they have moved in. As chicks were observed attempting to cross ditches even when within a few metres of the field entrance, bridges over ditches would probably not be used by lapwing broods. A simple way of perhaps reducing ditch entrapment would be for ditches to be dredged/cleaned out in sections of, for example, 20-40m lengths. This may allow any trapped chick or brood to travel along the ditch to a less deep section which could be accessed which would then allow the chick or brood to exit the ditch to the adjacent field. The drainage value of such a ditch would need to be established. A less severe slope to field boundary ditches would also benefit grey partridge (a red-listed BoCC[9] species) breeding in the study area. Partridges nest on ditch slopes and gamekeepers have to remove eggs to an incubator as chicks fall to their deaths on hatching (J. Bell, pers comm, pers. obs.). Also the removal of ditches should not be considered as some of the less deep ditches may provide foraging opportunities for lapwing chicks, especially late in the season. The presence of ditches has also been associated with higher densities of reed bunting and skylark (*e.g.* Parish *et al.* 1994, 1995), both red-listed BoCC species that breed in the study area (*pers, obs.*). Radio-marking, however, only indicated a small proportion of chicks died through ditch entrapment and eradicating this form of mortality completely may not contribute much to lapwing productivity at the site. This may be particularly true as most deaths from ditch entrapment occurred immediately post-hatching so surviving chicks would be exposed to other mortality factors. It could also be true, however, that those chicks that were considered to have been depredated may have exposed themselves to a higher risk of predation by entering a ditch. Ditch engineering changes would have to be negotiated with farmers as most field boundary ditches are under their jurisdiction rather than that of local government or the Environment Agency. In fact, drainage of the study site and surrounding area is, perhaps, a key factor governing the local agriculture and, therefore, the fate of the lapwing population. Spring cereals are farmed partly because some of the low-lying land is too wet during the winter to allow access to the agricultural machinery needed to cultivate autumn sown crops. Improvements in drainage (both in fields and in the watercourses) have allowed more and more fields to be autumn sown. This indicates that lapwing (indeed, biodiversity) conservation in the area may need to embrace more than agricultural practice and policy but also other land use concerns.

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[9] Birds of Conservation Concern (see 1.2.2).

To conclude, it is apparent that the nature of farming at Altcar is still able to support a productive lapwing population and that the practices that allow this (mainly mixed spring farming) need to be maintained and encouraged. Lapwings on Altcar produced enough nestlings to maintain the population. Not enough of the chicks that hatched, however, survived until fledging. Priority management needs to be aimed at enhancing lapwing chick survival with a halt or reversal of the decline in the area spring farmed. At Altcar, as well as elsewhere in the UK, lapwings need to be conserved on farmland as this is where most lapwing breed. Farmers need formal conservation agreements to maintain or improve conditions for wildlife on their land. Such agreements, administered under the CAP by MAFF and FRCA (Farming and Rural Conservation Agency), could also be endorsed by national and local government under Biodiversity Action Plans. Land designation or environmental protection schemes under the CAP would ensure that farmers could achieve conservation targets, for which they would receive payments, as well as producing high quality food. This may need a shift away from the crop subsidies of the CAP towards payments for environmental measures. The Agenda 2000 reforms do not include a significant shift away from subsidies and the CAP continues to be Europe's most damaging environmental policy (Young 1999).

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