Thesis
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Linking grassland management, invertebrates and Northern Lapwing productivity.

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Abstract

Numbers of lapwings (*Vanellus vanellus*) breeding in Britain and Ireland have declined over the last 20 years. It has been suggested that intensification of agricultural practices has contributed to the decline by reducing food abundance and availability and the suitability of nesting and chick rearing habitat. Much of the previous research has been conducted on arable habitats while very little is still known of the effects of grassland improvement on lapwing food supply and breeding success.

This thesis investigates the effects of grassland management techniques, i.e. fertiliser application, drainage and re-seeding on the invertebrate food supply and breeding success of lapwings at the Loch Gruinart Nature Reserve on Islay. The study was carried out using a farm-scale factorial experiment manipulating timing of fertiliser and water levels.

The key findings were that both water and fertiliser treatments had a significant effect on earthworm biomass, an important component of adult lapwing diet and surface invertebrates, important in chick diet. Lapwing nest placement was affected by both water and fertiliser treatment, however this was dependent on field. Ditches were selected over rigs as preferred nest sites, probably because chick food supply and availability on ditches is greater than rigs. Sward structure interacted with predator activity to affect nest survival. In fields where predator activity was low nests were more successful in longer sward, in fields where predator activity was high nests were more successful in shorter vegetation, benefiting from early detection of predators.

Chick foraging behaviour and condition was influenced by surface invertebrate abundance and vegetation structure. Lapwing broods favoured areas of short sward for foraging; these areas included late fertilised treatments and ditches. Foraging rates in short sward were significantly greater than in long sward, explaining the difference in treatment preference. No effect of treatment was observed in determining egg or clutch size, however chicks which hatched in treatments with abundant food supplies were heavier and survived for longer.

The use of the farm-scale experiment has allowed us to demonstrate the complex and multifactorial impacts of two commonly used farming practices on the food supply, behaviour, life history and productivity of a declining farmland bird species.

Declaration

This thesis is a result of my own research, and no part of this thesis has been submitted in application for a higher degree at this or any other institution. All collaborative involvement has been duly acknowledged.

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CONTENTS

Chapter 1

General introduction & study site

Farmland Bird Declines

Populations of farmland birds have suffered widespread declines and range contractions throughout Europe since the 1950s. It is now widely accepted that post war changes in agricultural practices have contributed to the declines (Siriwardena *et al.* 2001, Wilson *et al.* 1999, Fuller *et al.* 1999, O'Connor & Shrubb 1986). During and after the second world war, agricultural policy in Europe and later in the European Union changed, offering financial incentives to farmers to modernise farming methods and increase food production. These changes were delivered by means of subsidies provided by the Common Agricultural Policy (CAP) of which a modified version is still functional today. In Britain, changes in lowland farmland practices that occurred after the introduction of the CAP included complete mechanisation of practices such as mowing and ploughing (O'Connor & Shrubb 1986), a great increase in drainage of wetland habitats (Jefferson & Grice 1998, Self *et al.* 1994) and the more widespread use of inorganic fertilisers and the introduction of synthetic pesticides (Fuller, 1999). In the 1970s intensification of farming practices increased including a switch from spring to autumn sowing of cereal crops and the simplification of crop rotations with the loss of grass leys (O'Connor & Shrubb 1986, Evans 1997). On grassland habitats silage production replaced hay and stocking rates increased (O'Connor & Shrubb 1986).

The relationship between farmland bird declines and agricultural intensification has been tested in various ways. On a community level, long-term monitoring schemes such as the Common Bird Census (CBC) have identified downward population trends and range contractions of some farmland bird specialists. Many of these species are now on the 'Red List' of birds of conservation concern (Gregory *et al.* 2002). The declines in farmland bird populations parallel declines in both plant and invertebrate food supply on farmland (Wilson *et al.* 1999, Benton *et al.* 2002) and habitat loss, such as changes in the sowing of cereal crops (Chamberlain *et al.* 2000). Secondly, many autecological studies have demonstrated negative behavioural (e.g. habitat use) and demographic (e.g. hatching success and chick survival) responses of farmland birds to agricultural intensification (e.g. Donald *et al.* 2002, Baillie, *et al.* 1997, Green 1984). While the use of field experiments in identifying the mechanisms of population declines with changes in management has been limited, they have proved to be powerful in understanding and quantifying the impact of a particular component of agricultural change (Potts 1986, Green & Stowe 1993).

Agricultural intensification can impact bird populations in two ways affecting them: 1. directly, through removal of habitat or increased mortality due to disturbance and 2. indirectly, by altering food resources or quality of nesting sites (Fuller 1999). For example, the change in timing of sowing cereal crops has contributed to the decline of skylarks *Alauda arvensis* by changing the vegetation structure, thus reducing the amount of suitable nesting habitat (Chamberlain & Crick 1999, Donald & Vickery 2000, Donald *et al.* 2002). Declines of invertebrates on farmland are thought to be responsible for the decline in gamebird species by reducing chick survival (Potts 1970 & 1980, Green 1984).

The impacts of changes in arable farming practices on farmland birds over the last 10 years are well documented (Siriwardena *et al.* 2001, Wilson *et al.* 1999). Grassland habitats, on the other hand, which have been subjected to the same degree of intensification, have received very little attention despite recent declines in species associated with grassland habitats (Vickery *et al.* 2001).

The Northern Lapwing

The Northern Lapwing *Vanellus vanellus*, locally known in many areas of Britain and Ireland as "peewits", are terrestrial plovers, which are closely associated with farmland. They are conspicuous in their appearance and behaviour especially during the breeding season where males can be seen corkscrewing and tumbling in the air. This behaviour along with their high-pitched screech, makes them one of the most widely recognised and popular birds of the British countryside.

Lapwings breed in most of Europe including Iceland, but more sparsely through North Africa across South Russia and North China to Ussuriland. The Netherlands, Belarus and Great Britain hold 80-90% of the total European breeding population. Their wintering grounds range from the Atlantic littoral (Ireland to Iberia) and the coastal plains of North West Africa through the Mediterranean (Hagemeijer & Blair 1997).

In the early 19th century, lapwings in Britain and Ireland were widely distributed and a common bird of the countryside (Holloway 1996). Since then they have undergone a series of population fluctuations. In the 1830s lapwing populations suffered a decline due to egg collecting, netting of autumn flocks and the drainage and enclosure of farmland. Numbers then increased briefly following the introduction of the Lapwing Act of 1926 and then suffered another decline in the 1950s (Holloway 1996).

Population trends documented by the British Trust for Ornithology (BTO) / Joint Nature Conservancy Council's (JNCC) Common Bird Census (CBC) suggest that the decline in numbers since the 1950s has accelerated in the last 20 years (Baillie *et al.* 2002). Other surveys reveal declines in England and Wales of 38 % between 1982 and 1989 (O'Brien & Smith 1992) and of 49% between 1987 and 1998 (Wilson *et al.* 2001). The Scottish population has suffered a decline of 28% between 1994 and 1998 as documented by the British Trust for Ornithology (BTO) / Royal Society for the Protection of Birds (RSPB) / Joint Nature Conservancy Council's (JNCC) Breeding Bird Survey (BBS) (Wilson & Browne 1999), and a 13% decline in lowland areas between 1992 and 1997 (Tharme 1998). In addition there has been a marked range contraction from the southwest of England, northwest Scotland, parts of Wales and throughout Ireland between breeding atlas periods

1968-1972 (Sharrock 1976) and 1988-1991 (Gibbons *et al.* 1993). Despite this, lapwings remain widely distributed in Britain (Gibbons *et al.* 1993). The decline in Britain is consistent with the rest of Europe where 50% of European countries have experienced range contractions and a decline in numbers during the period 1970-1990, by 20-50% (Hagemeijer & Blair 1997). However, eastern European countries, such as Russia, Poland, Ukraine, Romania, Lithuania and Croatia, all regions where farming practices are not yet fully industrialised, report mostly stable numbers (Hagemeijer & Blair 1997).

In order to obtain a better understanding of the change in population dynamics, analysis of British lapwing ringing recoveries was undertaken by Peach *et al.* (1994). It was shown that mean adult annual survival rates were at 0.705 in the period 1930–1988, but since 1960 have increased to 0.752. Further analysis revealed that while the proportion of birds surviving their first year had fluctuated markedly, no long-term trend was evident, concluding that the recent decline in lapwings in Britain could not be attributed to a reduction in adult or first year survival. Peach *et al.* (1994) therefore suggested a reduction in chick productivity was contributing to the overall decline of lapwings in Britain and identified that to replace adult losses lapwings need to produce 0.83 - 0.97 fledglings per pair per year. Analysis of nest record data from the BTO's Nest Record Scheme shows an increase in failure rates at egg stage from 40% to 49% in the same period of decline (Baillie *et al.* 2002). It appears therefore that a reduction in breeding success is responsible for the overall decline, however the mechanisms are still poorly understood.

Farmland is now considered the most important habitat type for lapwings (Hudson *et al.* 1994). In a survey of England and Wales in 1987, 96% of breeding lapwings of that population were recorded on agricultural land (Shrubb & Lack 1991) and 85% of the Scottish population were recorded on farmland (Thom 1986). It is now widely recognised that a reduction in habitat quality through agricultural intensification is responsible for declines in breeding lapwing populations in Britain (e.g. Lister 1964, Green & Cadbury 1987, Galbraith 1988b, Baines 1990, Gibbons *et al.* 1993, Hudson *et al.* 1994) and elsewhere in Europe (e.g. Schifferli 2000, Hutchinson 1989, Hagemeijer & Blair 1997, Berg 1992, Beintema & Müskens 1987).

Factors affecting breeding lapwing on farmland

Nest habitat

Nest site selection in lapwings is determined by vegetation height (e.g. Spencer 1953, Galbraith 1988a, Berg *et al.* 1992, Hudson *et al.* 1994), predator avoidance (e.g. Baines 1990, Berg *et al.* 1992) and philopatry (Thompson *et al.* 1994).

The impacts of agricultural intensification on nesting lapwings are well documented. On arable habitats the switch from spring to autumn sown cereal crops has reduced the amount of suitable habitat available for nesting (Shrubb 1990). A change from hay to silage production through drainage and fertiliser input on grassland habitats has had negative impacts on nesting lapwings. Silage production involves earlier, fast growing swards unsuitable for nesting (Lister 1964). Lapwings leave areas when the sward height reaches 15cm and avoid intensively managed grass crops where the sward is too dense and tall for nesting (Lister 1964, Shrubb & Lack 1991). In the Netherlands, the promotion of grass growth achieved through drainage and fertilizer application has caused lapwings and other wader species to breed 1-2 weeks earlier than in the early 1900s (Beintema & Müskens 1987). An increase in nest mortality through trampling by livestock (Beintema & Müskens 1987, Shrubb 1990), destruction by farm machinery (Baines 1990, Kruk *et al.* 1996) and increases in the risk of detection by predators (Baines 1990) have also occurred.

In lowland Britain, lapwings nest on both grassland and arable habitats. Arable, especially spring cereals are preferred for nesting (Shrubb 1990). In an analysis of nest record cards, Shrubb (1990) found that hatching success on arable was greater than pasture. It appeared that lapwings nesting in spring cereals benefited from easier nest placement due to sparse vegetation cover, less predation risk due to clearer views around the nest and no trampling from stock (Shrubb 1990).

The role of food in selecting nest sites is much debated. While food supply during the pre-breeding season is important in providing energy for male territorial displays and egg production in females (Galbraith 1989a), it is not considered important in determining nest site selection on arable or grassland habitats (Baines 1990, Galbraith 1989a). However, other studies attribute preference for arable as a nesting habitat in part to the availability of earthworms early in the season (Berg *et al.* 2002, Berg 1993, Blomqvist & Johansson 1995). Proximity to good chick rearing habitat is important in determining chick survival (e.g. Shrubb 1990, Galbraith 1989a, Johansson & Blomqvist 1996), but in many cases this is not a key factor in determining nest placement (e.g. Galbraith 1989a, Kirby & Tyler 1999).

Philopatry and breeding site fidelity are also important factors in determining where lapwings nest (Thompson *et al.* 1994). However recent research by Berg *et al.* (2002) suggests that nest site choice is not driven by past experience but rather by environmental conditions on arrival in the spring.

Previous work on lapwing nesting habitat selection on farmland has focussed on the comparison of behavioural and demographic responses between grassland and arable habitats. However, the mechanisms underlying these responses within grassland habitat types are still poorly researched and understood.

Chick-rearing habitat

Lapwing chicks are precocial and after hatching broods are moved to suitable chick- rearing areas by adults (Cramp & Simmons 1983). While hatching success is high on arable habitats, and fledging success of arable clutches is dependent on proximity to grassland habitats that provide good chick-rearing areas (e.g. Shrubb 1990, Galbraith 1989a, Johansson & Blomqvist 1996). It has been suggested that vegetation height on arable habitats constrains the ability of chicks to forage and that food supply is less plentiful on arable than on grassland habitats (Galbraith 1988a). Galbraith (1988a,b) found that chicks that did not leave their natal arable fields deteriorated in body condition.

Chick-rearing areas tend to be associated with short vegetation and high soil moisture (e.g. Milsom *et al.* 2002, Berg 1992, Baines 1990, Jackson & Jackson 1980). It has been suggested that these areas provide more abundant and accessible food than nesting sites (Redfern 1982, Galbraith 1988b, Berg 1992) as well as allowing easier detection of predators (Galbraith 1988b). However, grassland improvement (i.e. fertiliser application and drainage) has resulted in a loss of suitable chick rearing habitat available to lapwing broods. Lapwing chicks now have to mover greater distances to find suitable foraging areas and these long distance movements are associated with reduced survival (Blomqvist & Johansson 1995).

Lapwing food supply

The importance of food in determining breeding success in birds is widely acknowledged. It has been suggested that a reduction in food abundance and availability, through grassland improvement, is one of the main factors contributing to lapwing decline in Britain (Vickery *et al.* 2001, Wilson *et al.* 2001). Previous studies have shown how adult food supply prior to breeding can influence chick survival through egg quality (Blomqvist & Johansson 1995, Galbraith 1988b). Chick survival can also be determined by proximity to an abundant food source (Galbraith 1988b, Baines 1990). Despite this very little is known about the effects of grassland management on the abundance and availability of lapwing food supply.

Many studies have demonstrated that Lumbricidae (earthworms), Coleoptera (beetles) and fly larva (particularly Tipulidae) are be the most important components of both lapwing adult and chick diet during the breeding season (Baines 1990, Galbraith 1989b & Bientema *et al.* 1991). Early in the breeding season lapwings are found feeding in areas where earthworm densities are high (Galbraith 1989a, Baines 1990, McKeever unpublished data). Earthworm biomass during this period is important in determining lapwing egg size, which has implications for chick survival (Galbraith 1988c, Blomqvist & Johansson 1995). Lapwing chick diet is varied and opportunistic (Hudson *et al.* 1994), including beetles, leatherjackets, spiders and earthworms (Galbraith 1989b, Baines 1990, Beintema *et al* 1991, Johansson & Blomqvist 1996).

Recent research has quantified a negative response of some species of terrestrial earthworms to winter flooding where recreation of lowland wet grassland has been attempted (Ausden *et al.* 2001). Earthworm responses to fertiliser can be positive or negative depending on the rate of application (Edwards 1984) although in general very little is known about the effects of either drainage or fertiliser application on surface invertebrate abundance.

In a recent review by Vickery *et al.* (2001), the need for more research into the effects of grassland management and their impacts on bird populations, in particular how food abundance is affected by fertiliser application, was highlighted.

Study site

Islay

Islay is the southern most of the Scottish Inner Hebrides, lying west of mainland Scotland and north of Ireland. It has an area of 614 km^2. Islay's climate is hyper-oceanic with lower summer and higher winter temperatures than the mainland (Boyd & Bowes 1983). Sea level *c.*7000 years ago was about 8-10m above its present level. Extensive and shallow mudflats linked Loch Gruinart and Loch Indaal. This area was probably attractive to considerable numbers of wildfowl and waders. At this time Islay's climate encouraged the growth of a variety of tree species, including alder, hazel, birch, willow and oak. Insect and woodland bird populations flourished. At the beginning of the Neolithic period (*c.*5,500 years ago) farming practices were introduced and land clearance made way for crops and grazing. Today, Islay's mosaic of fertile farmland, heath, moorland and machair habitats attracts a diverse assemblage of breeding and wintering birds.

Loch Gruinart RSPB Reserve

The Loch Gruinart Reserve (Figure 1) was purchased by the RSPB in 1984 in response to increased threats to the internationally important numbers of wintering Greenland Barnacle geese *Branta leucopsis* and Greenland Whitefronted geese *Anser albifrons flavirostris.* It is a major farm holding which comprises a variety of habitat types including farmland, heather moorland, intertidal mudflats, salt marsh and woodland and has been designated a site of Special Scientific Interest (SSSI) (part) Special Protection Area (SPA) and RAMSAR site. The reserve includes the most important roosting and feeding areas for Barnacle geese on Islay. The reserve has fulfilled its role as a refuge for geese, which still remains a priority. In 1994 the management direction of the reserve expanded to encompass the wide variety of habitats and species of high priority such as Corncrake *Crex*

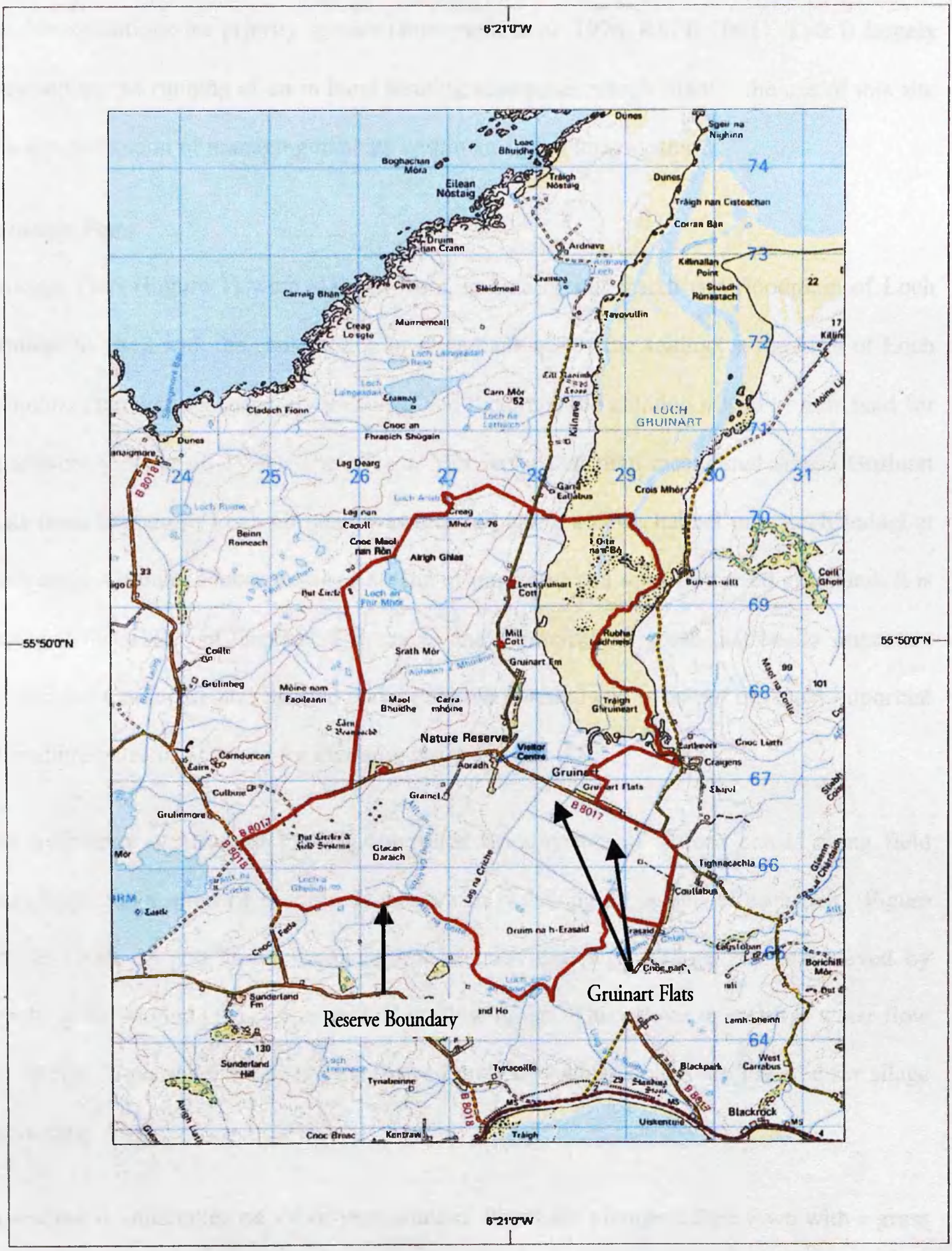

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Figure 1 Map of the RSPB Loch Gruinart Nature Reserve, Isle of Islay, Scotland.

crex, Hen Harrier *Circus cyaneus*, chough *Pyrrhocorax pyrrhocorax* and breeding waders. The reserve habitats are dynamic and require continual management work to maintain suitable conditions for priority species (Beaumont *et al.* 1996, RSPB 2001). This is largely achieved by the running of an in hand farming enterprise, which enables the use of this site as a demonstration of managing habitats within an agricultural system.

Gruinart Flats

Gruinart Flats (Figure 1) were claimed from an area of salt marsh and floodplain of Loch Gruinart in 1812 with the construction of a sea bank across the saltings at the head of Loch Gruinart. This was subsequently breached and then repaired creating 400ha of new land for agriculture (Self *et al.* 1994). The Gleann Mòr River that then meandered across Gruinart Flats from Eresaid to Loch Gruinart was directed along a new channel into Loch Indaal at Uiskentuie. Gruinart Flats comprises 86.1ha of improved and semi-improved grassland. It is managed for wintering Greenland Barnacle and Whitefronted geese, nationally important numbers of Corncrake and Spotted crake *Porzana porzana* and is one of the most important agricultural sites in Scotland for breeding waders.

The hydrology of Gruinart Flats is controlled by a system of sluiced canals along field boundaries and a series of shallow ditches which run along the length of each field (Figure 2a). In fields 25 and 26-31 water control of individual rigs (Figure 2b) is achieved by attaching 90° angled pipes on individual outflow drains. This allows or restricts water flow out of rigs. High water levels are maintained until July when sluices are lowered for silage harvesting.

Reseeding is undertaken on a five-year rotation. Fields are ploughed then sown with a grass seed mix (40% ryegrass, 29% timothy, 19% fescues and 12% clover) at a rate of 42kg/ha. Reseeding takes place in the autumn after a cut of silage has been taken in August. Cattle

Figure 2a Aerial photograph of Gruinart Flats, view to west.

Figure 2b Aerial photograph of Gruinart Flats showing 'rig' and 'ditch' structure of fields, view to south.

then graze silage aftermath until the end of September. Cattle are used to produce an optimum sward height of *c.*10cm for grazing Barnacle and Whitefronted Geese. Goose grazing results in favourable conditions for breeding waders including Lapwing (175-200 pairs) and Redshank *Tringa totanus* (50-100 pairs) by cropping the sward to a suitable height for nesting and chick rearing.

Fertiliser is applied to the Flats to promote grass growth for corncrake cover, silage for winter feed, to maintain the mineral balance of the soil and achieve successful reseeds. A 15:8:15 NPK blend is applied at the rate of 750kg/ha each year.

Aims of study

Despite the recent declines in the number of lapwing breeding on improved lowland grassland in Britain (Baillie 2002, Wilson *et al* 2001, Wilson & Browne 1999, Tharme 1998, Gibbons *et al.* 1993), very little is known of the factors causing the decline. Many authors suggest that a change in management in particular fertilising, reseeding and drainage have affected lapwings by creating habitat unsuitable for nesting and chick rearing and reducing food availability for chicks (e.g. Baines 1990, Galbraith 1988b, Beintema & Müskens 1987, Berg *et al.* 1992, Blomqvist & Johansson 1995) thereby reducing productivity. This thesis investigates the effects of grassland management (drainage, fertilising and reseeding), using a large farm-scale factorial experiment, on lapwing invertebrate food supply and lapwing breeding success.

Thesis outline

Chapter 2 investigates long-term spatial and temporal trends in lapwing breeding success at Gruinart flats between 1995 and 1999. These results are used to compare and contrast with results from the experiment. Chapter 3 outlines the experimental design and tests the hypothesis that manipulating water levels and fertiliser application affects soil moisture, sward height and the abundance of surface and subsurface invertebrates. In Chapter 4 the response of lapwing nesting behaviour (nest density and hatching success) to treatments is investigated. The direct (sward manipulation) and indirect (food supply) impacts of grassland management are assessed. Chapter 5 investigates chick behaviour in relation to treatment. In particular, the role of food and vegetation structure in determining habitat use by lapwing chick is examined. The effects of treatment on aspects of lapwing life history (clutch and egg size, chick body condition and chick survival) are examined in Chapter 6. Finally, Chapter 7 concludes with a general discussion of the results found, leading to management recommendations for the study site. How these recommendations might be applied to the wider countryside will also be discussed.

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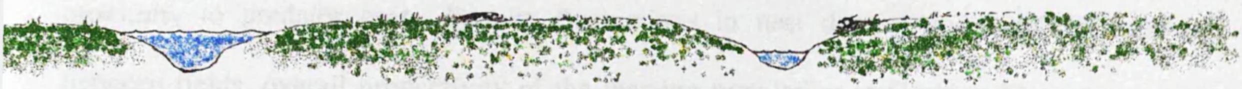
Chapter 2

Spatial and temporal trends of Northern Lapwing productivity at Gruinart Flats 1995-1999



Abstract

Lapwings breeding at the RSPB Loch Gruinart Nature Reserve were monitored from 1995 – 1999. Pair density of the Flats population remained constant throughout the study ranging from a peak number of 109 pairs in 1995, reaching a low count of 81 pairs in 1998, with numbers recovering in 1999 to 100 pairs. Nest density over the study period was dependent on field. Marked decreases were observed in 2 fields, increases were observed in 2 fields while nest density in 3 fields remained constant over the study period. The vicinity of ditches was preferred over rigs as nest sites. Variation in hatching success between years was explained by lay date. Nests initiated early in the season had a higher chance of survival to hatching than those initiated later in the season. Hatching success between first and replacement clutches varied depending on field. Fledging success increased over the study period. Survival of first and replacement broods to fledging was dependent on natal field proximity to predator nests. Despite fluctuations in nest density and hatching success between fields, overall productivity of the lapwing population at Gruinart Flats appears to have increased steadily over the study period.

2.1 Introduction

Numbers of lapwing breeding in Britain and Ireland have declined over the last 20 years (O'Brien & Smith 1992, Baillie *et al.* 2002, Wilson *et al.* 2001). It has been suggested that intensification of agricultural practices has contributed to the decline by reducing the amount of suitable breeding habitat and by reducing invertebrate food availability to chicks (Chamberlain & Crick 2002, Beintema *et al.* 1991, O'Brien & Smith 1992).

In lowland areas, grassland improvement has been identified as one of the main causes of lapwing decline (e.g. Chamberlain & Crick 2002, O'Brien & Smith 1992, Shrubb & Lack 1991, Shrubb 1990). This often involves a switch from hay to silage production which has resulted in an increase in drainage, fertilising and reseeding and these practices create habitat that is unsuitable for nesting and chick rearing.

The Loch Gruinart RSPB Reserve on Islay is one of the most important agricultural sites in Scotland for breeding waders. When the reserve was acquired by the RSPB in 1984, management of Gruinart Flats was primarily aimed at providing grasslands suitable for over-wintering geese. This management included fertilising in the spring and reseeding on a 7-year rotation. In 1990 management of the site was expanded to benefit other species, such as breeding waders and corncrake. This resulted in a change to the spring farming operations on the Flats (Beaumont *et al.* 1996). Practices such as ploughing, fertilising and rolling were delayed until later in the season and thereafter, numbers of breeding Lapwing on the reserve increased from 100 pairs in 1990 to just over 300 pairs in 1994 (Figure 1).

With increasing concern over declining lapwing populations elsewhere in the UK, the Loch Gruinart population offered the chance to study the breeding ecology of and apparently increasing population. In 1995 a pilot study was undertaken on the Flats, which held the highest densities of breeding waders on the reserve, to quantify Lapwing productivity. This included intensive monitoring of nest survival and chick survival throughout the breeding season. Productivity in the first year of the study (1995) was found to be particularly low with just 0.16 chicks per pair fledged (Welstead 1995), well below the 0.76 chicks per pair required to maintain a stable population (Peach *et al.* 1994). This posed many questions on how the current management was affecting productivity and Lapwing monitoring was therefore continued on the site from 1996-1999.

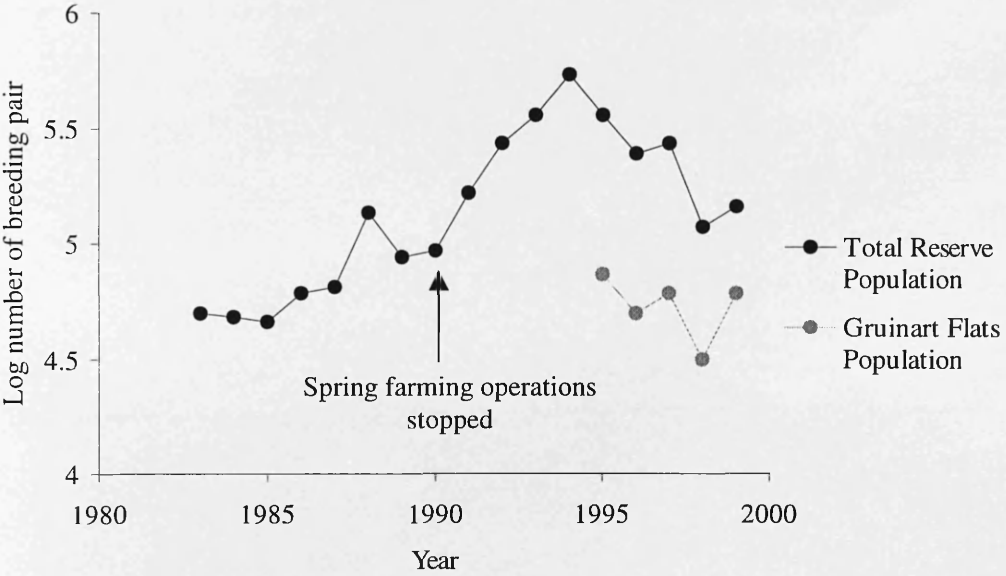


Figure 1 **Breeding Lapwing population at Loch Gruinart RSPB Reserve 1995-1999.**

Numbers of breeding pairs were taken from Breeding Wader Survey data. Survey methods are described in Bibby, Burgess & Hill (1992).

In this chapter, data from the 'Lapwing productivity monitoring project 1995-1999' are analysed to investigate the temporal and spatial trends of lapwing nest density, nest survival and chick survival in relation to management (reseeding) and within-field topography (rig/ditch effect). These baseline results will be used to compare with results from the experiment to follow.

The data presented in this chapter were collected by the RSPB as part of the 'Lapwing productivity monitoring project 1995-1999' (Rout 1999). Contributions made by data collectors, namely Fiona Rout, Julia Welstead and James Gordon and project managers Mike Peacock and David Beaumont are gratefully acknowledged.

2.2 Methods

2.2.1 Nest Density

Nests were found by locating 'scraping' or 'incubating' birds at the beginning of the breeding season. Observations were made using a Kowa TSN telescope with a x30 magnification wide angled lens and 8x42 magnification binoculars from a landrover used as a mobile hide. All fields were monitored daily for new nests. As a nest was initiated, its location was mapped along with a brief habitat description and how to re-locate it using reference points. Nest location within fields (rig / ditch) was also noted. Nests located up to 1.5m from the centre of each ditch (see Figure 2) were recorded as ditch nests.

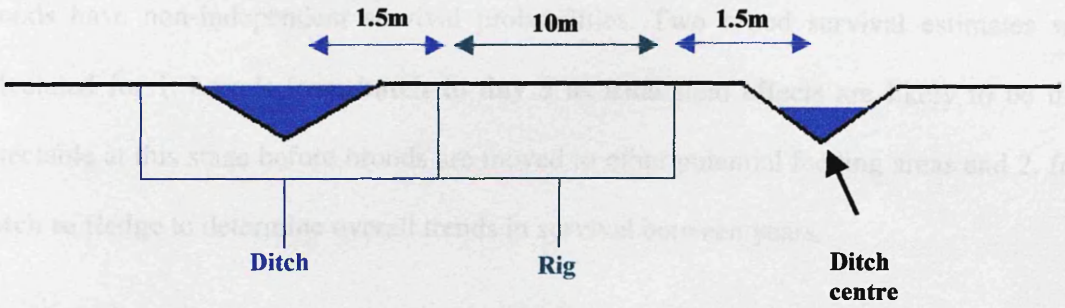


Figure 2 **Rig and Ditch boundaries.**

Diagram not to scale.

2.2.2 Nest survival

All nests were monitored daily until hatching or failure. Initiation date of each nest and date of hatching or failure was recorded. A nest without an incubating adult after 5 consecutive days was recorded as a failure. All nests initiated after the date of the first confirmed replacement attempt were included in the analysis as replacement nests (Kirby & Tyler 1999).

2.2.3 Brood survival

Hatched broods stayed in close proximity to the nest for 3-4 days where numbers of chicks hatching were recorded. Chicks were ringed using BTO metal rings and colour rings to allow individual identification on re-location. Numbers of chicks per brood were monitored every 3 days for survival and their location noted to monitor movement within and between fields. Brood survival estimates were derived using the modified Kaplan Meier procedure described in Flint *et al.* (1995). This estimator controls for the assumption that chicks within broods have non-independent survival probabilities. Two brood survival estimates were calculated for 1. broods from **hatch to day 5** as natal field effects are likely to be more detectable at this stage before broods are moved to other potential feeding areas and 2. from **hatch to fledge** to determine overall trends in survival between years.

2.2.4 Data analysis

Generalised linear models in S-plus were used to test the effects of 'year' and 'field' on nest density, nest and brood survival. GLMs allow the analysis of non-gaussian error distributions through the use of linearising link functions (McCullagh & Nelder 1983). Minimal models are arrived at by stepwise deletion (McCullagh & Nelder 1983). Model residuals are checked for normality. Predicted fits were used to display results controlling for other terms remaining in the model. Rig and ditch are nested in field to control for repeated measures.

2.3 Results

2.3.1 Nest Density

Vegetation structure and predator avoidance are important factors determining nest site selection in lapwings (Redfern 1982, Beintema & Müskens 1987, Berg *et al.* 1992). In this section, the effects of 1. proximity of lapwing nests to avian predator perches, such as known buzzard *Buteo buteo* nests and 2. field management, on lapwing nest density are examined.

Firstly, two predator indices per field were derived according to their proximity to avian predator nests or potential predator nests (Appendix 1, Figures 1 & 2). The 'distance from buzzard nest' index was calculated from the mean distance of lapwing nests to the nearest buzzard nest over the study period. The 'distance from woodland' index was calculated from the mean distance of lapwing nests to the nearest woodland (potential avian predator nests and perches) over the study period.

Nest density varied significantly within fields over time as shown by the year x field interaction (Table 1, Figure 3). It appeared that nest density increased over the study period in fields 29, 30. Nest density in fields 25, 28 and 32 appear to have remained constant. Field age and both predation indices did not predict this variation (Table 1).

Nest distribution within fields varied significantly, with more nests initiated on ditch edges than rigs (Table 1, Figure 4).

Table 1 Generalised linear model of nest density 1995-1999.

Minimal model

Term	**d.f**	**Deviance**	***P*-value**
NULL	69	263.32	
Field	6	31.62	<0.001
Field (Rig/Ditch)	7	167.14	<0.001
Year	4	10.48	0.032
Year x Field	24	39.98	0.021
Terms dropped			
Field age	1	0.426	0.410
Distance from woodland	1	1.189	0.275
Distance from buzzard nest	1	0.111	0.738

Nest density, being count data, has a poisson distribution. The effects of year, field, field age and 2 predator indices were analysed using a log-linear GLM. (Rig/Ditch) was nested in Field to control for within-field variation. Model residuals were Normal.

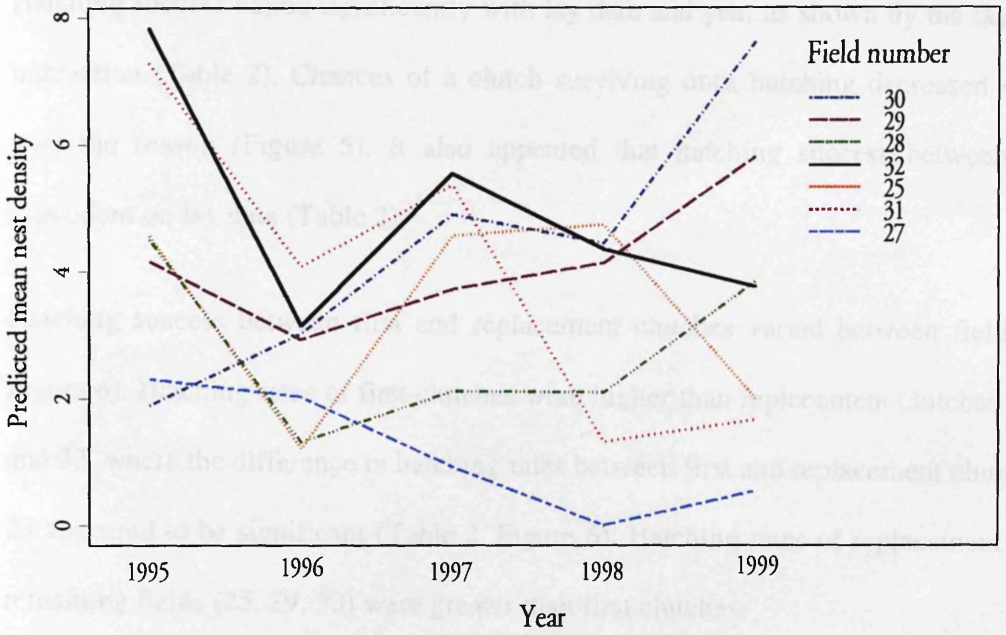


Figure 3 **Variation in nest density in fields between years**

The predicted values control for terms remaining in the minimal model (Table 1).

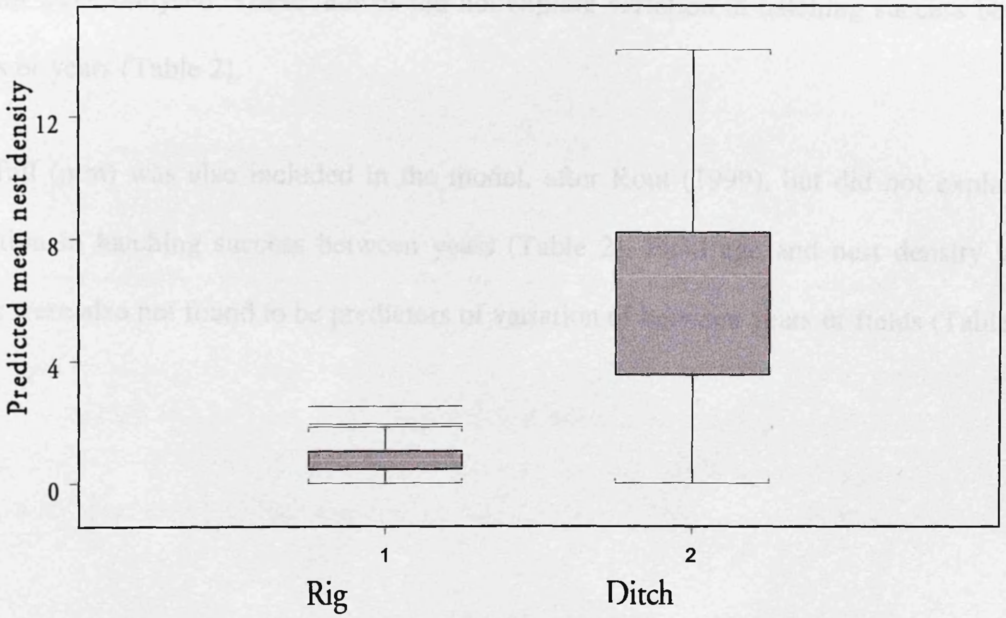


Figure 4 **Variation in nest density within fields.**

The predicted values control for terms remaining in the minimal model (Table 1).

2.3.2 Hatching Success

Hatching success varied significantly with lay date and year as shown by the lay date x year interaction (Table 2). Chances of a clutch surviving until hatching decreased significantly over the season (Figure 5). It also appeared that hatching success between years was dependent on lay date (Table 2).

Hatching success between first and replacement clutches varied between fields (Table 2, Figure 6). Hatching rates of first clutches were higher than replacement clutches in fields 28 and 32, where the difference in hatching rates between first and replacement clutches in field 28 appeared to be significant (Table 2, Figure 6). Hatching rates of replacement clutches in remaining fields (25, 29, 30) were greater than first clutches.

The effects of two predation indices were investigated in the model. The effects of 'distance from buzzard nest' index and the 'distance from woodland' index used in the previous section were analysed. These indices did not explain variation in hatching success between fields or years (Table 2).

Rainfall (mm) was also included in the model, after Rout (1999), but did not explain the variation in hatching success between years (Table 2). Field age and nest density within fields were also not found to be predictors of variation of between years or fields (Table 2).

Table 2 Generalised linear model of nest survival 1995-1999.

Minimal model

Term	d.f	Deviance	*P*-value
NULL	624	866.43	
Year	4	29.38	<0.001
Clutch	1	8.68	0.0032
Lay date	1	26.37	<0.001
Field	5	26.32	<0.001
Year x Lay date	1	25.31	<0.001
Clutch x Field	5	18.59	0.002
Terms dropped			
Field (Rig/Ditch)	6	7.96	0.240
Field Age	1	0.08	0.775
Weather	1	0.259	0.610
Distance from woodland	1	2.17	0.140
Distance from buzzard nest	1	1.07	0.300
Nest density	1	1.41	0.23

The response variable is binary, indicating whether hatching occurred or not. Variation in nest survival over time and between fields was analysed using a logistic regression GLM. (Rig/Ditch) was nested in Field to control for within-field variation. Variation in hatching success between clutches, lay date, predator index and weather were also tested. Model residuals appeared Normal.

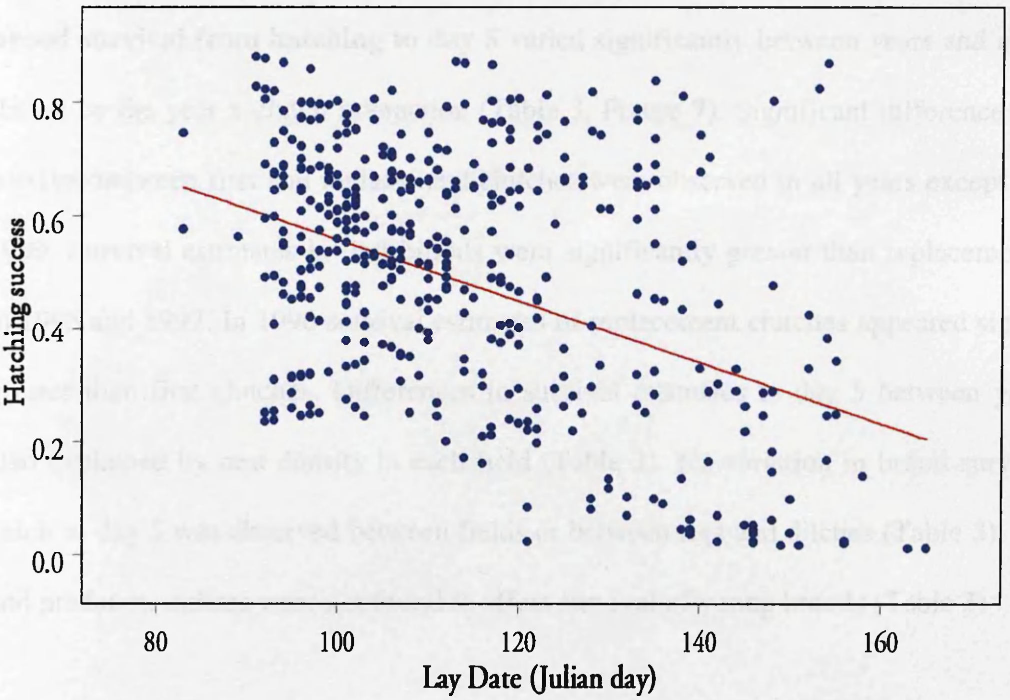


Figure 5 **Variation in hatching success with lay date.**

The values shown control for terms remaining in the minimal model (Table 2).

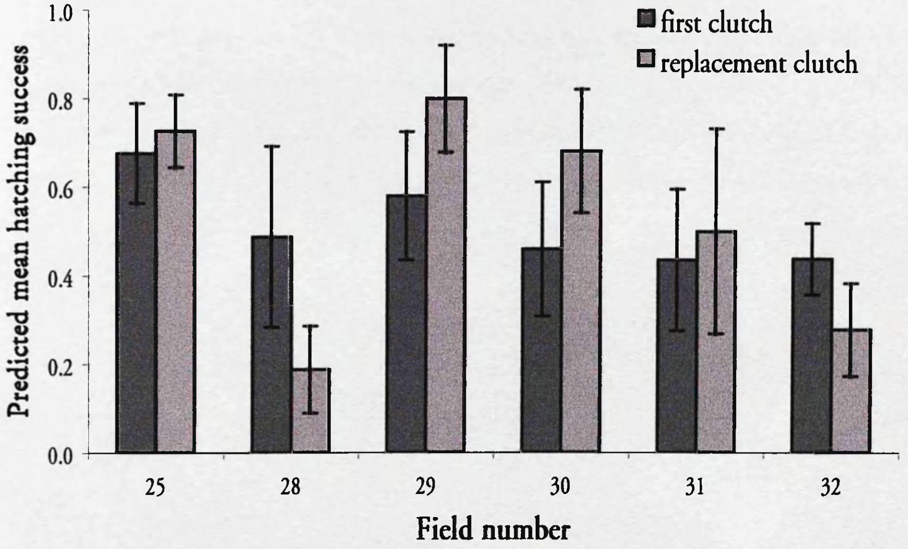


Figure 6 **Variation in hatching success between first and replacement clutches within fields**

The predicted values shown control for terms remaining in the minimal model (Table 2).

2.3.2 Brood survival

Brood survival from hatching to day 5 varied significantly between years and clutches as shown by the year x clutch interaction (Table 3, Figure 7). Significant differences in brood survival between first and replacement clutches were observed in all years except 1998 and 1999. Survival estimates in first broods were significantly greater than replacement broods in 1995 and 1997. In 1996 survival estimates of replacement clutches appeared significantly greater than first clutches. Differences in survival estimates to day 5 between years were also explained by nest density in each field (Table 3). No variation in brood survival from hatch to day 5 was observed between fields or between rigs and ditches (Table 3). Field age and predation indices were not found to affect survival of young broods (Table 3)

Table 3 General linear model of brood survival 1995-1999 (hatch – day 5).

Minimal model

Term	d.f	Deviance	*P*-value
NULL	287	768.95	
Year	4	59.27	<0.001
Clutch	1	0.182	0.765
Nest density	1	0.056	0.866
Year x Clutch	1	25.30	0.015
Year x Nest density	4	20.96	0.036
Terms dropped			
Field	6	19.05	0.167
Field (Rig / Ditch)	9	21.49	0.328
Field Age	1	0.210	0.750
Distance from woodland	1	1.50	0.391
Distance from buzzard nest	1	0.006	0.953

The response variable has a binomial distribution. Variation in brood survival estimates (hatch – day 5) over time and between fields was analysed using a logistic regression GLM weighted by brood size. The model parameter was over-dispersed, therefore a quasi-likelihood GLM was applied with the appropriate "logit" link and "mu(1-mu)" variance functions for the Binomial family. (Rig/Ditch) was nested in Field to control for within-field variation. Model residuals appeared Normal.

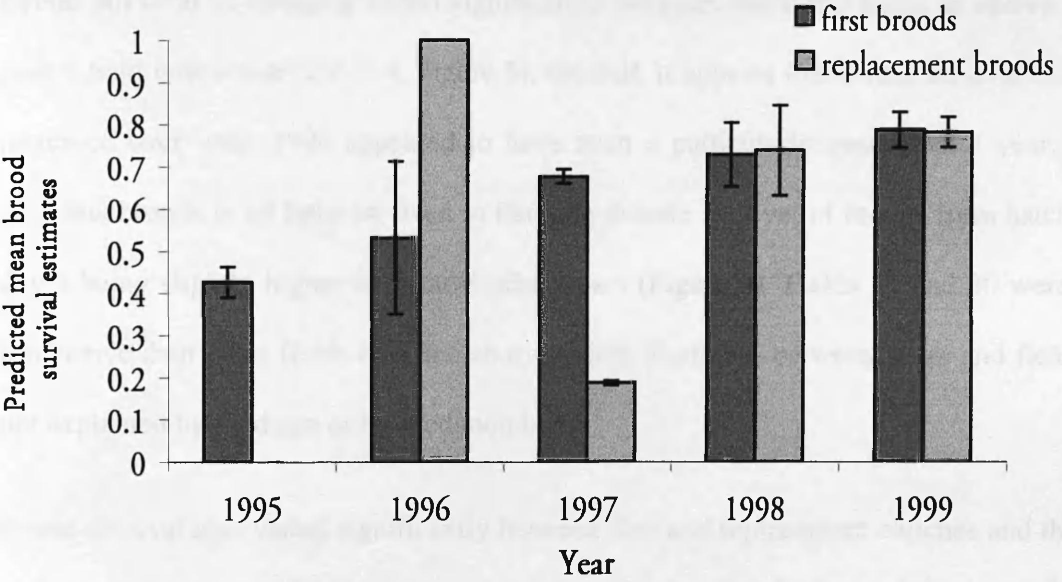


Figure 7 **Variation in brood survival between first and replacement clutches over time**

The predicted values shown control for terms remaining in the minimal model (Table 3).

Brood survival to fledging varied significantly between years and fields as shown by the year x field interaction (Table 4, Figure 8). Overall, it appears that brood survival estimates increased over time. 1996 appeared to have been a particularly unsuccessful year, where very few broods in all field survived to fledging despite survival of broods from hatching to day 5 being slightly higher than most other years (Figure 7). Fields 29 and 30 were more productive than other fields over the study period. Variation between years and fields was not explained by field age or by predation index.

Brood survival also varied significantly between first and replacement clutches and this was dependent on the proximity of their natal field to buzzard nests (Table 3, Figure 9). In fields close to buzzard nests (Fields 28 & 29) the survival of replacement clutches to fledging appeared to be significantly greater than first clutches, while in fields more distant from buzzard nests (Fields 25, 32, 30, 31 & 27) survival of first broods appeared to be greater than replacement broods. This result highlights the importance of replacement broods in maintaining the recruitment of young to the population.

No variation in survival from broods that hatched on rigs and ditches was observed (Table 4).

Table 4 General linear model of brood survival 1995-1999 (hatch – fledge).

Minimal model

Term	d.f	Deviance	*P*-value
NULL	287	481.27	
Year	4	102.21	<0.001
Clutch	1	11.9	0.001
Field	6	51.01	<0.001
Field (Rig / Ditch)	8	11.87	0.235
Distance from Buzzard nest	1	0.0001	0.991
Year x Field	19	36.18	0.038
Distance from Buzzard nest x Clutch	1	5.28	0.031
Terms dropped			
Field Age	1	0.003	0.950
Distance from woodland	1	1.56	0.210

The response variable has a binomial distribution. Variation in brood survival estimates (hatch – fledge) over time and between fields was analysed using a logistic regression GLM weighted by brood size. (Rig/Ditch) was nested in Field to control for within-field variation. Model residuals appeared Normal.

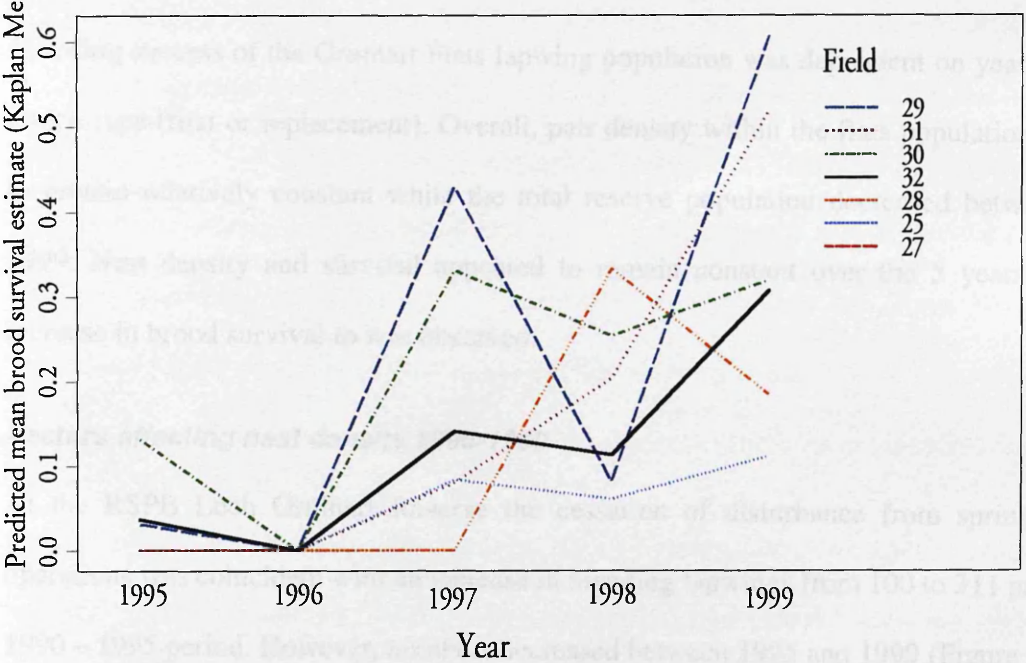


Figure 8 **Variation in brood survival to fledging between fields over time.**

The predicted values shown control for terms remaining in the minimal model (Table 4).

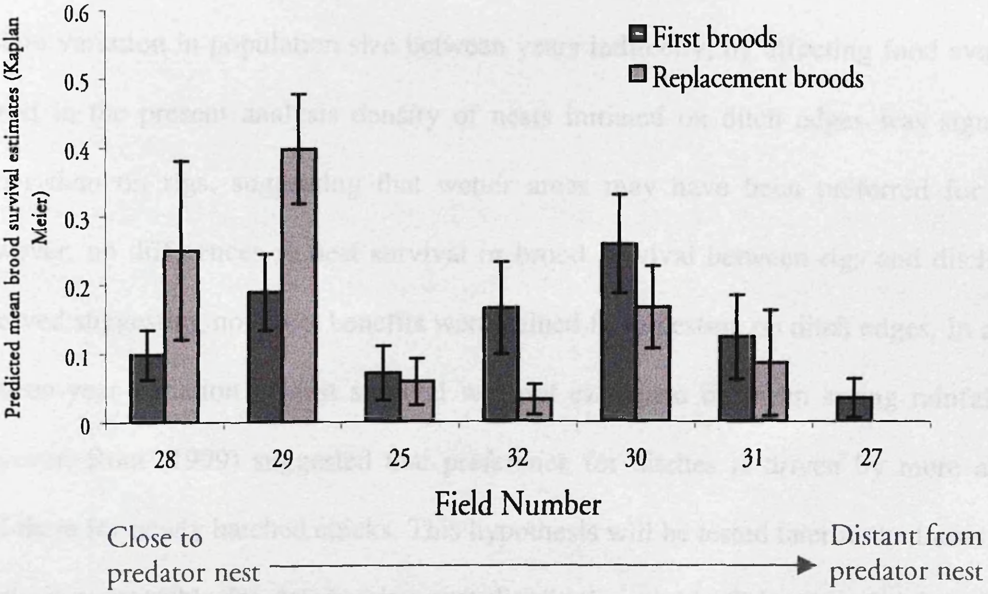


Figure 9 **Variation in brood survival to fledging between first and replacement clutches with field proximity to predator nest.**

The predicted values shown control for terms remaining in the minimal model (Table 4).

2.4 Discussion

Breeding success of the Gruinart Flats lapwing population was dependent on year, field and clutch type (first or replacement). Overall, pair density within the flats population appeared to remain relatively constant while the total reserve population decreased between 1995-1999. Nest density and survival appeared to remain constant over the 5 years while an increase in brood survival to was observed.

Factors affecting nest density 1995-1999

At the RSPB Loch Gruinart Reserve the cessation of disturbance from spring farming operations was coincident with an increase in breeding lapwings from 100 to 311 pairs in the 1990 – 1995 period. However, numbers decreased between 1995 and 1999 (Figure 1). While the overall reserve population declined, numbers of birds using Gruinart Flats remained relatively constant.

In a long-term study by Berg *et al.* (2002) in Sweden, spring flooding index was thought to explain variation in population size between years indirectly, by affecting food availability. Indeed in the present analysis density of nests initiated on ditch edges was significantly higher than on rigs, suggesting that wetter areas may have been preferred for nesting. However, no differences in nest survival or brood survival between rigs and ditches were observed suggesting no direct benefits were gained from nesting on ditch edges. In addition, between-year variation in nest survival was not explained by mean spring rainfall (mm). However, Rout (1999) suggested that preference for ditches is driven by more abundant food there for newly hatched chicks. This hypothesis will be tested later in the thesis. If food supply is responsible for determining nest distribution within fields then it is possible that food supply is responsible for between-field variation in nest density and may have contributed to declines in certain fields.

Another important factor in determining nest site choice in lapwings is vegetation height (e.g. Beintema & Müskens 1987, Redfern 1982). This factor was unlikely to affect lapwings at Gruinart as over wintering geese grazed the sward short and fertiliser was not applied until the end of May, thereby leaving a suitable sward height throughout the nesting period. Rout (1999) suggests that density of *Juncus* might affect nest site suitability of lapwings at Gruinart. However, *Juncus* density is positively related to field age (Rout 1999), i.e. old fields hold higher densities of *Juncus* than fields recently reseeded fields and field age did not significantly predict the variation in nest density between fields or years in this analysis.

Berg *et al.* (1992) observed that lapwings avoided nesting in close proximity to potential predator perches or nest sites. Proximity to woodland and buzzard nests was not found to influence nesting lapwings within fields in this analysis. In addition to woodland there are many fence posts and telegraph poles around the site which can act as potential predator perches which were too many to take into account in this analysis. This measure only considers the effect of avian predators, mammalian predators which occur at the site, such as otter, were not included in the predator index.

Factors affecting nest survival

Previous studies have recognised disturbance from farm machinery and predation as the main causes of lapwing nest failure on agricultural land (e.g. Shrubb 1990, Baines 1990, Galbraith 1988b).

Disturbance from farm machinery during fertiliser application was not thought to contribute to nest failure in this study. When fertiliser was applied in late May the majority of first and replacement clutches had hatched and those still being incubated were marked and avoided by tractors. The effects of earlier fertilising on nest survival will be tested later in the thesis.

Data on causes of nest failure were not recorded in this study. Rout (1999) suggested nest predation is the most obvious cause of lapwing nest failure, however nest proximity to buzzard nests or woodland did not explain variation in hatching success in the present analysis.

Variation in nest survival between first and replacement clutches was dependent on field. Berg *et al.* (1992) also observed differences in hatching success between first clutches and replacement clutches. However they found that greater hatching success of replacement clutches occurred when the loss of first clutches has been attributed to destruction from farm machinery. In the absence of nest destruction from machinery which occurred in this study, hatching success of first clutches was greater than replacement clutches in all but 2 fields. This result was replicated as clutches laid earlier in the season had higher hatching success than those laid later in the season. In the absence of significant disturbance from farm machinery at Gruinart it might be assumed that predation has contributed to the decline in 1999. Rout (1999) suggested that increased numbers of corvids observed at the study site in that year might explain the high failure rates of first clutches, however corvids were only counted in 1998 and 1999 and so this hypothesis cannot be tested.

This analysis highlights the importance of replacement clutches for the Flats' lapwing population. In fields where hatching success of first clutches is low, replacement clutches partially compensate this loss. However, previous studies have shown survival of replacement broods to be lower than early broods (Galbraith 1988a).

Factors affecting brood survival

Previous studies have shown the importance of extrinsic factors (such as food supply, predation, habitat structure and weather) and intrinsic factors (egg size) on the survival of lapwing chicks (Galbraith 1988 a & b, Beintema & Visser 1989).

In this study, between-year variation in brood survival from **hatch to day 5** appears to be influenced by season, i.e. broods hatched earlier in the season (first clutches) survived better than broods that hatched later in the season. This is likely to be related to food supply where food availability is more abundant earlier in the season (Galbraith 1988a). Rout (1999) hypothesised that food abundance on ditch edges was greater than rigs and that chicks hatched on ditches might survive better. However, no differences in survival between rigs and ditches were observed in this study. Between-year variation in survival of broods to day 5 were also predicted by nest density in fields. Previous studies have highlighted the importance of larger colonies in protecting young chicks from predator attacks (Hudson *et al* 1994), but proximity to predators did not influence chick survival to day 5 in this study.

When survival estimates of chicks from **hatch to fledge** were considered there were significant differences between fields suggesting that natal field appears to affect the survival of chicks to fledge but not the survival of chicks to day 5. Proximity of natal fields to buzzard nests predicted differences in chick survival between first and replacement broods. It appears that mortality of first clutches is greater than replacement clutches in fields close to buzzard nests, however this apparent mortality might also be explained by brood movement away from fields where predation pressure is high. Migration is more likely to explain why no effect of proximity to buzzard nest was observed in young chicks. Young chicks remain close to the nest until they are more mobile and then are moved by their parents. Higher survival in replacement clutches in fields close to buzzard nests could then be explained by taller vegetation later in the season providing extra cover for broods.

This analysis gives an outline of the factors which influence the spatial and temporal trends in breeding success at Gruinart Flats. Understanding the mechanisms driving these trends, such as the effects of management (water level manipulation and fertilising) on invertebrate food supply and breeding success will be addressed in the following chapters.

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APPENDIX I

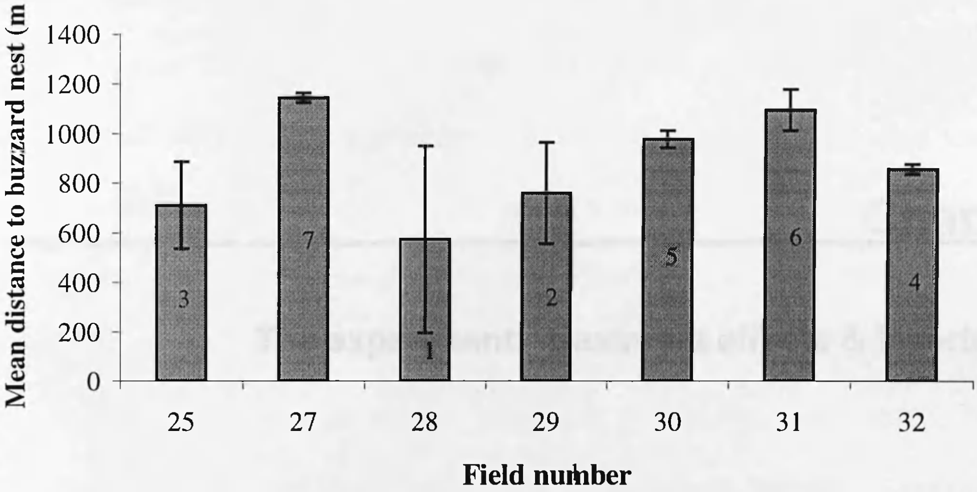

Figure 1 **Ranking of lapwing nest proximity to nearest buzzard nest within fields.**

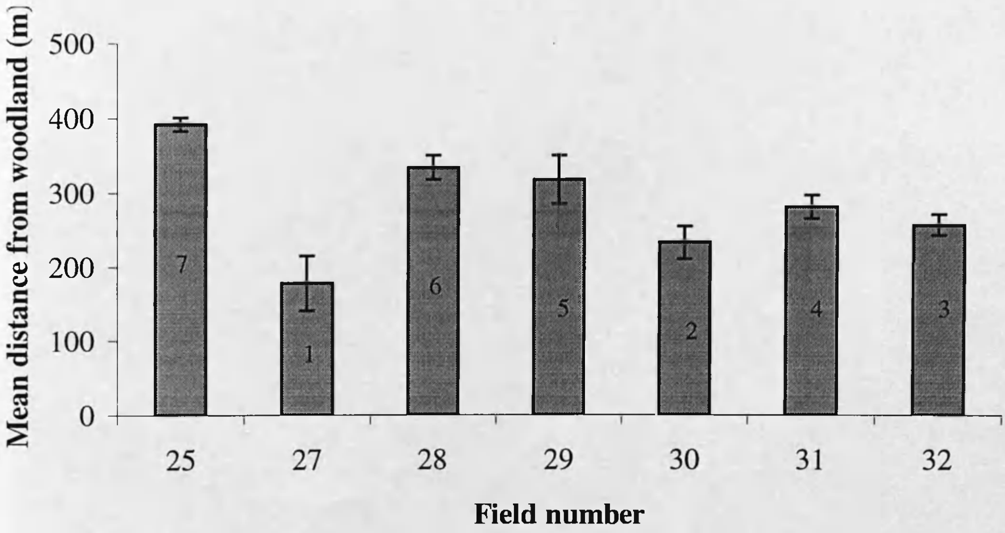

Figure 2 **Ranking of lapwing nest proximity to woodland within fields.**

Chapter 3

The experiment: treatment effects & invertebrates

Abstract

The effects of grassland management practices on the invertebrate food supply of birds has been suggested as a possible mechanism for the decline in farmland birds associated with grassland habitats (Wilson *et al.* 2001). However, the mechanisms are poorly understood (Vickery *et al.* 2001). Here, the effects of two commonly used grassland management practices, fertilising and drainage, on the invertebrate food supply of breeding adult and chick lapwings are examined using a farm-scale factorial experiment. The experiment took the form of a 2 x 3 factorial design with 2 water (high, low) and 3 fertiliser treatments (application early, mid and late season) generating 6 treatment combinations. Both water and fertiliser treatment had a significant effect on earthworm biomass, important for pre-breeding adults (e.g. Galbraith 1989a, Baines 1990). Applying fertiliser early in the season had a positive effect on earthworm biomass when soil moisture was low and an adverse effect when soil moisture is high. Significant spatial and temporal variation was also observed. Water and fertiliser treatments significantly affected numbers of surface invertebrates, important in chick diet (e.g. Beintema *et al.* 1991, Johansson & Blomqvist 1996). Surface invertebrates were most abundant on early and late fertilised treatments when soil moisture was low. When soil moisture was high surface invertebrate abundance on fertiliser treatments did not differ. Spider numbers responded to treatment in a similar way to surface invertebrates, showing that the responses to treatment may be shared between groups. Significant spatial and temporal variation in surface invertebrate and spider number was also observed.

3.1 Introduction

The importance of food supply in influencing bird populations is well known, however its precise effects are seldom easy to quantify (Newton 1998). For example, food shortage can affect bird species by reducing population size through lowering their breeding success. However, this type of effect may be difficult to detect because of the time lag between the food shortage and resultant decrease in population (Newton 1998). Food manipulation experiments have identified how food shortage prior to and during the breeding season can limit egg production (Pons & Miggot 1995) and can result in poor chick growth and survival (Green 1984) thereby affecting breeding success.

Over the past 50 years changes in agricultural practice have been blamed for the decline in bird species associated with farmland habitats. Links between changing management practices, reductions in invertebrate food availability and farmland bird populations on a large scale have recently been demonstrated (Benton *et al.* 2002). On a finer scale, the effects of reduced invertebrate food availability on the breeding success of birds associated with arable habitats are well documented (Wilson *et al.* 1999). However the impacts of grassland management on invertebrate populations and how they affect birds dependent on those habitats has received very little attention despite recent declines in those species (Vickery *et al.* 2001).

The role of food supply during the lapwing breeding season is well documented. Previous studies have shown how adult food supply prior to breeding can influence chick survival through egg quality (Blomqvist & Johansson 1995, Galbraith 1988b). Chick survival can also be determined by proximity to an abundant food source (Galbraith 1988b, Baines 1990).

In a survey of England and Wales in 1987, 96% of breeding lapwings were recorded on agricultural land (Shrubb & Lack 1991), and in Scotland 85% of lapwings were recorded on farmland (Thom 1986). It is no surprise therefore that changes in agricultural practice have been linked to the decline in numbers of breeding lapwings in Britain (O'Brien & Smith 1992, Gibbons *et al.* 1993, Tharme 1998, Wilson *et al.* 2001) and elsewhere in Europe (Hagemeijer & Blair 1997). On grassland, direct effects such as disturbance from livestock and farm machinery have been shown to affect nest survival (Beintema & Müskens 1987, Shrubb 1990, Berg *et al.* 1992). However, very little information is available on the effects of grassland management on lapwing food supply. Previous studies have highlighted differences in invertebrate abundance between grassland habitat types and how this affects lapwing productivity (Baines 1990). However no attempts have been made to understand how management techniques affect the invertebrate food supply of lapwings.

Adult lapwing diet during the breeding season comprises a wide range of soil invertebrates including earthworms and leatherjackets (Tipulidae), and ground dwelling beetles (Coleoptera) and other arthropods (Hogstedt 1974, Cramp 1983). Early in the breeding season lapwings are found feeding in areas where earthworm densities are high (Galbraith 1989a, Baines 1990, McKeever unpublished data). Earthworm biomass during this period is important in determining lapwing egg size, which has implications for chick survival (Galbraith 1988c, Blomqvist & Johansson 1995). Lapwing chick diet is varied and opportunistic (Hudson *et al.* 1994), including beetles, leatherjackets, spiders (Araneae) and earthworms (Galbraith 1989b, Baines 1990, Beintema *et al* 1991, Johansson & Blomqvist 1996).

Recent research has quantified a negative response of some species of terrestrial earthworms to prolonged winter flooding where re-creation of lowland wet grassland has been attempted

(Ausden *et al.* 2001). Earthworm response to fertiliser can be positive or negative depending on the rate of application (Edwards 1984). Very little is known about the effects of drainage and fertiliser application on surface invertebrate abundance. In a recent review by Vickery *et al.* (2001) the need for more research into the effects of grassland management and their impacts on bird populations, in particular how food abundance is affected by fertiliser application, was highlighted.

In this Chapter we tested the hypothesis that lowland wet grassland management affects lapwing food availability. This was undertaken by first examining the effects of manipulating water levels and the timing of fertiliser applications on soil moisture and sward height. Secondly the effects of these manipulations on lapwing food supply were investigated using a farm-scale factorial experiment.

3.2 Methods

3.2.1 Experimental design

The study area was divided up into a series of experimental units (for detailed description of study site, see chapter one). The unit size was determined by lapwing territory size in previous years. Unit size consisted of 2 rigs and 2 ditches (*c.*1ha), which was expected to hold up to 6 nests. Figure 1 shows rig and ditch boundaries for the purpose of this study. Fifty-four units of comparable size were created allowing adequate replication of treatments for the experiment. Rigs that held no lapwing territories in previous years, as well as 'corncrake corridors' (Beaumont *et al.* 1996), were excluded from the design.

The experiment took the form of a 2x3 factorial design: water (HIGH, LOW) x fertiliser (EARLY, MID and LATE season application) generating 6 treatment combinations. With a sample size of 54 units, this allowed 9 replicates per treatment. Power analysis was used to test the robustness of a 2 x 3 design replicated 9 times (Table 1). The effect size used was the standard deviation of nest success to hatching in each unit, calculated from the 1995-1999 data set.

The effect of field age (i.e. number of years since re-seed, see Table 2) was monitored in addition to water and fertiliser treatments. Field age in this study encompasses the management technique and the associated differences in vegetation composition that occur with age. Variation in vegetation composition ranges from ryegrass *Lolium perenne*, timothy *Phleum pratense* and clover *Trifolium repens* dominated grassland in recently reseeded fields to *Agrostis capillaries*, *A. stolonifera* and *Ranunculus repens* dominated grassland 7 years after reseeding (Evans 1985). Field age was not incorporated into the experimental design but was controlled for in all analyses.

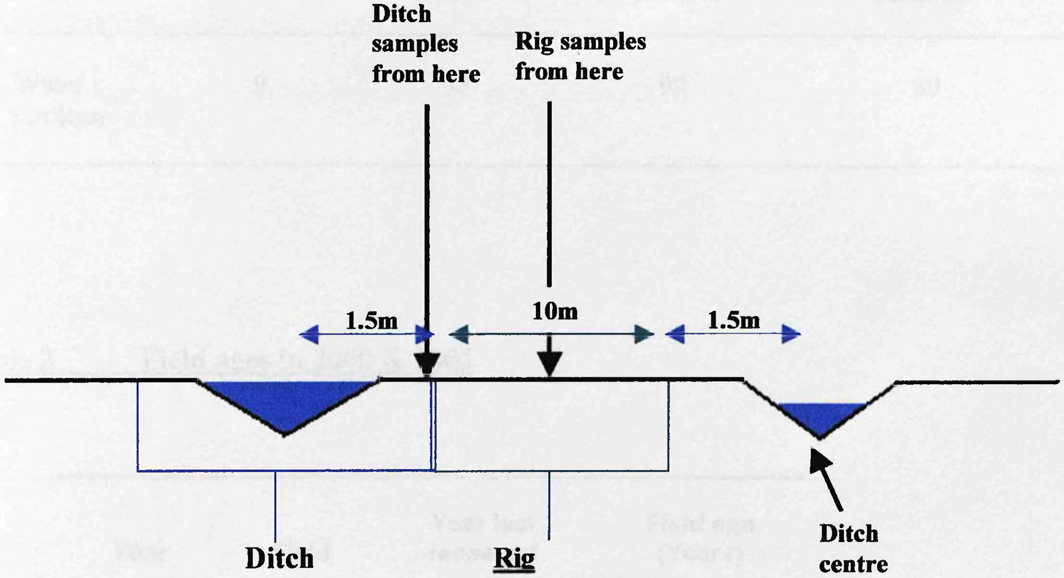

Figure 1 Diagram showing rig and ditch sample points.

Diagram not to scale

Table 1 Power calculations for water x fertiliser factorial design

Effect size = standard deviation of nest success to hatching between units 1995-1999. Power was calculated to 95% probability level.

Factors	N	% Power water	% Power fertiliser	% Power water x fertiliser
Water x fertiliser	9	98	99	30

Table 2 Field ages in 2000 & 2001

Year	Field	Year last reseeded	Field age (Years)
2000	25	1997	3
	27	1995	5
	28	1994	6
	29	1996	4
	*30	1993 & 1999	7 & 1
	31	1995	5
	32	1997	3
2001	25	1997	4
	27	1995	6
	28	1994	7
	29	1996	5
	*30	1999 & 2000	1 & 2
	31	2000	1
	32	1997	4

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* Half of field 30 was reseeded in 1999 and the remainder in 2000. Prior to this field 30 was last reseeded in 1993.

Throughout the study, blocking by field encompasses a wide range of between-field variations such as distance from predator nests and perches and other features such as soil type.

Water x fertiliser treatments were allocated randomly over the study area, except in Field 32 (Figure 2). Details of how treatments were applied and their effects are given below.

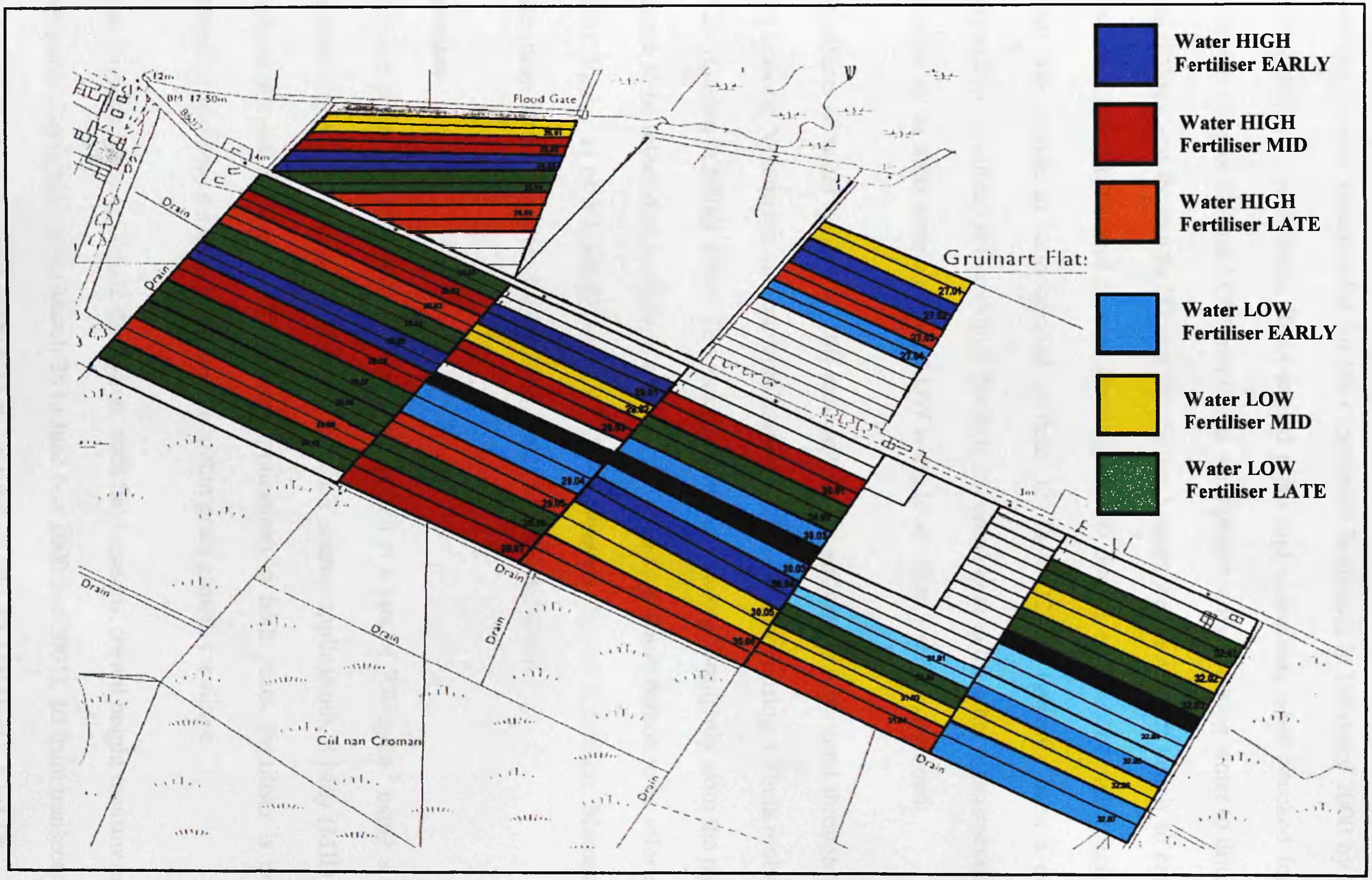

Figure 1 Map of Gruinart Flats showing allocation of treatments in fields.

Water

Water levels were manipulated for the experiment beginning in February 2000 by clearing outflow drains in each ditch. Right-angled pipes and extensions were attached for HIGH treatments (Figure 3a) and LOW treatments were prepared by allowing water to drain freely from ditches into the canals (Figure 3b). Sluice heights were set in the canals to encourage flow from low ditches and prevent flooding of low ditches in times of high precipitation. Water was unable to be controlled in field 32. Field 32 has typically been a dry field (personal observation) with minimal flooding in comparison to the other experimental fields; therefore all its units were allocated LOW water level status for the experiment.

The effects of water control on soil moisture within units were monitored throughout both field seasons. Volumetric soil moisture content (θ) was measured using a Theta probe – type ML2x (Gaskin & Miller 1996). Ten measurements were taken fortnightly from the rig centre (hereon to be referred to as rig) and 1m from the ditch edge (from hereon to be referred to as ditch) (Figure 1) of 3 x HIGH and 3 x LOW treatments chosen at random. Measurements were taken fortnightly from March 28 to June 6 in 2000 and 2001.

Fertiliser

Fertiliser (15:8:15 NPK blend) pellets were applied at a rate of 750kg/ha^{-1} using a tractor-mounted hopper on three dates: 19 April (EARLY season application), 8 May (MID season application) and 30 May (LATE season application) in both years. Fertiliser is normally applied in mid-May on Islay to produce optimum grass growth for silage.

Sward heights were monitored throughout both field seasons. Sward height measurements were taken fortnightly (from March 28 to June 6 in 2000 and 2001), 10 from transects along the rig and 10 from the ditch (Figure 1) of 2 x EARLY and 2 x MID and 2 x LATE treatments chosen at random. Measurements were taken using a sward stick at 2m intervals along transects.

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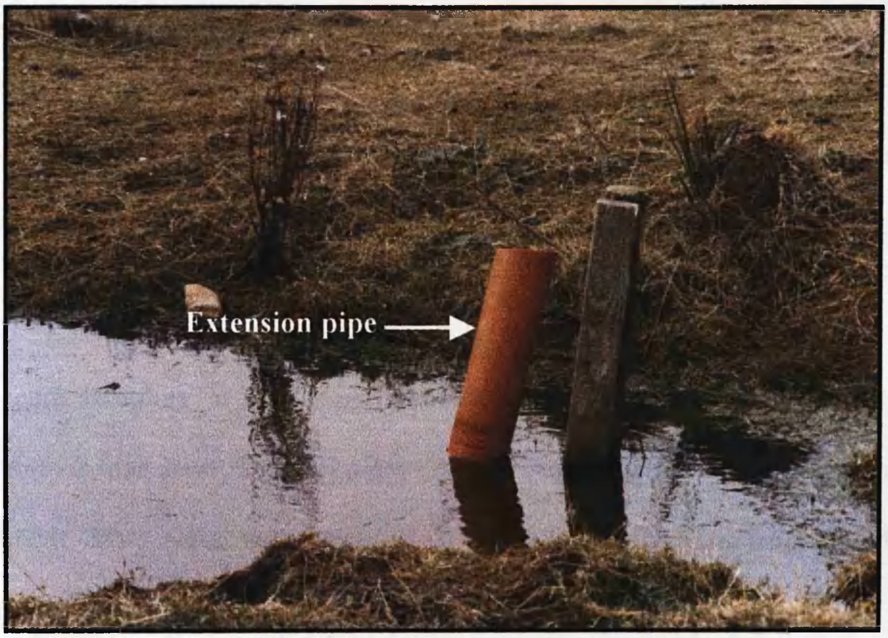


Figure 3a **Photograph of HIGH water ditch - showing extension pipe preventing water flow out of ditch.**

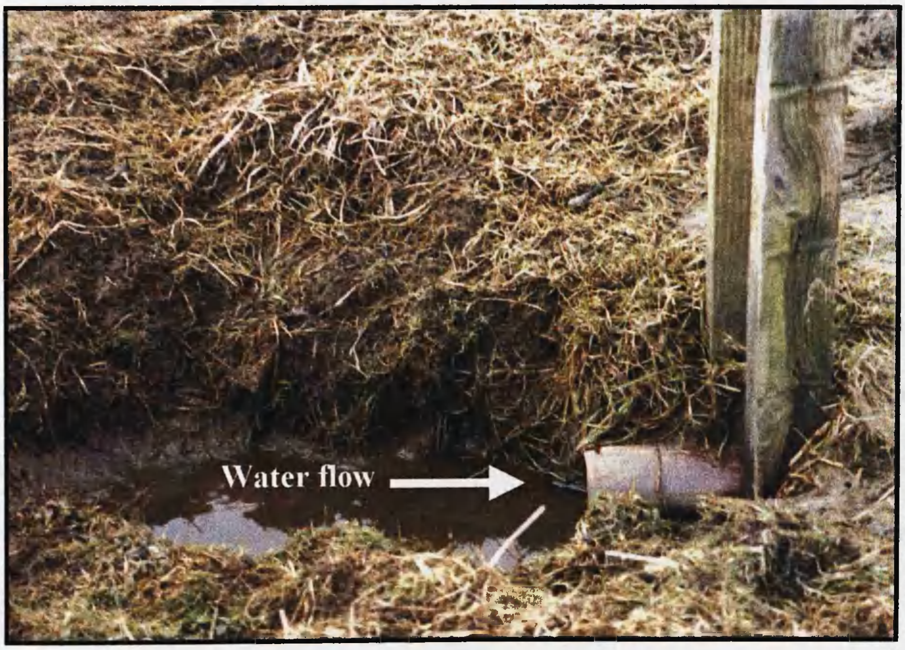


Figure 3b **Photograph of LOW water ditch - showing water flow out of ditch.**

3.2.2 Invertebrates

Soil invertebrates

Soil invertebrates were sampled using soil cores. In 2000, soil cores were sampled from each treatment type in March and again in June. Ten cores (10 x 6 cm, height x width) were taken from the rig and ten from the ditch.

Soil core sampling in 2001 was modified. Treatments were sampled fortnightly from 28 March to 6 June 2001. Ten soil cores (14cm x 8cm, height x width) were sampled from each treatment. Five cores were taken from the rig and five 1m from the ditch (Figure 1). Treatments sampled were chosen at random.

Soil cores from both years were sorted by hand and earthworms were preserved in 70% alcohol. Earthworm density (number) and wet biomass (g) were calculated. Tipulid larvae occurred in very low numbers and were excluded from the analysis.

Surface invertebrates

Surface invertebrates were caught using pitfall traps (plastic cups; 100mm in diameter). Pitfall samples were collected from each treatment type every fortnight from 28 March to 6 June 2001. Treatments sampled each fortnight were chosen at random. Within each treatment ten pitfalls were set, five on the rig and five 1m from the ditch, spaced at 2m intervals. Trapping fluid used was propylene glycol. Wire mesh (2cm mesh) was placed over each trap to prevent capture of wader chicks and small mammals.

Pitfall traps reflect not only the relative abundance of species caught, but also their activity and behaviour. Pitfall traps are more likely to catch species which forage more actively (Blake *et al.* 1994). Lapwings feed by visual cues and active invertebrates are more likely to be taken (Baines 1990). Pitfall trapping is therefore an appropriate method of catching potential lapwing food. However, pitfall efficiency can be affected by vegetation height (Greenslade 1964).

On collection, samples were placed in glass vials with 70% alcohol, to preserve them for identification. Invertebrates were identified to family level and counted. Only invertebrates >3mm in body length were included in the analysis. Animals smaller than this are not considered important in Lapwing chick diet (Beintema *et al.* 1991).

Spider abundance

Spiders are considered an important component of Lapwing food (Beintema *et al.* 1991, Baines 1990, Galbraith 1989b). Spiders were identified to species (Roberts 1993) and the effects of treatment on mean spider number were investigated to examine if similar trends were found to the total surface invertebrate catch. The help of Dr. D. J. Beaumont is acknowledged for identifying spiders to species level.

3.2.3 Data analysis

Generalised linear models in S-plus were used to test the effect of fertiliser and water treatment on soil moisture, sward height and invertebrates in this chapter. GLMs allow the analysis of non-gaussian error distributions through the use of linearising link functions (McCullagh & Nelder 1983). Minimal models were arrived at by stepwise deletion (McCullagh & Nelder 1983). Model residuals were checked for normality. Predicted fits were used to display results controlling for other terms remaining in the model. Rig and ditch were nested in field to control for repeated measures.

3.3 Results

3.3.1 Treatment effects on physical environment

Water

Soil moisture in HIGH water treatments was significantly greater than in LOW water treatments (Table 3, Figure 4). Therefore manipulating water levels of individual ditches had a significant effect on soil moisture of rigs. There was a tendency for soil moisture to vary between rigs and ditches (Table 3). Soil moisture in both HIGH and LOW treatments decreased throughout the season as expected (Table 3, Figure 5). Soil moisture varied significantly between fields (Table 3), in particular, soil moisture in field 32 was significantly lower than other fields.

Table 3 Generalised linear model of volumetric soil moisture content (θ).

Minimal Model

Term	d.f.	Deviance	*P*-value
NULL	59	2.52	
Water treatment	1	0.089	0.009
Week	1	0.593	<0.001
Field	6	0.341	0.001
Field (Rig/Ditch)	7	0.182	0.061
Field x Water	5	0.169	0.030
Week x Field	6	0.209	0.020

The response variable was volumetric soil moisture content (θ). Distribution of the response variable appeared to be Poisson. A log-linear model was used to test the effects of water treatment. Field (Rig/Ditch) was added to control for between and within field variation. The dispersion parameter calculated for the log-linear model was too large (>2). A quasi likelihood GLM was applied. Quasi likelihood allows the estimation of the dispersion parameter in under or over dispersed regression models by supplying the appropriate link and variance functions. In this case we used the "log" link and "mu" variance functions for the Poisson family. Model residuals were Normal.

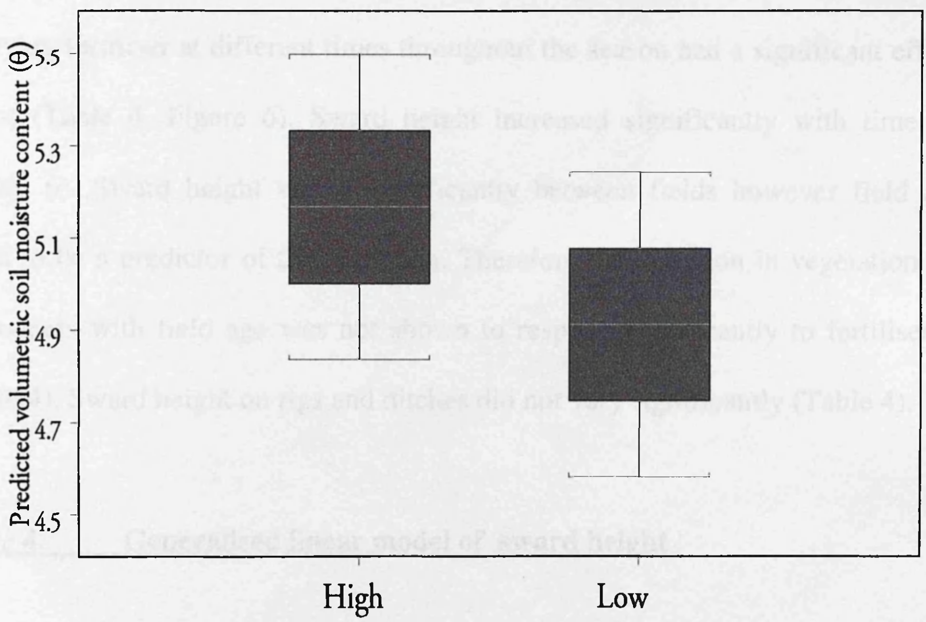


Figure 4 **Variation in volumetric soil moisture content (*6*) with water treatment.**

The predicted values shown control for factors remaining in the minimal model (Table 3).

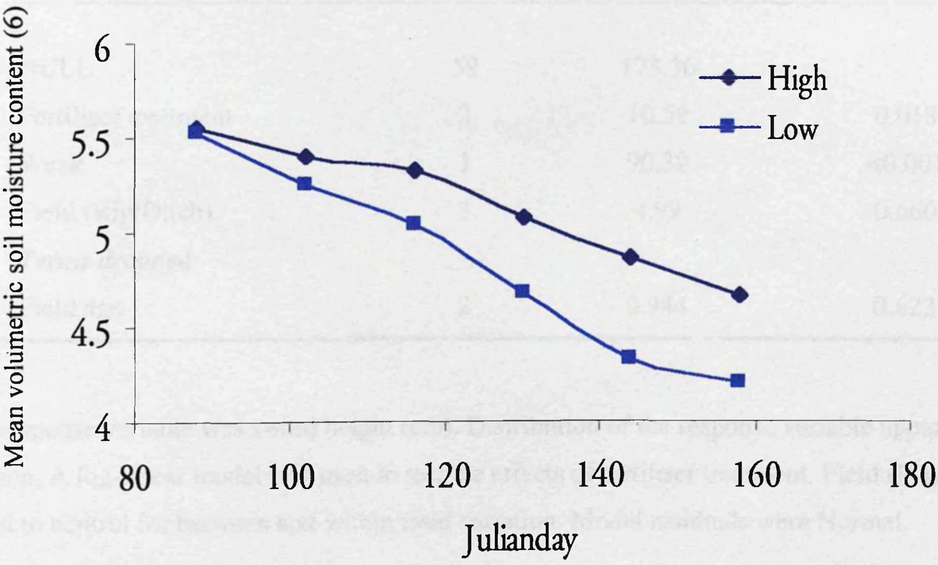


Figure 5 **Variation in volumetric soil moisture content (*6*) with time.**

The predicted values shown control for factors remaining in the minimal model (Table 3).

Fertiliser

Applying fertiliser at different times throughout the season had a significant effect on sward height (Table 4, Figure 6). Sward height increased significantly with time as expected (Figure 6). Sward height varied significantly between fields however field age was not found to be a predictor of this variation. Therefore the variation in vegetation composition that occurs with field age was not shown to respond significantly to fertiliser application (Table 4). Sward height on rigs and ditches did not vary significantly (Table 4).

Table 4 Generalised linear model of sward height

Minimal Model

Term	d.f	Deviance	*P*-value
NULL	59	173.36	
Fertiliser treatment	2	10.59	0.018
Week	1	90.39	<0.001
Field (Rig/Ditch)	3	4.99	0.660
Terms dropped			
Field age	2	0.944	0.623

The response variable was sward height (cm). Distribution of the response variable appeared to be Poisson. A log-linear model was used to test the effects of fertiliser treatment. Field (Rig/Ditch) was added to control for between and within field variation. Model residuals were Normal.

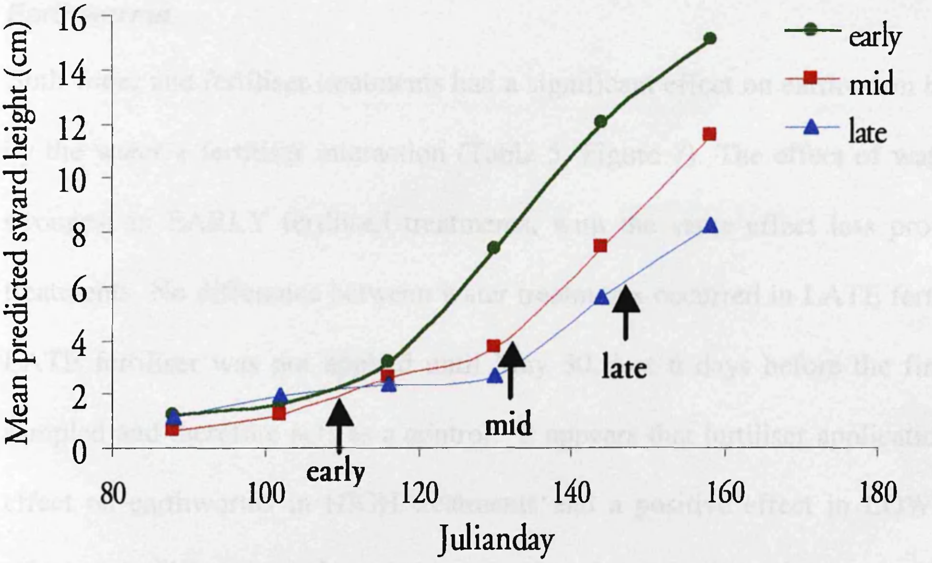


Figure 6 **Variation in sward height with fertiliser treatment**

Predicted soil sward heights in **EARLY, MID** and **LATE** treatments. The predicted values shown control for factors remaining in the minimal model (Table 4). Arrows indicate date of fertiliser application.

3.3.2 Treatment effects on Lapwing food supply

Earthworms

Both water and fertiliser treatments had a significant effect on earthworm biomass as shown by the water x fertiliser interaction (Table 5, Figure 7). The effect of water treatment was strongest in EARLY fertilised treatments, with the same effect less pronounced in MID treatments. No difference between water treatments occurred in LATE fertilised treatments, LATE fertiliser was not applied until May 30, just 6 days before the final soil cores are sampled and therefore acts as a control. It appears that fertiliser application had a negative effect on earthworms in HIGH treatments and a positive effect in LOW treatments. The effect of fertiliser on earthworm biomass therefore was dependent on soil moisture content and the effect of water is equally dependent on the timing of fertiliser application. Earthworm biomass did not differ significantly between treatments after fertiliser application indicating earthworm response to fertiliser was not a direct effect of fertiliser but rather the interaction of timing of fertiliser and water treatment (Table 5).

Variation in earthworm biomass between fields interacted significantly with water and fertiliser treatments, julianday and year (Table 5). This suggests that variation between treatments, day and year depended on the field sampled. Between-field variation was not found to be related to field age (Table 5).

Earthworm biomass varied significantly within fields. Rigs held greater earthworm biomass than ditches (Table 5, Figure 8). This trend was consistent between treatments and fields.

Table 5 Generalised linear model of mean earthworm biomass.

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	111	1972.41	
Water	1	33.72	0.023
Fertiliser	2	88.90	0.001
Year	1	15.41	0.121
Julianday	1	71.38	0.001
Field	6	228.82	<0.001
Field (Rig / Ditch)	7	273.54	<0.001
Water x Fertiliser	2	67.21	0.007
Water x Field	4	46.71	0.127
Fertiliser x Field	9	220.41	0.001
Julianday x Field	5	153.33	<0.001
Year x Field	5	181.90	<0.001
Year x Field (Rig/Ditch)	7	226.11	<0.001
Water x Fertiliser x Field	2	78.36	0.003
Terms dropped			
Field age	1	1.43	0.635
Fertiliser presence	1	3.44	0.479

The response variable was mean earthworm biomass. Earthworm biomass is count data; therefore the distribution appeared to be Poisson. A log-linear model was used to test the effects of fertiliser and water treatment on earthworm biomass. The dispersion parameter calculated for the log-linear model was too large (>2). A quasi likelihood GLM was applied. Field (Rig/Ditch) was included to control for between and within field variation. Presence of fertiliser (1/0) was included to control for fertiliser treatments which had not yet received fertiliser due to timing of sampling. Year and Julianday were included to control for between and within seasonal variation. Model residuals were Normal.

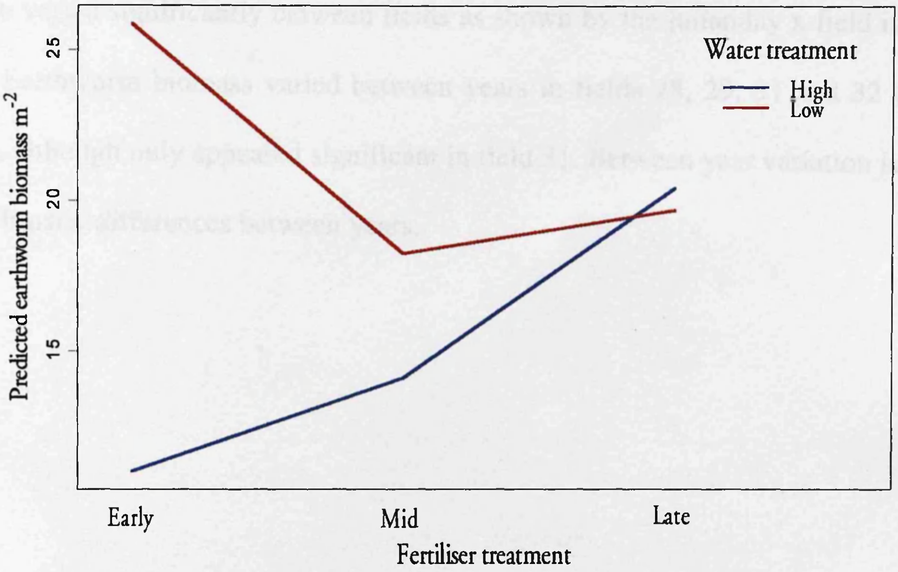


Figure 7 **Variation in earthworm biomass with water and fertiliser treatment.**

The effects of water x fertiliser interaction on earthworm biomass. Interaction plot controls for terms remaining in minimal model (Table5).

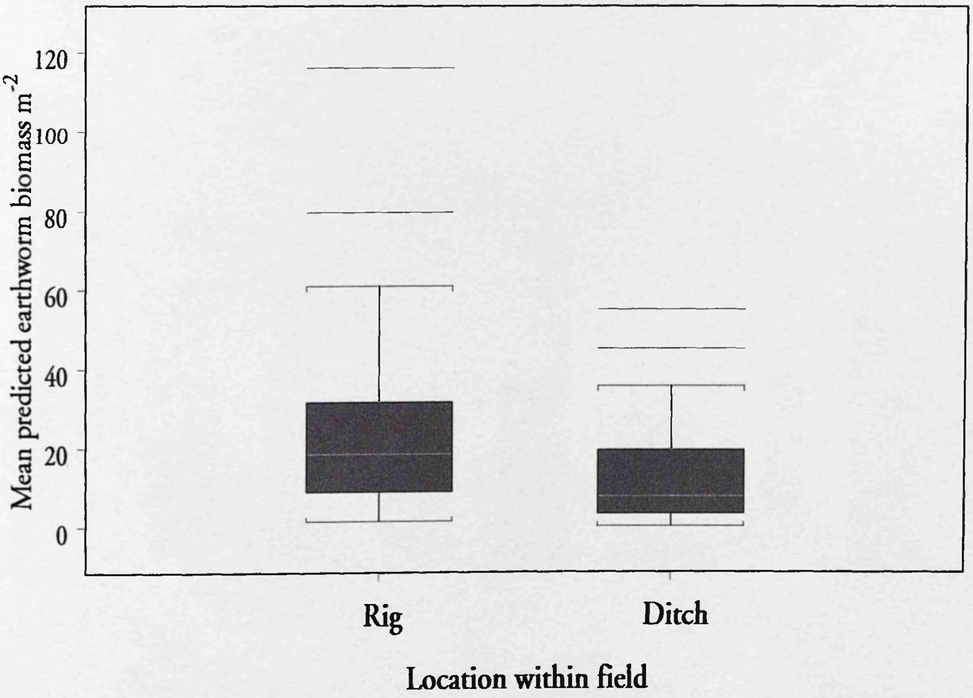
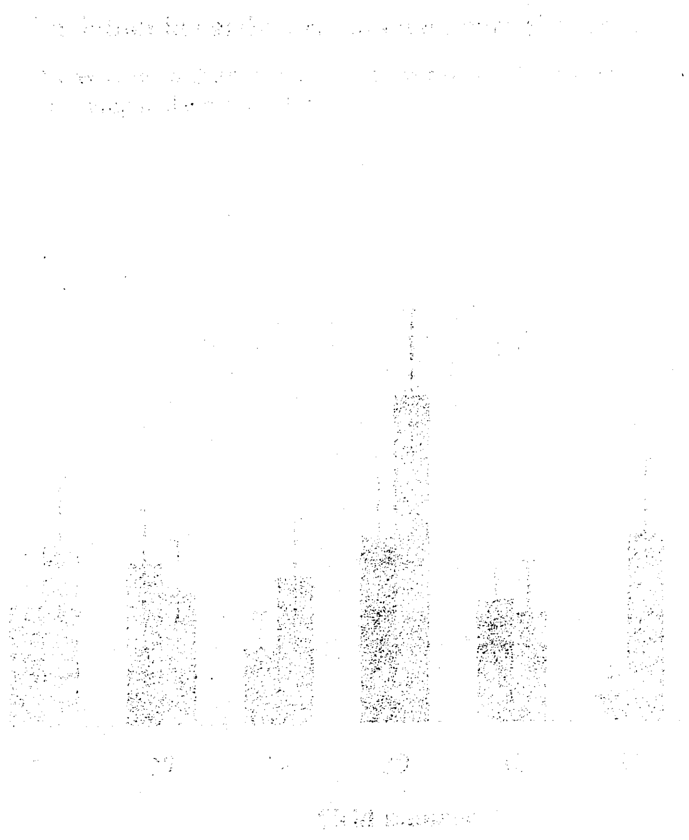


Figure 8 **Variation in earthworm biomass within fields.**

Variation in earthworm biomass g between Rigs and Ditches. The predicted values shown control for terms remaining in the model (Table 5).

Earthworm biomass decreased over the season (Table 5, Figure 9). The rate of decrease over time varied significantly between fields as shown by the julianday x field interaction (Table 5). Earthworm biomass varied between years in fields 28, 29, 31 and 32 (Table 5, Figure 10), although only appeared significant in field 31. Between year variation is likely to be due to climatic differences between years.



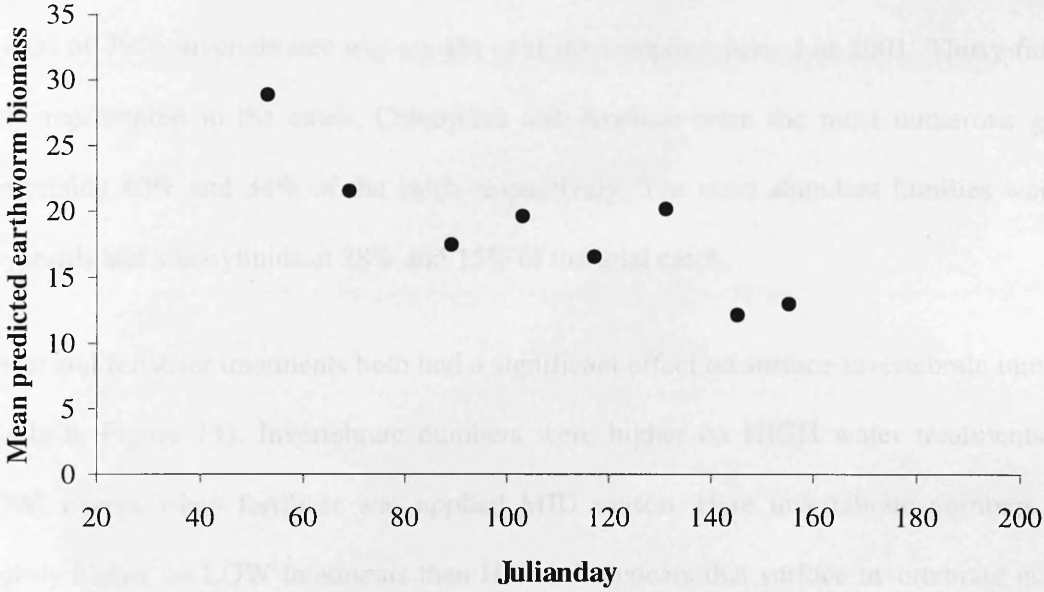


Figure 9 **Variation in earthworm biomass over the season.**

Decrease in earthworm biomass g over time. The predicted values shown control for terms remaining in the model (Table5).

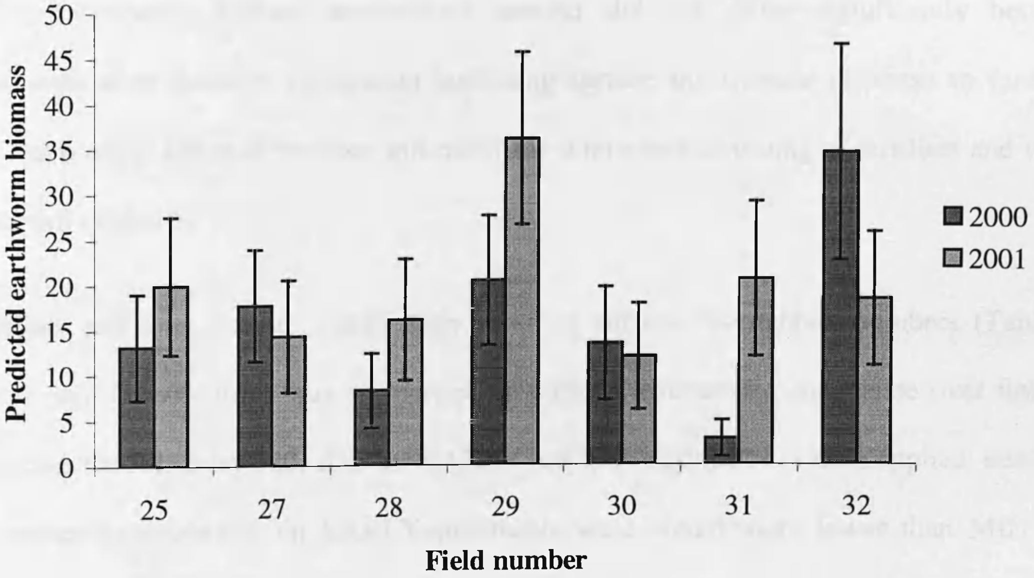


Figure 10 **Variation in earthworm biomass between years & fields.**

Variation in earthworm biomass g between years. Plot is controlled for terms remaining in minimal model.

Surface invertebrate abundance

A total of 7986 invertebrates was caught over the sampling period in 2001. Thirty families were represented in the catch. Coleoptera and Araneae were the most numerous groups comprising 40% and 34% of the catch respectively. The most abundant families were the linyphiids and staphylinids at 28% and 15% of the total catch.

Water and fertiliser treatments both had a significant effect on surface invertebrate numbers, (Table 6, Figure 11). Invertebrate numbers were higher on HIGH water treatments than LOW, except when fertiliser was applied MID season. Here invertebrate numbers were slightly higher on LOW treatments than HIGH. It appears that surface invertebrate number is dependent on soil moisture especially in EARLY and LATE fertilised treatments. The negative effect of soil moisture in MID fertilised treatments is puzzling. Vegetation length is known to constrain the efficiency of pitfall traps (Greenslade 1964) but this does not appear to be the case in this study as invertebrate activity in EARLY treatments is equal to that in LATE treatments. Surface invertebrate number did not differ significantly between treatments after fertiliser application indicating surface invertebrate response to fertiliser was not a direct effect of fertiliser but rather the interaction of timing of fertiliser and water treatment (Table 6).

Fertiliser and time interact significantly to affect surface invertebrate numbers (Table 6, Figure 12). Overall there was an increase in surface invertebrate abundance over time as expected. On Julianday 130, after the EARLY fertiliser treatment has been applied, numbers of surface invertebrates on EARLY treatments were significantly lower than MID and LATE fertiliser treatments (Figure 12). This negative response to fertiliser treatment was observed on MID treatments, however it was not significant. No negative response was observed on LATE treatments.

Table 6 Generalised linear model of mean surface invertebrate number.

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	59	369.8	
Water	1	0.25	0.611
Fertiliser	2	5.99	0.049
Julianday	1	126.77	<0.001
Field	6	66.15	<0.001
Field (Rig / Ditch)	7	47.15	<0.001
Water x Fertiliser	2	7.19	0.027
Fertiliser x Julianday	2	13.38	0.001
Fertiliser x Field	10	51.30	<0.001
Fertiliser x Field x Julianday	3	7.19	0.037
Terms dropped			
Field age	1	2.65	0.103
Fertiliser presence	1	0.296	0.586

The response variable was mean surface invertebrate number. Distribution appeared to be Poisson. A log-linear model was used to test the effects of fertiliser and water treatment on surface invertebrate number. Field (Rig/Ditch) was included to control for between and within field variation. Presence of fertiliser (1/0) was included to control for fertiliser treatments which had not yet received fertiliser due to timing of sampling. Year and Julianday were included to control for between and within seasonal variation. Model residuals were Normal.

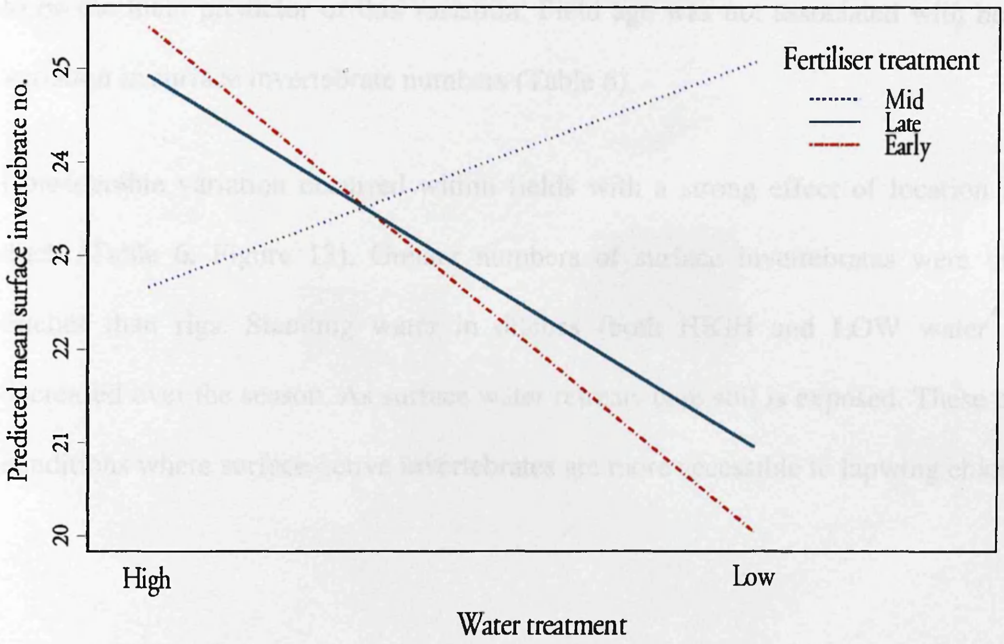


Figure 11 **Variation in surface invertebrate number with water and fertiliser treatment.**

The predicted values shown control for terms remaining in the model (Table 6).

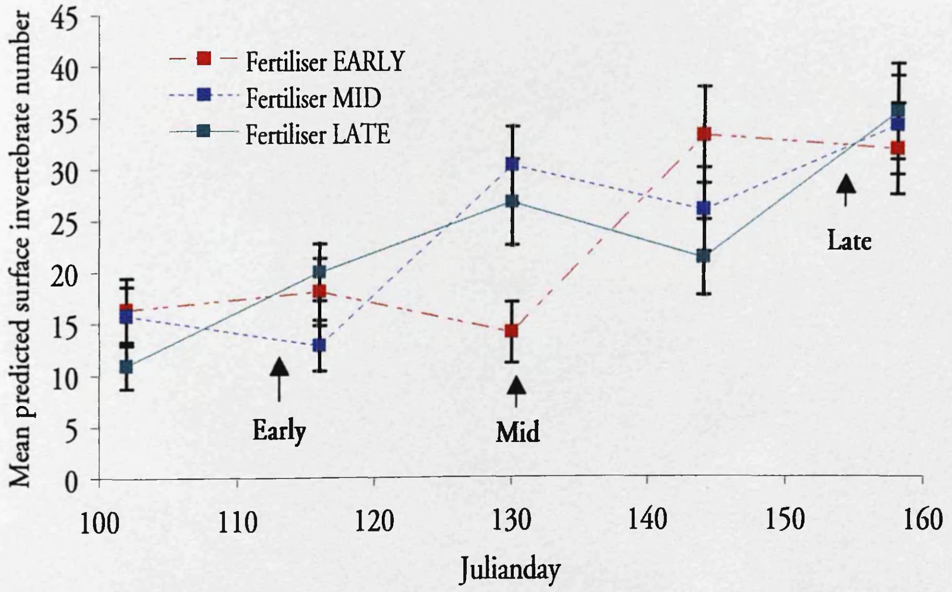


Figure 12 **Variation in surface invertebrate number between fertiliser treatments with date.**

The predicted values shown control for terms remaining in the model (Table 6). Arrows indicate date fertiliser treatments were applied.

Numbers of surface invertebrates varied significantly between fields. Fertiliser was observed to be the main predictor of this variation. Field age was not associated with between-field variation in surface invertebrate numbers (Table 6).

Considerable variation occurred within fields with a strong effect of location i.e. rig and ditch (Table 6, Figure 13). Greater numbers of surface invertebrates were observed on ditches than rigs. Standing water in ditches (both HIGH and LOW water treatments) decreased over the season. As surface water retreats bare soil is exposed. These areas create conditions where surface-active invertebrates are more accessible to lapwing chicks.

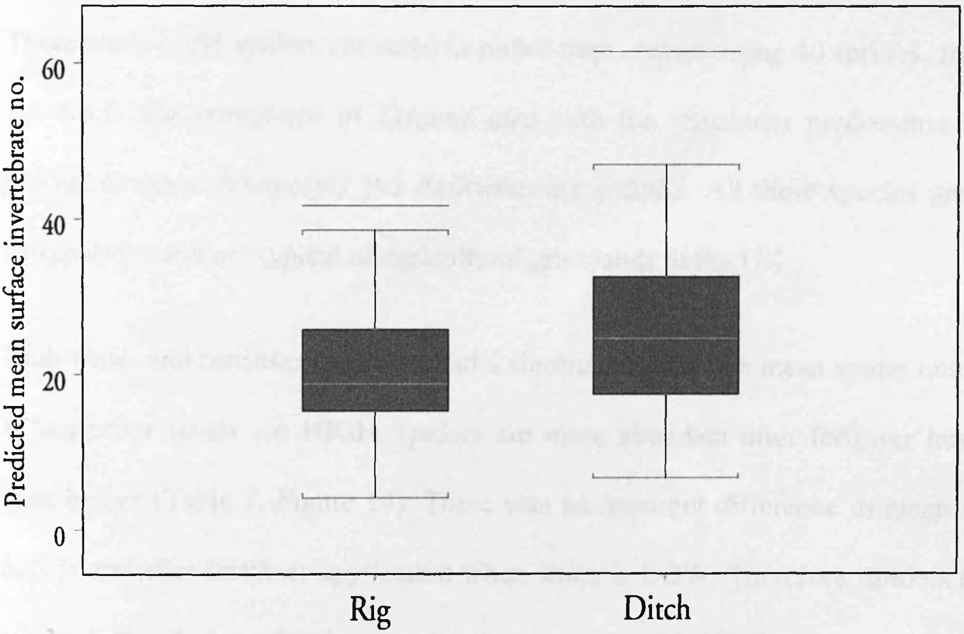


Figure 13 **Variation in surface invertebrate number caught in pitfall traps between rigs and ditches.**

The predicted values shown control for terms remaining in the model (Table 6).

Spider abundance

There were 2,264 spiders collected in pitfall traps, representing 40 species. Just over 50% of the catch was comprised of *Erigone atra* with the remainder predominantly *Oedothorax fuscus*, *Erigone dentipalpis* and *Bathyphantes gracilis*. All these species are of the family Linyphiidae and are typical of agricultural grasslands in the UK.

Both water and fertiliser treatment had a significant effect on mean spider number (Table 7). When water levels are HIGH, spiders are more abundant after fertiliser has been applied than before (Table 7, Figure 14). There was no apparent difference in mean spider number before and after fertiliser application when water is LOW. Therefore, spiders only appear to respond directly from fertiliser application when water is HIGH.

Spider number within fertiliser treatments varied significantly after fertiliser application (Table 7, Figure 16). Spider abundance benefited from fertiliser application in both EARLY and MID fertiliser treatments where greater numbers of spiders were observed after fertiliser was applied. Numbers of spiders in late treatments did not appear to vary significantly after fertiliser application. Overall, spider number appeared greatest on MID and LATE fertiliser treatments than EARLY suggesting preference for shorter sward.

Table 7 Generalised linear model of mean number of spiders

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	59	183.09	
Water treatment	1	0.237	0.626
Fertiliser treatment	2	15.86	<0.001
Fertiliser presence	1	5.35	0.020
Julian day	1	3.56	0.058
Field	6	68.88	<0.001
Field (Rig/Ditch)	7	16.55	0.020
Field age	1	3.66	0.055
Fertiliser presence x Fertiliser treatment	2	41.04	<0.001
Water treatment x Fertiliser presence	1	6.35	0.011
Fertiliser treatment x Julianday	2	22.20	<0.001

The response variable was mean spider number. Distribution appeared to be Poisson. A log-linear model was used to test the effects of fertiliser and water treatment on spider number. Field (Rig/Ditch) was included to control for between and within field variation. Presence of fertiliser (1/0) was included to control for fertiliser treatments which had not yet received fertiliser due to timing of sampling. Year and Julianday were included to control for between and within seasonal variation. Model residuals were Normal.

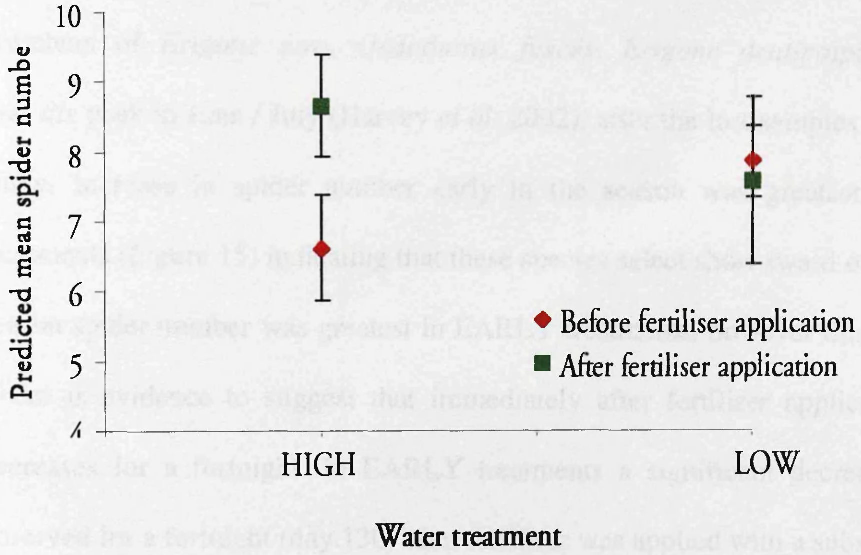


Figure 14 **Variation in spider number with water treatment before and after fertiliser application.**

The predicted values shown control for terms remaining in the model (Table 7).

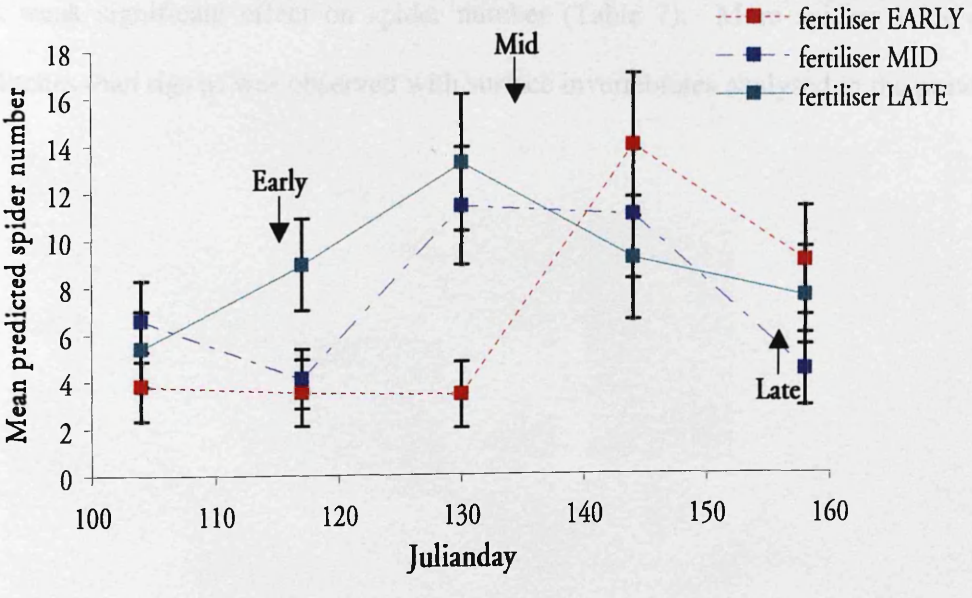


Figure 15 **Variation in spider number between fertiliser treatments over time.**

The predicted values shown control for terms remaining in the model (Table 7). Arrows indicate date fertiliser treatments were applied.

Fertiliser treatment also interacted significantly with julianday (Table 7, Figure 15). Numbers of *Erigone atra*, *Oedothorax fuscus*, *Erigone dentipalpis* and *Bathyphantes gracilis* peak in June / July (Harvey *et al.* 2002), after the last samples are collected for this study. Increase in spider number early in the season was greatest in LATE fertilised treatments (Figure 15) indicating that these species select short sward over long. Later in the season spider number was greatest in EARLY treatments, however this was not significant. There is evidence to suggest that immediately after fertiliser application spider number decreases for a fortnight. In EARLY treatments a significant decrease in numbers was observed for a fortnight (day 130) after fertiliser was applied with a subsequent recovery.

Spider number differed significantly between fields (Table 7) and within fields (Table 7, Figure 17). Between field variation might be attributed to field age, which was found to have a weak significant effect on spider number (Table 7). More spiders were caught from ditches than rigs as was observed with surface invertebrates analysed in the previous section.

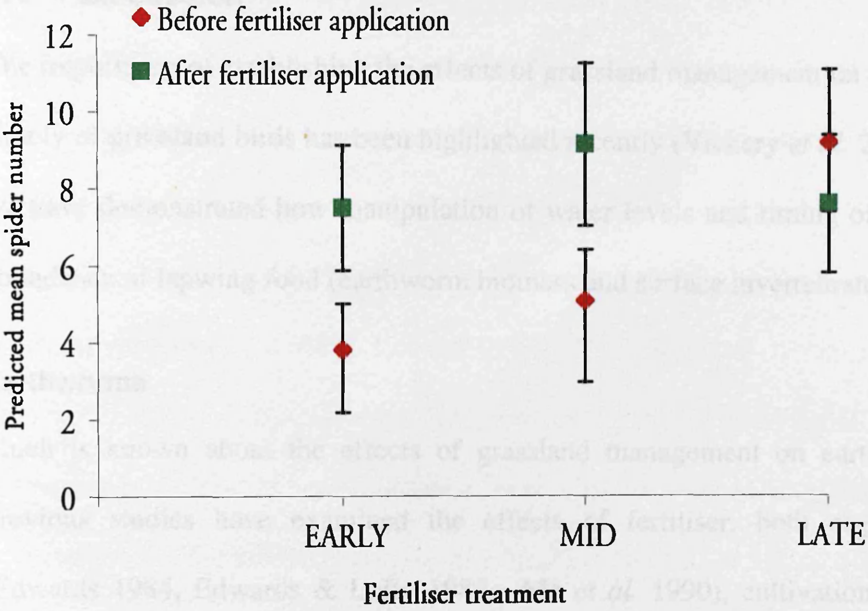


Figure 16 **Variation in spider number between fertiliser treatments before and after fertiliser application.**

The predicted values shown control for terms remaining in the model (Table 7).

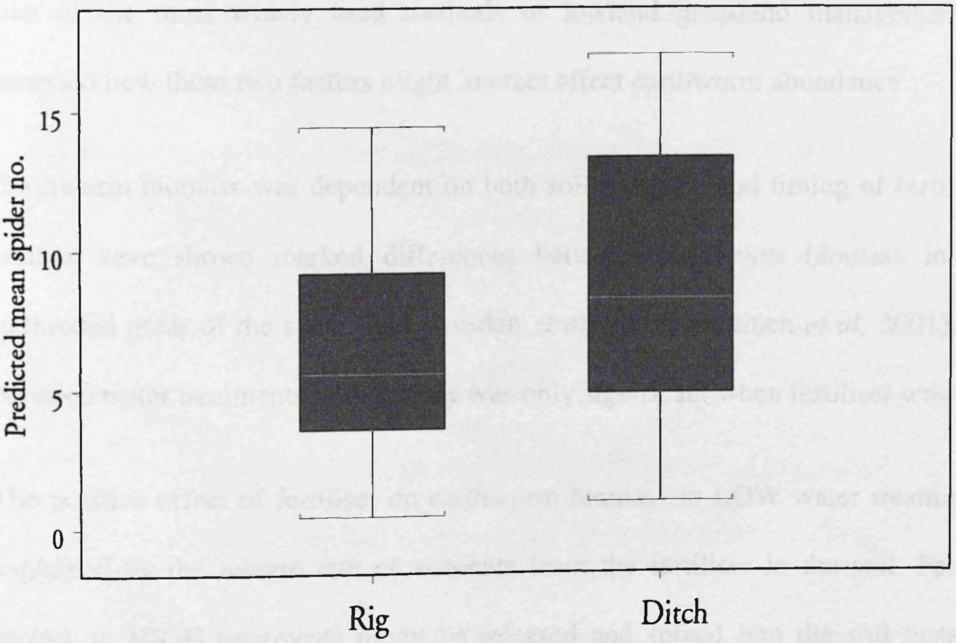


Figure 17 **Variation in spider number between rigs and ditches.**

The predicted values shown control for terms remaining in the model (Table 7).

3.4 Discussion

The importance of establishing the effects of grassland management on the invertebrate food supply of grassland birds has been highlighted recently (Vickery *et al.* 2001). In this chapter we have demonstrated how manipulation of water levels and timing of fertiliser can affect abundance of lapwing food (earthworm biomass and surface invertebrate number).

Earthworms

Much is known about the effects of grassland management on earthworm populations. Previous studies have examined the effects of fertiliser, both organic and inorganic (Edwards 1984, Edwards & Lofty 1982a, Ma *et al.* 1990), cultivation (Edwards & Lofty 1982b) and compaction (Hansen & Englestad 1999) by using field experiments. Other studies have demonstrated the relationship between earthworm biomasses and soil moisture content (Ausden *et al.* 2001, Nuutinen *et al.* 2001). Fertiliser application and drainage are two of the most widely used methods of lowland grassland management. This study assessed how these two factors might interact affect earthworm abundance.

Earthworm biomass was dependent on both soil moisture and timing of fertiliser. Previous studies have shown marked differences between earthworm biomass in flooded and unflooded areas of the same field (Ausden *et al.* 2001, Nuutinen *et al.* 2001). The contrast between water treatments in this study was only significant when fertiliser was applied.

The positive effect of fertiliser on earthworm biomass in LOW water treatments might be explained by the release rate of nutrients from the fertiliser in the soil. Fertiliser pellets spread on HIGH treatments might be released and spread into the soil faster than under LOW water treatments. Fertiliser on LOW treatments therefore might act like a lower dose over a longer period of time. Low rates of inorganic fertiliser have been shown to have positive effects on earthworm populations (Zajonc 1975).

Terrestrial earthworms vacate recently flooded fields, probably due to lack of oxygen (Ausden 2001) and the development of noxious gases (Mather & Christensen 1988). It is likely that a combination of oxygen depletion in HIGH water treatments and fertiliser dissolving into solution has a negative effect on earthworm biomass. Application of NPK fertiliser on some soil types has an acidifying effect creating adverse conditions for earthworms (Ma *et al.* 1990, Hansen & Engelstad 1999). It is possible that the adverse effects of fertiliser chemicals are enhanced when dissolved faster in HIGH water treatments. No difference in earthworm biomass was observed between HIGH and LOW water treatments when fertiliser was applied LATE. This is probably caused by lower soil moisture in HIGH water treatments by the time LATE fertiliser is applied (Chapter 3, Figure 5).

The variation in earthworm biomass between rigs and ditches might be explained by the species composition therein. Semi – aquatic species commonly found in flooded areas are smaller than terrestrial species found in drier soils (Ausden *et al.* 2001), however variation in species combination between rigs and ditches did not occur (Bishop, unpublished data).

A significant seasonal decline in earthworm biomass was observed in this study. As the season progresses and soil dries out earthworms are forced to burrow deeper into the soil (Edwards & Lofty 1977, Edwards & Lofty 1982b). The rate of decline in LOW water treatments was not, as expected, greater than HIGH treatments suggesting that a reduction in soil moisture over time may not be the sole predictor of seasonal decline.

Reseeding has been shown to affect earthworms through disturbance caused by cultivation (Edwards 1984). However, in this study it was not found to influence earthworm biomass. It appears that water level, timing of fertiliser and seasonal effects are of greater importance in determining earthworm biomass.

Surface invertebrates

The response of surface invertebrate number to sward height was dependent on soil moisture. There is evidence to suggest that surface invertebrates require a specific sward height when soil moisture is low. When soil moisture is high the surface invertebrate response is positive and no apparent significant variation with sward height occurs. The effect of drainage on surface invertebrates associated with grassland is not well documented. It is known that arthropods of arable land in Southern Britain benefit from irrigation (Frampton, van den Brink & Gould 2000). Soil moisture has been suggested as one of the main predictors of variation in arthropod number between improved and unimproved grassland habitats in northern England (Baines 1990).

Few studies exist on the effects of fertiliser on abundance of surface invertebrates. In this study temporal increases of surface invertebrates were dependent on fertiliser treatment; there was evidence of a short-term decrease in number after fertiliser was applied indicating a short-term direct effect of fertiliser application. Edwards and Lofty (1975) found reductions in Collembola, Diptera and Coleoptera in permanent pasture receiving fertiliser compared with unfertilised pasture. However this study is the first to consider the combined effects of fertiliser application at different times during the season with varying water levels. Previous authors have also shown that as management intensity increases species diversity and size of Coleoptera (Morris & Rispin 1987, Seipel 1990, Foster *et al.* 1997), Hemiptera and Araneae (Siepel 1990) decreases. Decrease in abundance and over time a decrease in animal size and species diversity will have negative impacts on birds that depend on these invertebrates for food.

Spiders

Spiders numbers were greatest on treatments with high soil moisture after fertiliser had been applied suggesting spiders benefit directly from fertiliser application. Higher numbers of spiders in ditches than rigs is also likely to reflect the higher soil moisture in ditches. In contrast, Downie *et al.* (2000) in a study of linyphiids over 18 land-use categories across Scotland showed that soil moisture has a negative effect on abundance.

Spider preference for fertiliser treatments varied before and after fertiliser application. Spider number was greatest on treatments with short sward after fertiliser was applied. Downie *et al.* (2000) showed that vegetation height was not a significant determinant of linyphiid number. In this study over 50% of the spiders caught were *Erigone atra*, a species associated with short vegetation.

Temporal increases of spiders were also influenced by fertiliser treatment. Increases were greatest on short sward early in the season with a shift to longer grass later in the season. *Erigone atra* are commonly found at ground level on low vegetation (Harvey *et al.* 2002), therefore higher numbers of these spiders were expected on short sward. However it is likely that this result might reflect the activity of spiders rather than actual number, in which case they are more likely to be detected by lapwing chicks. There also appears to be the same short-term negative affect of fertiliser as observed with other surface invertebrates.

Conclusions

Water and fertiliser treatments are very important in determining the abundance of invertebrates which are important in the diet of lapwings. Earthworms are positively affected by fertiliser treatment when soil moisture is low. However previous studies have shown that lapwings, in particular lapwing chicks find great difficulty in feeding in conditions of dry soil and long vegetation (Hudson *et al.* 1994, Baines 1990, Galbraith 1987, 1988). Earthworm biomass in HIGH and LOW treatments are equal when fertiliser is applied LATE. The short sward and better penetrability created by LATE fertiliser HIGH water should attract more chicks for feeding. Optimum conditions for surface invertebrates (particularly spiders) are also provided by LATE fertiliser and HIGH water treatments.

Questions to be answered later in the thesis from these results are:

1. Does food availability influence where lapwings nest?
2. Does food availability determine egg size in lapwings?
3. Does food availability influence lapwing hatching success?
4. Do food availability and/or accessibility influence where lapwing chicks feed and their foraging behaviour?
5. Does food availability in treatments where lapwing chicks feed influence their condition, growth patterns and ultimately their survival?

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Chapter 4

Grassland management and lapwing nesting behaviour

Abstract

Recent research has revealed a decrease in lapwing nest survival rates over the past 30 years (Baillie *et al.* 2002). While much is known of the direct effects of agricultural intensification such as nest destruction from machinery and trampling by livestock (Beintema & Müskens 1987), very little is known of the threats posed by changes in habitat structure (Lister 1964) and food supply. Here, the effects of grassland management practices, namely fertiliser application and drainage, on lapwing nest placement and hatching success are investigated using a farm-scale factorial experiment. Both water and fertiliser treatment significantly influenced nest density, however this was dependent on field. Significant within-field variation occurred, where nest density on ditches was significantly higher than rigs. Fertiliser treatment had a significant effect on hatching success. In fields with low predator activity hatching success in early fertilised treatments was greatest. In fields with high predator activity hatching success was highest in treatments where fertiliser was applied later in the season.

4.1 Introduction

Changes in agricultural practice have been implicated as the cause of severe declines in farmland bird populations over recent decades (e.g. O'Connor & Shrubb 1986, Fuller 1999, Siriwardena *et al* 2001). The impacts of these changes can be classified as direct and indirect. Direct impacts include loss of suitable nesting habitat, for example hedgerow removal, which has been suggested as one of the major contributors of linnet *Carduelis cannabina* decline (Fuller *et al.* 2001). Indirect effects include a reduction in food availability, for example Benton *et al.* (2002) found that changes in farmland bird populations in Scotland were closely linked to changes in agricultural practice through their effects on invertebrate abundance.

While much is known about the effects of agricultural activities on birds associated with arable systems, the effect of grassland management on farmland birds has received little attention (Vickery *et al.* 2001). The direct and indirect effects of fertilising, reseeding and drainage on ground nesting species is poorly understood and more research is required on their effects and in particular their interaction effects with predators and weather (Vickery *et al.* 2001).

Numbers of breeding lapwings in Britain have declined by 49% between 1987 and 1998, particularly in lowland areas (Wilson *et al.* 2001). In addition failure rates at the egg stage have increased from 40% to 49% between 1968 and 1998 (Baillie *et al.* 2002). The loss of suitable nesting habitat and alteration of food supply through grassland improvement are thought to be the main causes of lapwing decline in lowland Britain (Chamberlain & Crick 2002, Fuller 1999, Beintema & Müskens 1987).

The direct impacts of grassland management on breeding lapwings are well documented. Over the last 50 years agricultural intensification has led to the loss of considerable areas of lowland wet grassland in Britain (O'Brien & Self 1994) and lapwings in these areas have declined by 38% between 1982 and 1989 (O'Brien & Smith 1992). Increased use of fertilisers has paralled a change from hay to silage production and an increase in stocking rates. Silage production results in fast, dense growing swards unsuitable for nesting lapwings (Lister 1964), an increase in nest mortality through trampling by livestock (Beintema & Müskens 1987, Shrubb 1990), destruction by farm machinery (Baines 1990, Kruk *et al.* 1996) and increases in the risk of detection by predators (Baines 1990).

Little is known of the indirect effects of grassland management on lapwing nest site selection and hatching success (i.e. what role food supply has on lapwing nest site selection, and ultimately hatching success). Previous studies that have identified links between food supply and breeding success have focused on differences between arable and grassland habitats (Galbraith 1988a, 1988b). However, one study comparing improved and unimproved grassland sites found that while earthworm densities were highest on improved fields, lapwing nest density was highest on unimproved fields (Baines 1990). Baines (1990) suggested that other factors such as sward structure and soil moisture content were more important factors in determining breeding field selection, however this has never been investigated. It is clear then that more research is needed in this area to attain a better understanding of what factors determine nest site selection and hatching success of lapwings on grassland.

The effects of manipulating water levels and timing of fertiliser on lapwing food supply in this study have already been established. In this chapter the hypothesis that lowland wet grassland management affects the nesting behaviour of lapwings will be investigated.

4.2 Methods

The effects of experimental grassland management on lapwing nests were monitored in years 2000 and 2001 of the study. Details of experimental design are outlined in Chapter 3. Aspects of nesting behaviour studied in detail were nest density and nest survival to hatching.

4.2.1 Nest density

Nests were found by locating 'scraping' or 'incubating' birds at the beginning of the breeding season. Observations were made using a Kowa TSN telescope with a x30 magnification wide angled lens and 8x42 magnification binoculars from a landrover used as a mobile hide. All fields were monitored daily for new nests. As a nest was initiated, its location was mapped along with a brief habitat description and how to re-locate it using reference points. Nest location (rig / ditch) was also noted. Nests located up to 1.5m from the centre of each ditch were recorded as ditch nests.

4.2.2 Nest Survival

All nests were monitored daily until hatching or failure. Initiation date of each nest and date of hatching or failure was recorded. A nest without an incubating adult on two consecutive days was recorded as a failure. Replacement nests were easily identified as they were usually initiated in the same territory approximately one week after failure of the first clutch occurred. Later in the season nests in new territories that occurred were assumed to be replacement attempts by pairs which failed in the surrounding area.

4.2.3 Predators

Between-field variation encompasses a range of factors, the most important of which in this chapter is predation. Predator pressure was quantified from daily observations of predator activity within each field over the study period. As a predator was observed, the species was recorded along with location (field) and lapwing response. One hundred and sixty predator observations were recorded over the study period (Appendix 1, Table 1). Fields were ranked according to the proportion of predator activity observed over the study period (Appendix 1, Figure 1) and this index was included in the analysis.

4.2.4 Data analysis

Generalized linear models in S-plus are used to test the effect of treatment on nest site selection and hatching success. GLMs allow the analysis of non-gaussian error distributions through the use of linearising link functions (McCullagh & Nelder 1983). Minimal models are arrived at by stepwise deletion (McCullagh & Nelder 1983). Model residuals are checked for normality. Predicted fits were used to display results controlling for other terms remaining in the model. Rig and ditch are nested in field to control for repeated measures.

4.3 Results

Two hundred and seventy nests (121 first clutches and 86 replacement clutches) were initiated in the study area over the two-year period. Average nest density in the study area was 2.9 nests ha^{-1}, with 76% of units holding at least one nest. First-egg lay dates ranged from 29th March – 22nd May in 2000 and 3rd April – 22nd May in 2001.

4.3.1 Nest density

Nest site choice by lapwings was not expected to be influenced by treatment before water and fertiliser manipulations took effect (24th April and 29th April respectively, see Chapter 3). On the other hand, numbers of nests initiated after treatments took effect were too few to analyse. Fertiliser presence was included in the model in addition to fertiliser treatment (timing of fertiliser) to control for variation in nest density before and after fertiliser application.

Numbers of nests initiated in water treatments varied significantly before and after fertiliser application. Numbers of nests initiated before fertiliser was applied were significantly greater than those initiated after fertiliser application (Figure 1). Numbers of nests initiated in fertiliser treatments also varied significantly before and after fertiliser application where numbers initiated before fertiliser was applied were significantly greater than those initiated after fertiliser application (Figure 2).

Table 1 Generalised linear model of nest density.

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	171	954.1	
Water treatment	1	3.60	0.204
Fertiliser treatment	2	0.297	0.935
Fertiliser presence	1	393.71	<0.001
Year	1	1.84	0.363
Field	6	42.69	0.004
Field (Rig/Ditch)	7	225.33	<0.001
Field Age	1	19.77	0.003
Field x Fertiliser presence	6	48.05	0.001
Field x Fertiliser treatment	12	79.28	<0.001
Year x Field	6	46.99	0.002
Water x Fertiliser presence	1	25.86	<0.001
Water x Field	5	47.38	<0.001
Fertiliser treatment x Field age	2	33.69	<0.001

Nest density being count data has a poisson distribution. The effects of water and fertiliser treatment were analysed using a log-linear GLM. Field (Rig/Ditch) was included to control for between and within field variation. Fertiliser presence (1/0) was included to control for nests initiated before and after fertiliser application. Year was included to control for variation between years. The dispersion parameter calculated for the log-linear model was too large (>2). A quasi likelihood GLM was applied with the appropriate "log" link and "mu" variance functions for the Poisson family. Model residuals were Normal.

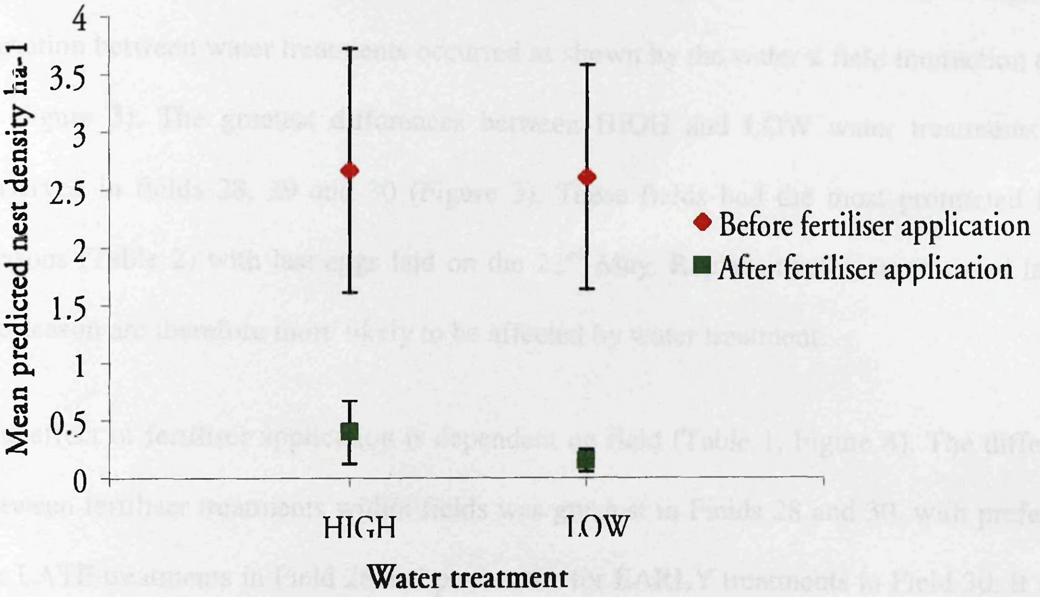

Figure 1 **Variation in nest density between water treatments before and after fertiliser application.**

The predicted values shown control for factors remaining in the minimal model (Table 1).

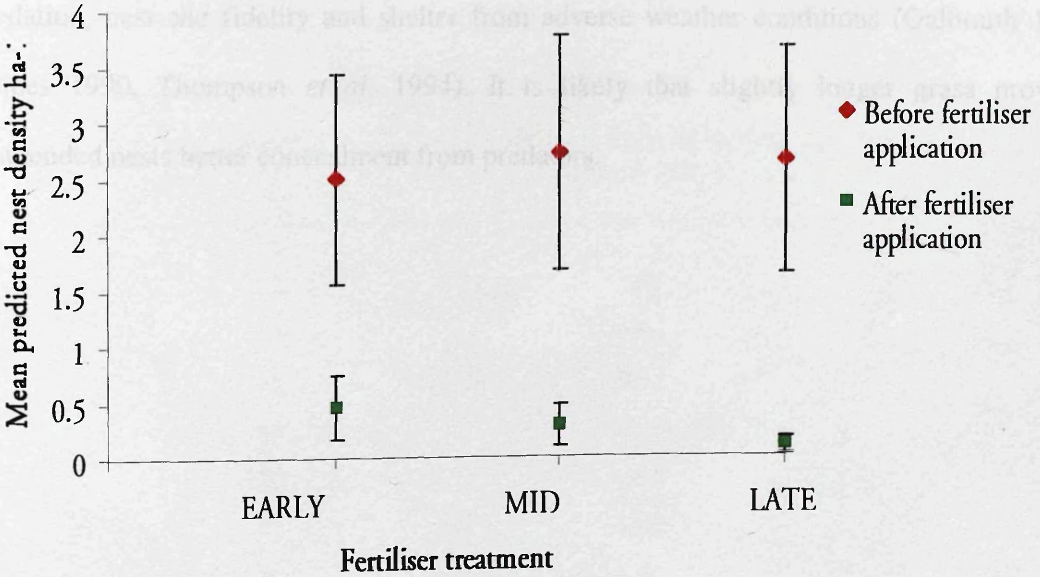

Figure 2 **Variation in nest density between fertiliser treatments before and after fertiliser application.**

The predicted values shown control for factors remaining in the minimal model (Table 1).

When total nest density was analysed significant treatment effects occurred. Significant variation between water treatments occurred as shown by the water x field interaction (Table 1, Figure 3). The greatest differences between HIGH and LOW water treatments were observed in fields 28, 29 and 30 (Figure 3). These fields had the most protracted laying seasons (Table 2) with last eggs laid on the 22^{nd} May. Replacement nests initiated later in the season are therefore more likely to be affected by water treatment.

The effect of fertiliser application is dependent on field (Table 1, Figure 4). The difference between fertiliser treatments within fields was greatest in Fields 28 and 30, with preference for LATE treatments in Field 28 and preference for EARLY treatments in Field 30. It is not clear if this preference is driven by sward height as the majority of nests are initiated before EARLY fertiliser treatment takes effect. However, placement of relay clutches is more likely to be affected by fertiliser treatment later in the season. Other factors important in nest site selection by lapwings, in addition to vegetation height, include avoidance of nest predation, nest site fidelity and shelter from adverse weather conditions (Galbraith 1989, Baines 1990, Thompson *et al.* 1994). It is likely that slightly longer grass provides unattended nests better concealment from predators.

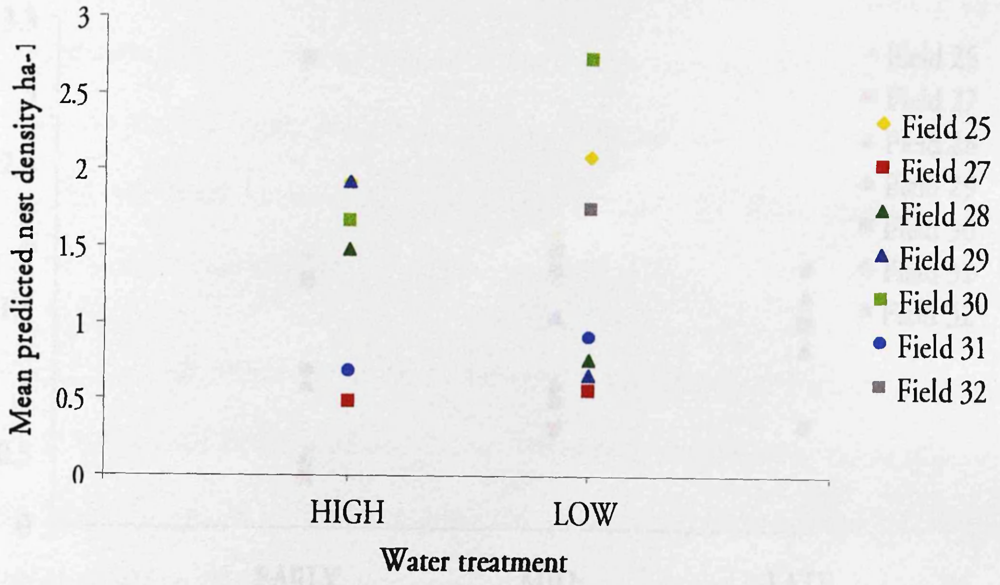

Figure 3 **Variation in nest density between water treatments within fields.**

Difference in nest density / ha^{-1} between rigs and ditches. The predicted values shown control for factors remaining in the minimal model (Table 1).

Table 2 **Duration of laying season (days) in each field.**

Mean number of days between initiation of first and last nests was calculated for each field in both years.

Field	Mean length of laying season (days)
25	26
27	17.5
28	**53.5**
29	**41.5**
30	**46.5**
31	24.5
32	38

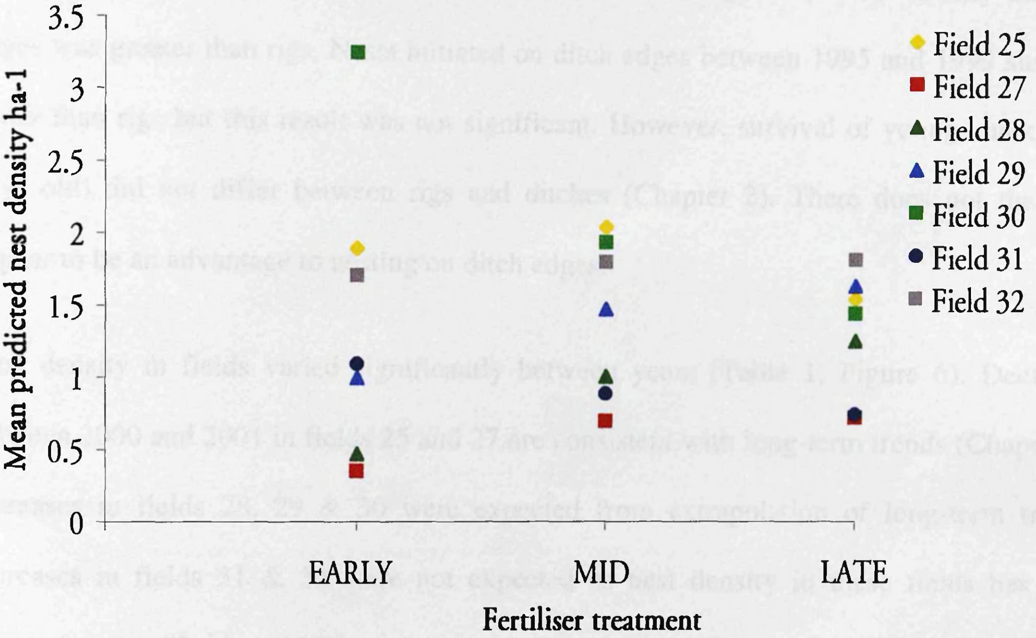

Figure 4 **Variation in nest density between fertiliser treatments within fields.**

The predicted values shown control for factors remaining in the minimal model (Table 1).

Nest density within fields varied significantly (Table 1, Figure 5). Nest density on ditch edges was greater than rigs. Nests initiated on ditch edges between 1995 and 1999 survived better than rigs but this result was not significant. However, survival of young chicks (1-5 days old) did not differ between rigs and ditches (Chapter 2). There does not therefore appear to be an advantage to nesting on ditch edges.

Nest density in fields varied significantly between years (Table 1, Figure 6). Decreases between 2000 and 2001 in fields 25 and 27 are consistent with long-term trends (Chapter 2). Increases in fields 28, 29 & 30 were expected from extrapolation of long-term trends. Increases in fields 31 & 32 were not expected as nest density in these fields has been decreasing steadily since 1995.

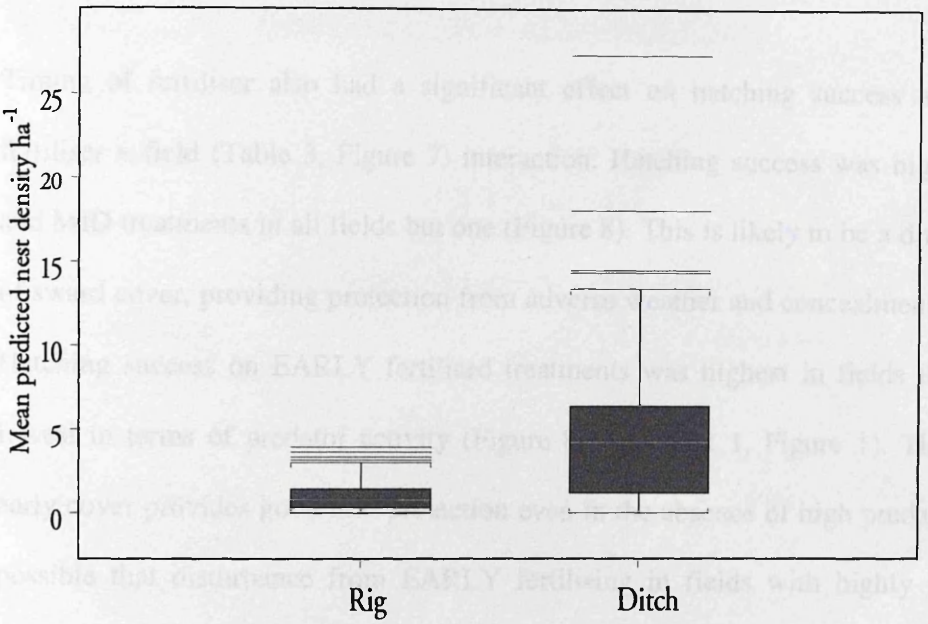

Figure 5 **Variation in nest density between rigs and ditches.**

The predicted values shown control for factors remaining in the minimal model (Table 1).

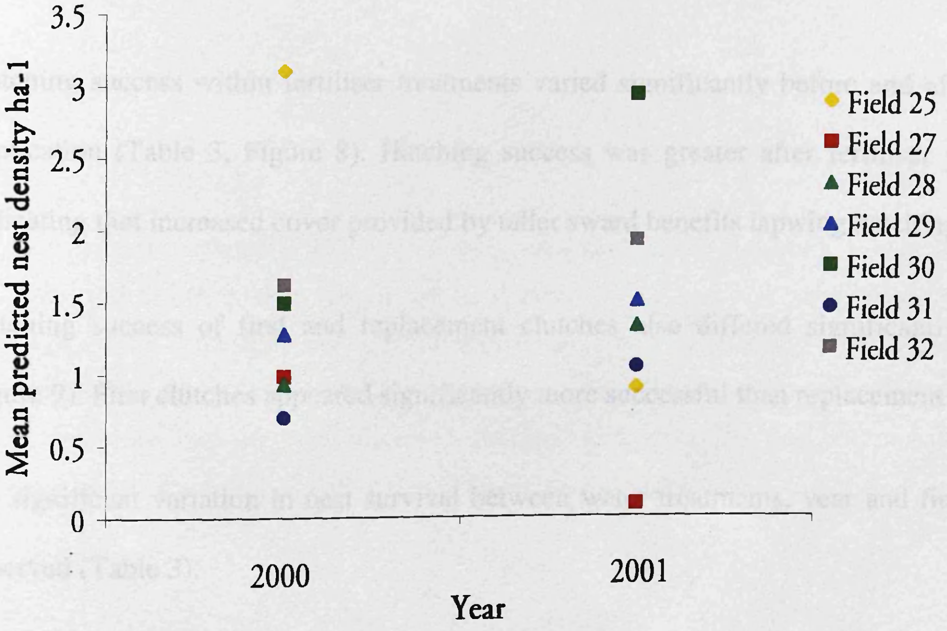

Figure 6 **Variation in nest density between years and fields.**

The predicted values shown control for factors remaining in the minimal model (Table 1).

4.3.4 Hatching success

Timing of fertiliser also had a significant effect on hatching success as shown by the fertiliser x field (Table 3, Figure 7) interaction. Hatching success was highest on EARLY and MID treatments in all fields but one (Figure 8). This is likely to be a direct consequence of sward cover, providing protection from adverse weather and concealment from predators. Hatching success on EARLY fertilised treatments was highest in fields that were ranked lowest in terms of predator activity (Figure 8; Appendix 1, Figure 1). This suggests that early cover provides good nest protection even in the absence of high predator activity. It is possible that disturbance from EARLY fertilising in fields with highly ranked predator activity (Figure 8; Appendix 1, Figure 1) contributed to their detection by predators and the ultimate failure of those nests. Fields 28 and 29 are adjacent and lie below Aoradh wood where ravens *Corvus corax* and rooks *Corvus frugilegus* nest. It is possible that these fields are more prone to nest predation in EARLY fertilised treatments than other fields.

Hatching success within fertiliser treatments varied significantly before and after fertiliser application (Table 3, Figure 8). Hatching success was greater after fertiliser was applied indicating that increased cover provided by taller sward benefits lapwing hatching success.

Hatching success of first and replacement clutches also differed significantly (Table 3, Figure 9). First clutches appeared significantly more successful than replacement clutches.

No significant variation in nest survival between water treatments, year and field age was observed (Table 3).

Table 3 Generalised linear model of hatching success

Minimal Model

Variable	d.f	Deviance	*P*-Value
NULL	212	287.33	
Fertiliser Treatment	2	9.81	0.009
Fertiliser presence	1	16.90	<0.001
Clutch	1	5.48	0.021
Field	6	18.42	0.008
Field (Rig/Ditch)	9	16.04	0.08
Field x Fertiliser treatment	10	20.80	0.032
Term dropped			
Field age	1	0.44	0.509
Water	1	0.86	0.361
Year	1	3.08	0.089

The response variable is binary, indicating whether hatching occurred or not. The effects of water and fertiliser treatments on hatching success were analysed using a logistic regression GLM. Fields were ranked in order of their predator activity (Figure 5). Field (Rig/Ditch) was included to control for between and within field variation. Fertiliser presence (1/0) was included to control for nests initiated before and after fertiliser application. Year was included to control for variation between years. Model residuals appeared Normal.

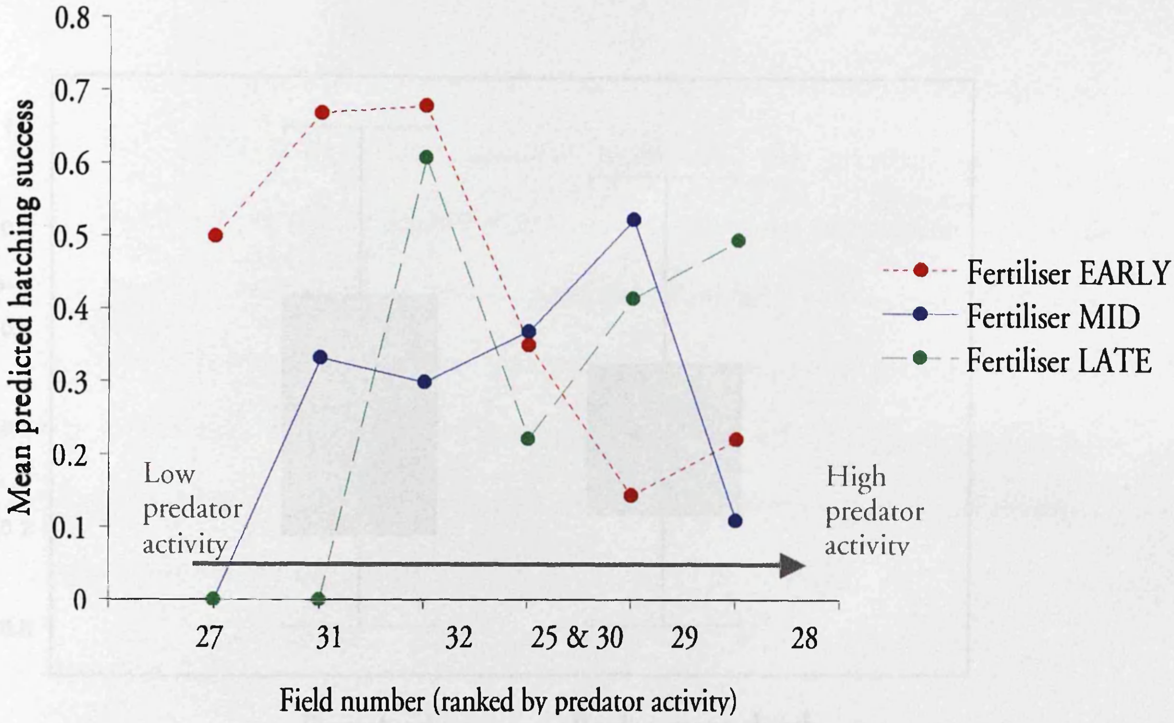

Figure 7 **Variation in hatching success between fertiliser treatments within fields.** The predicted values shown control for factors remaining in the minimal model (Table 3).

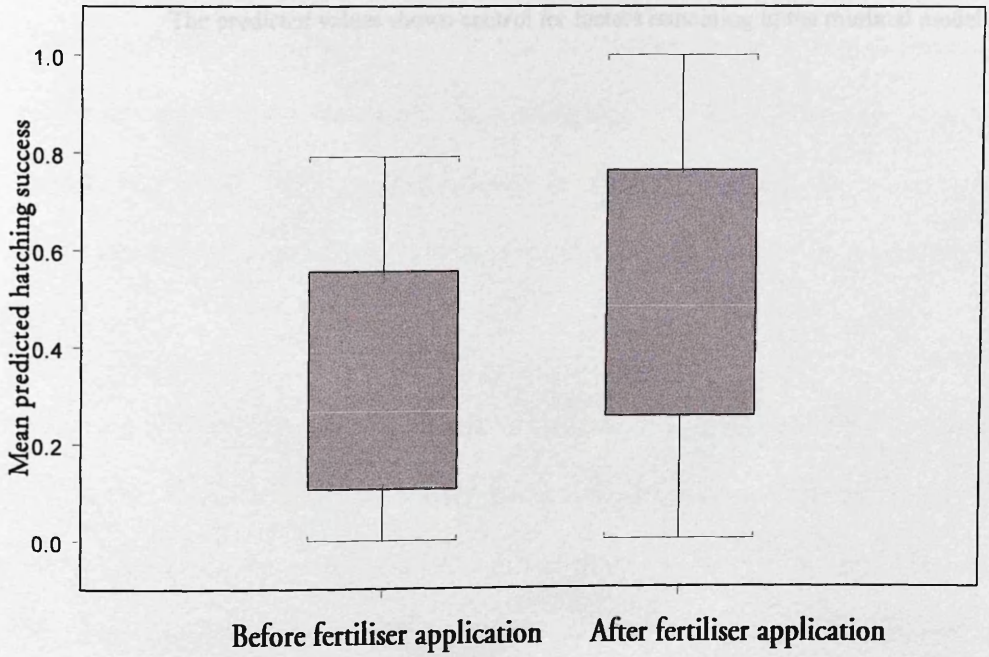

Figure 8 **Variation in hatching success before and after fertiliser application.** The predicted values shown control for factors remaining in the minimal model (Table 3).

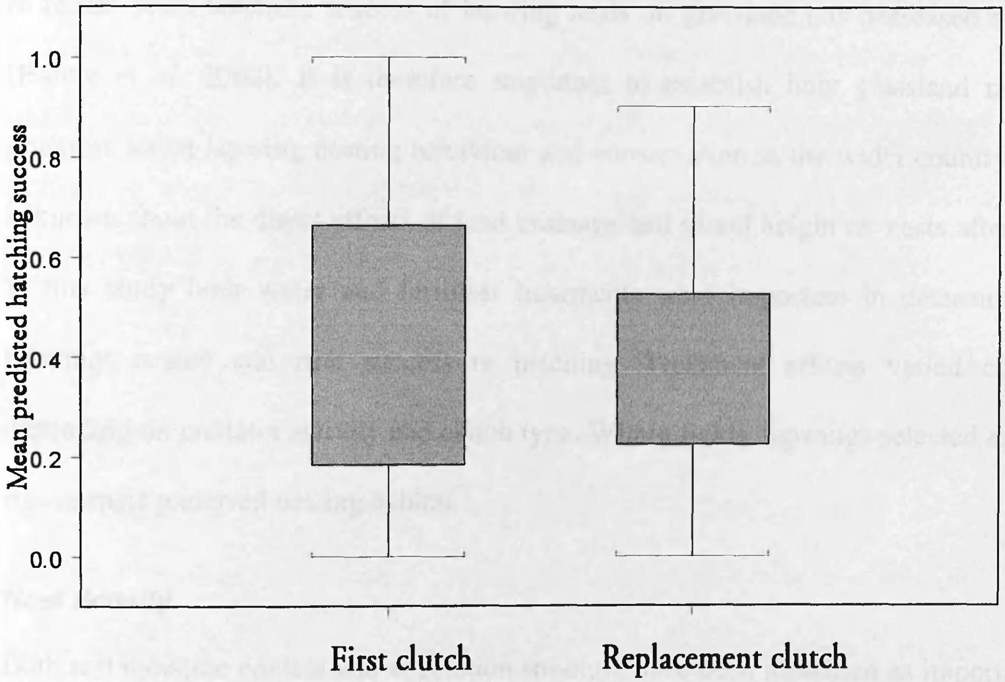

Figure 9 **Variation in hatching success between first and replacement clutches.**

The predicted values shown control for factors remaining in the minimal model (Table 3).

4.4 Discussion

In recent years hatching success of lapwing nests on grassland has decreased significantly (Baillie *et al.* 2002). It is therefore important to establish how grassland management practices affect lapwing nesting behaviour and conservation in the wider countryside. Little is known about the direct effects of land drainage and sward height on nests after initiation. In this study both water and fertiliser treatments were important in determining where lapwings nested and nest success to hatching. Treatment effects varied considerably depending on predator activity and clutch type. Within fields, lapwings selected ditches over rigs as their preferred nesting habitat.

Nest density

Both soil moisture content and vegetation structure have been identified as important factors in influencing lapwing nest site selection. For example, Baines (1990) suggested that differences in soil moisture content and vegetation type and structure between unimproved and improved fields in upland grassland systems is responsible for higher breeding densities of lapwings on unimproved fields. In a comparative study of lapwing breeding success between arable and rough grazing habitats in Central Scotland, Galbraith (1988b) found laying dates on arable were truncated because of the rapid increase in vegetation height from crop growth.

Associating bird populations with habitat is difficult as bird responses to habitat changes are often lagged (Weins 1989). This may be particularly relevant to lapwings as site fidelity and predator avoidance are also important factors when choosing nest sites (Thompson *et al.* 1994; Berg, Lindberg and Källebrink 1992) and therefore may override specific habitat features. O'Brien (2001) investigated the association between habitat and lapwing breeding densities in upland farmland in Northern Britain. He found that lapwing numbers were declining on sites despite the presence of apparently suitable habitat suggesting that other factors are influential in affecting lapwing density. In a 10 year study of lapwings in central Sweden, Berg *et al.* (2002) found low hatching success on arable habitats and much better hatching success on the less preferred grassland habitats. In addition, they found no increase in lapwing numbers on grassland after an extensive meadow restoration programme and attributed that to a lagged response in part due to natal site philopatry.

In the present study significant effects of water and fertiliser treatments were observed in fields which had the longest laying seasons, suggesting nests initiated later in the season were affected. This was expected as both water and fertiliser treatments did not take affect until after all first clutches and the majority of replacement clutches were initiated. Hart *et al.* (2002) found that sward height was not a predictor of lapwing density because of uniformity in the sward early in the season and suggested that sward height would have greater influence later. It is more likely therefore that factors such as predator avoidance, protection from adverse weather or site fidelity are more influential in determining where lapwings nest early in the breeding season.

It is unlikely that differences in food supply between water treatments (Chapter 3) was a determining factor in the selection of water treatments for nesting, as invertebrate responses to water treatment were dependent on timing of fertiliser. In addition invertebrate abundance did not vary significantly between water treatments within fields where significant differences in nest density occurred. This indicates that other field variables such as soil temperature or vegetation cover interact with water treatment in those fields to affect nest site choice.

The importance of the distance between nests and suitable chick-rearing habitat is well documented (Galbraith 1988b, Baines 1990, Berg *et al.* 1992, Blomqvist & Johansson

1995). In this study, lapwings favoured ditch edges over rigs as nesting habitat and this trend was consistent over all fields and treatments. One possible advantage of nesting by ditch edges is proximity to food supply. The surface area of moist bare soil increases in ditches as standing water retreats over the season; this creates conditions suitable for surface invertebrates which are an important and accessible source of chick food. Numbers of surface invertebrates at ditch edges were significantly higher than rigs (Chapter 3).

Hatching success

Many authors have identified destruction from farm machinery and predation as the main causes of lapwing nest failure on agricultural land (O'Brien 2001, Galbraith 1988b, Beintema and Müskens 1987). In a recent analysis of BTO nest record cards, Chamberlain and Crick (2002) found nest abandonment, weather, destruction by farm machinery or trampling and predation to be the main causes of lapwing nest failure from 1962 to 1999. Previous studies have considered the direct effects of trampling by livestock and farming methods such as harrowing, and rolling (Pearson and Stoate 1994) or differences in predation rates between habitats (Baines 1990). However very little is known about the direct or indirect effects of drainage and sward height on nest success.

Fertiliser treatment had a significant effect on lapwing hatching success at Gruinart flats. The effects of fertiliser treatment appeared to have been dependent on predator activity in each field. In relation to predator activity, hatching success was highest in treatments where sward was long and the proportion of predator activity was low. This result was replicated with significantly more lapwing nests surviving after fertiliser was applied. It is likely that nests initiated on treatments with early cover are provided with more concealment when pressure from predators is minimal. In contrast, when predator activity was high, failure rates in long sward were greater. It is probable that a combination of reduced predator detection in long grass, disturbance by applying fertiliser early and increased pressure by predators leaves lapwings unable to defend their nests effectively. However, Baines (1990) found nest predation higher on improved than unimproved grassland and attributed this to the ability of diverse vegetation and irregular background mosaics to provide camouflage for eggs. Potential nest predators observed at the study site included hooded crow, raven, common gulls, herring gulls, feral cat, otter and other mustelids. On the mainland, foxes have been associated with high nest predation of lapwings and other waders (O'Brien 2001, Grant *et al.* 1999) but do not occur on Islay.

Survival of first and replacement clutches differed significantly with survival of first clutches greater than replacement clutches. Previous studies have noted differences in hatching success between first and replacement clutches. Berg, Lindberg and Källebrink (1992) found hatching success in replacement clutches higher than first clutches, with disturbance from farming operations causing high nest mortality amongst first clutches. The same trends and causes of nest failure were observed by Berg *et al.* (2002). In this study there did not appear to be a direct adverse effect of fertiliser application on first or replacement clutches.

Since the cessation of spring farming operations at Gruinart flats in 1990, numbers of breeding pairs have increased from 150 to 300 in 1999. It is assumed that an increase in hatching success of first clutches in the absence of early cultivation and rolling has given rise to an increase in recruitment to the population. Since 1995 hatching success of replacement clutches in lapwings at Gruinart flats (1995-1999) has been significantly lower than first clutches (Chapter 2). Variation in hatching success between first clutches and replacement clutches in the present study was consistent with these trends. When hatching success in first clutches is low then hatching success amongst replacement clutches may become important in maintaining population levels, however this does not appear necessary at Gruinart Flats..

To conclude, the effects of fertiliser and water treatment on nest density were only apparent in fields where the laying season was protracted. Other factors, such as site fidelity are likely to have influenced nest placement at Gruinart Flats. This could not be integrated, however, due to the very small numbers of colour ringed adult birds observed. The effects of fertiliser treatment on hatching success within fields were dependent on the susceptibility of fields to predation events. It appears that heterogeneity of sward height benefits nest survival. Early cover benefits hatching success particularly those nests initiated in fields with low predator activity.

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APPENDIX 1

Table 1 Predator activity within fields over study period

Field (rank)	Species	No. Observations	Proportion of activity within field (%)
25 (4)	Buzzard	12	56
	Peregrine Falcon	5	21
	Raven	2	9
	Hooded crow	1	4
	Merlin	1	4
	Stoat	1	4
27 (1)	Buzzard	4	80
	Lesser Black backed gull	1	20
28 (7)	Raven	13	28
	Buzzard	12	26
	Hooded crow	9	20
	Hen Harrier	5	11
	Herring Gull	4	8
	Stoat	2	4
29 (6)	Buzzard	17	45
	Raven	8	20
	Hooded crow	8	20
	Herring Gull	3	7
	Lesser black backed gull	1	2
	Stoat	2	5
	Otter	1	2
30 (4)	Buzzard	11	50
	Hooded Crow	6	27
	Herring gull	4	18
	Otter	1	4
31 (2)	Pheasant	4	50
	Hen harrier	2	25
	Herring gull	2	25
32 (3)	Hooded crow	6	54
	Raven	3	27
	Buzzard	2	18

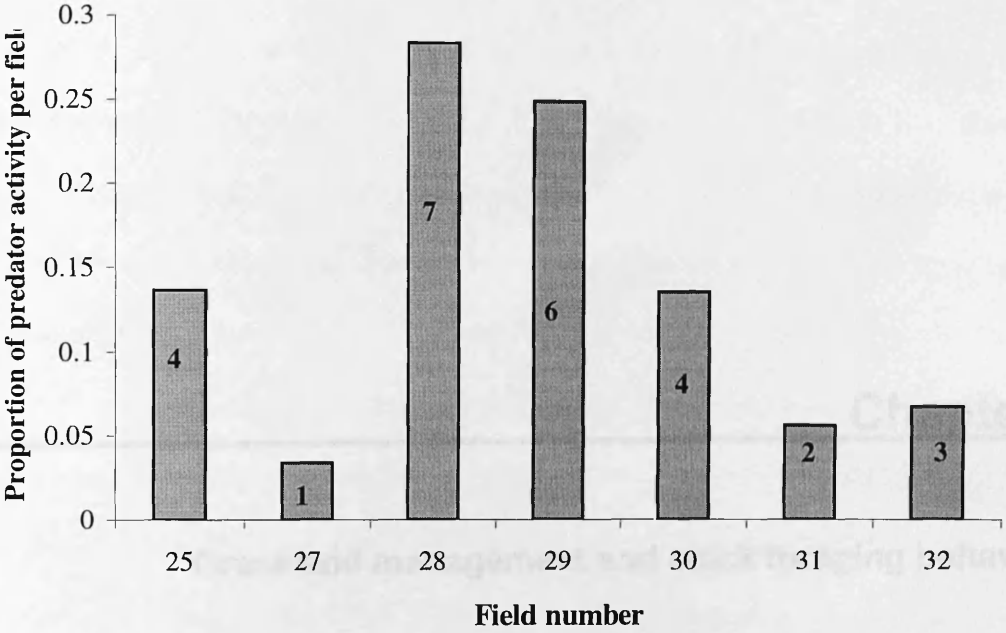


Figure 1 Ranking of fields in order of predator activity observed in fields over the study period.

Chapter 5

Grassland management and chick foraging behaviour

Abstract

While much is known of the impacts of agricultural change on nesting lapwings (Shrubb 1990, Baines 1990, Beintema & Müskens 1987) very little is known of how changes in grassland management may affect chick behaviour (Milsom et al 2002). Recent research has highlighted the importance of changes in habitat structure, brought about by changes in agricultural management practices, on the foraging success of farmland birds. Here, the effects of grassland management on chick foraging behaviour (habitat use and foraging success) are examined, with particular reference to food supply and habitat structure. Broods were found to significantly select areas of short sward for foraging, these areas included treatments that were fertilised late in the season and ditches. Areas with long sward (i.e. treatments fertilised early in the season and rigs) were actively avoided by foraging broods. No significant variation in preference for high or low water treatments was observed. Foraging success of chicks in varying sward heights was examined. It was found that foraging success and foraging rates in short sward were significantly greater than in long sward, explaining the difference in preference for treatments with short sward. Preference for short sward was also explained by variation in surface invertebrates. Early fertilising has a negative impact on the foraging behaviour of lapwing chicks by reducing food supply and detectability of food.

5.1 Introduction

Intensification of agricultural practices over the last 50 years has been blamed for the decline of many farmland bird species in Britain (Fuller *et al.* 1995, Chamberlain *et al.* 2000). Changes in habitat structure (O'Connor & Shrubb 1986, Fuller 1999, Vickery *et al.* 2001) and a reduction in summer invertebrate food availability (Benton *et al.* 2002, Potts 1986) and winter seed availability (Robinson & Sutherland 2002) have been suggested as three of the main causes of these declines. For example, changes in habitat structure such as the replacement of hay meadows with silage systems characterised by dense, fast growing swards which have reduced the availability of suitable nest sites for skylarks *Alauda arvensis* (Wilson *et al.* 1997). Reductions in invertebrate food supply through herbicide application to arable crops are thought to be responsible for reduced chick survival of the grey partridge *Perdix perdix* (Potts 1986). Factors affecting farmland birds associated with arable systems are now widely acknowledged and understood, however, the effect of lowland grassland improvement on farmland bird populations has received little attention (Vickery *et al.* 2001, Chamberlain & Fuller 2001). Vickery *et al.* (2001) highlighted many research gaps in understanding grassland management such as changes in food abundance and availability due to changes in sward structure through fertiliser input.

While grassland improvement has been blamed for the decline of lapwings breeding on lowland wet grassland (O'Brien and Smith 1992, Wilson *et al.* 2001), the mechanisms underlying the decline are still poorly understood. Grassland improvement is achieved through drainage, fertiliser application and reseeding, thus changes in habitat structure and food availability are factors most likely to affect breeding lapwings. Many previous studies investigating the effects of agricultural intensification on lapwing breeding success have addressed habitat selection of nesting adults (e.g. Redfern 1982, Galbraith 1988b, Baines

1990, Berg 1993) and factors affecting hatching success (Beintema & Müskens 1987, Shrubb 1990, Liker & Székley 1997). However, little is known about the impacts of grassland improvement on lapwing chick food supply, habitat use and their foraging behaviour (Johansson & Blomqvist 1996, Milsom *et al.* 2002).

Food availability, predation risk, and morphological constraints are important factors influencing habitat selection in birds (Hilden 1965). Lapwings require different habitat types for nesting and chick rearing (Redfern 1982, Galbraith 1988b, Blomqvist & Johansson 1996). Shortly after hatching, adult lapwings move broods to chick-rearing areas where the precocial young feed themselves (Cramp & Simmons 1983). Chick-rearing areas tend to be associated with short vegetation and high soil moisture (e.g. Milsom *et al.* 2002, Berg 1992, Baines 1990, Jackson & Jackson 1980). It is thought that these areas normally provide more abundant and accessible food than the vicinity of nest sites (Redfern 1983, Galbraith 1988b, Berg 1992) as well as allowing easier detection of predators (Galbraith 1988b).

The importance of an abundant food source for lapwing chick development and survival is well documented (Galbraith 1988a, Beintema & Visser 1989). Therefore establishing what factors determine food availability and accessibility for chicks is important in managing habitats to benefit lapwings. Fertiliser application and drainage have been shown to affect invertebrate abundance (Ausden *et al.* 2001, Downie *et al.* 2000, Seipel 1990), however these treatments may also affect prey availability through vegetation cover (Olsson *et al.* 2001). The effect of vegetation structure on the foraging success of birds has received much attention recently and is thought to be as important in determining habitat use and foraging success as food abundance (Moorcroft *et al.* 2002, Whittingham & Markland 2002). While food supply may be plentiful, vegetation structure or soil moisture might influence delectability or accessibility of food items thereby influencing intake rates (Whittingham & Markland 2002).

Milsom *et al.* (2002) found that foraging rates of lapwing chicks varied with soil moisture, however foraging rates in relation to food availability and sward (which were the suggested mechanisms responsible for variation in foraging rates) were not investigated. Galbraith (1988b) suggested that vegetation height can constrain the ability of lapwing chicks to use habitats by reducing their foraging efficiency by restricting their mobility, however this hypothesis has never been tested.

In this chapter the effects of manipulating sward height and soil moisture will be investigated on the habitat use and foraging behaviour of lapwing chicks. The results will also be interpreted in relation to food availability in treatments (see chapter 3).

5.2 Methods

1.2.1 Chick habitat use

On hatching, broods stayed close to their nest site for the first 3-4 days. Brood size was recorded and chicks were ringed with BTO metal rings and colour rings with a unique combination to allow individual identification on re-location. Broods were monitored every 2-3 days. Number of chicks per brood, activity (foraging or being brooded) and location within fields were recorded. Only broods with 3 or more observation days between age 3 days (age when usually moved by adults) and fledging were included in the analysis (Johansson & Blomqvist 1996). This resulted in data from field 27 being dropped from the analysis.

The majority of broods (90%) remained in their natal fields until fledging or failure. Preference for treatments was therefore analysed on 2 spatial scales, both over the whole study site ('potential range') and within fields ('actual range') (Grant *et al.* 1992, Milsom *et al.* 2002). The former assumes chicks are free to move in any direction after hatching, whereas the latter is more appropriate if brood movements are constrained within fields. Over the 'potential range' mean preference indices were derived for each treatment combination.

Preference for treatments by 50 broods within fields was investigated. Field 32 was dropped from water treatment analysis as just one water treatment was applied in that field (Chapter 2).

Habitat preference indices were calculated for each brood using the following equation (Manly 1974):

$P_i = \log(U_i + 1) / A_i$

Where P_i = preference index for area i, U_i = proportion of usage of area i and A_i = available area.

P_i values greater than 0.3 indicate selectivity while values below 0.3 indicate avoidance (Manly 1974).

5.2.2 Chick foraging rates

Lapwing chicks were observed foraging at Gruinart Flats between the 4th and 16th May 2002. Foraging rates in the form of 'peck rates' and 'successful peck rates' were collected. Pecks were defined as attempts to catch food whether successful or not. Successful pecks were defined as observed food intake. One chick per brood was followed for periods up to two hours. Within that time period chicks alternated between foraging bouts and being brooded by adult birds. Foraging bouts were timed and overall numbers of pecks and successful pecks in that time were recorded. After foraging bouts, 10 sward height and 10 soil moisture measurements were collected at random from where chicks were observed feeding. Chick foraging rates (overall and successful) were then calculated and analysed in relation to mean sward height, soil moisture and location within field (rig/ditch).

5.2.3 Data analysis

Variation in treatment preference by broods was determined using generalised linear models (GLMs) in S-plus. GLMs allow the analysis of non-gaussian error distributions through the use of linearising link functions (McCullagh & Nelder 1983). The effects of treatment on foraging rates were investigated using generalised linear mixed models (GLMMs) performed in Genstat 5 (Genstat 5 committee, 1993). This technique allows repeated measures on chicks from the same brood by fitting brood identity as a random effect. Minimal models are arrived at by stepwise deletion (McCullagh & Nelder 1983). Model residuals are checked for normality. Predicted fits were used to display results controlling for other terms remaining in the model.

5.3 Results

5.3.1 Chick habitat use

Over the study period (2000 & 2001) habitat use by 50 broods was monitored. The majority of broods remained in their natal fields until fledging or until broods had failed. Initially habitat preference indices were calculated for each treatment combination 'potential range' (Appendix 1, Table 1). Overall, HIGH water treatments appeared to score higher preference indices than LOW water treatments independent of fertiliser treatment, however this did not appear to be significant (Figure 1). Preference for LATE fertilised treatments was significantly greater than MID and EARLY treatments (Table 1, Figure 1). Significant variation between years also occurred in treatments 2, 3 and 5. Overall, lapwing broods actively selected treatments with short sward and high soil moisture and actively avoided treatments with long sward (see Chapter 3, Figures 5 & 6 for contrast and sward height between treatment types). Significant variation between years also occurred in treatments 2, 3 and 5. To control for the tendency of broods to remain in their natal field and use only the treatments available therein, treatment preference within fields ('actual range') was also assessed.

Table 1 Generalised linear model of preference indices

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	299	363.06	
Year	1	2.53	0.111
Treatment	5	35.63	<0.001
Year x Treatment	5	11.46	0.042

The response variable is habitat selectivity index (P_i). P_i has a binomial distribution. A logistic GLM was used to analyse the variation of P_i between treatments within years. Treatment = HIGH water, EARLY fertiliser; HIGH water, MID fertiliser; HIGH water, LATE fertiliser; LOW water, EARLY fertiliser; LOW water, MID fertiliser; LOW water, LATE fertiliser.

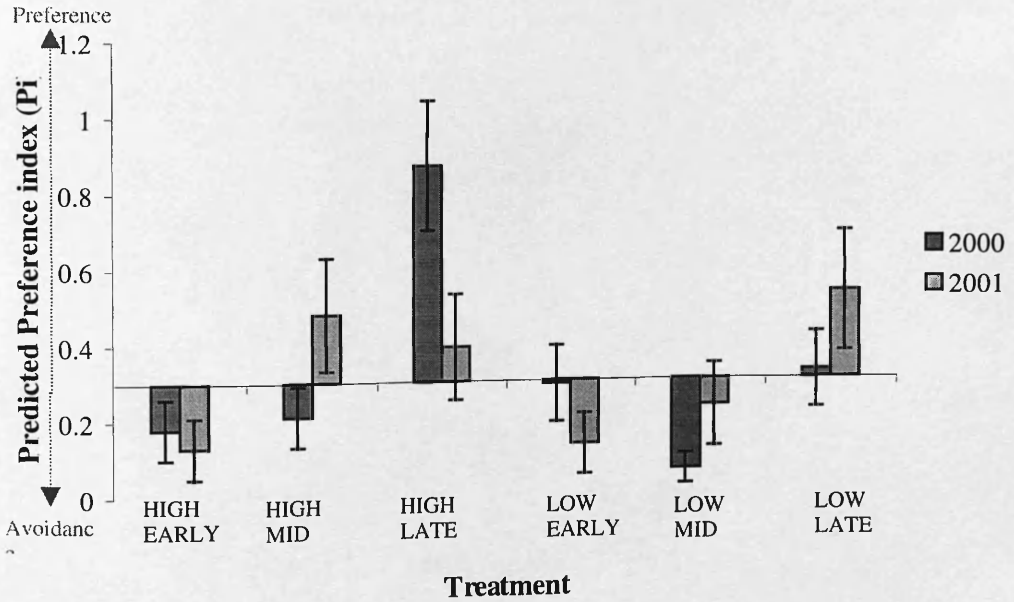


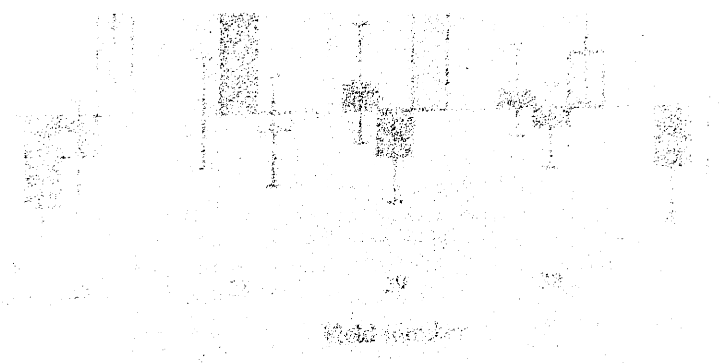
Figure 1 Preference indices of lapwing broods for treatment combinations in all fields 'potential range'.

The predicted values and standard errors shown control for terms remaining in the model (Table 1).

Not all treatment combinations were available in individual fields therefore analysis of water and fertiliser treatment preferences were analysed independently of each other within fields. Due to the small numbers of broods per field, broods from both years were grouped for the analysis.

Fertiliser treatments

When habitat use for fertiliser treatments within fields was considered it was found that LATE fertilised treatments scored significantly higher preference indices than MID and EARLY (Table 2, Figure 2) EARLY treatments were actively avoided in proportion to their availability in 2 fields out of 5, and MID treatments in field 29 and LATE treatments in field 28 were avoided out of all treatments available. Avoidance of late treatments in field 28 might be explained by 80% of those treatments having LOW water level status because LOW LATE treatments are not as attractive to lapwing chicks as HIGH LATE (Figure 1).



Habitat preference indices of lapwing broods for [illegible]

Table 2 Generalised linear model of preference indices.

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	149	199.52	
Fertiliser	2	9.7	0.002
Field	4	5.62	0.280
Fertiliser x Field	8	11.8	0.023

The response variable is habitat selectivity index (P_i). P_i has a binomial distribution. A logistic GLM was used to analyse the variation of P_i between treatments within years.

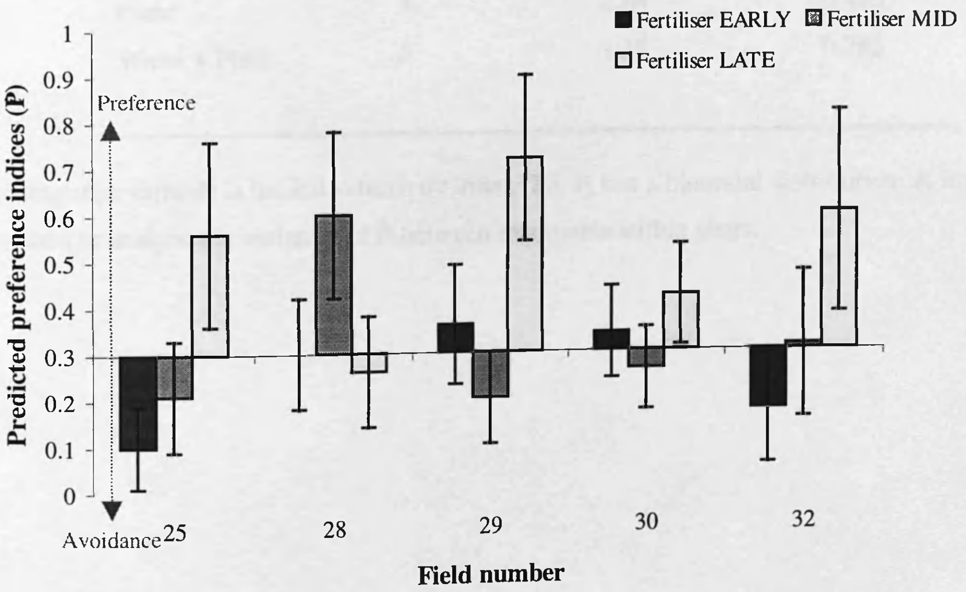


Figure 2 **Habitat preference indices of lapwing broods for FERTILISER treatments within 'actual range'.**

The predicted values and standard errors shown control for terms remaining in the model (Table 2).

Water treatments

Selection for water treatments within fields was also derived (Appendix 1, Table 3). Analysis showed HIGH treatments were avoided in field 25), however this was not significant (Table 3, Figure 3). In remaining fields no difference in preference for one water treatment over the other was observed (Table 3, Figure 3). No significant preference for water treatment was therefore observed in the 'actual range' or 'potential range'.

Table 3 Generalised linear model of preference indices.

Minimal Model

Term	d.f.	Deviance	*P*-value
NULL	107	90.60	
Terms dropped			
Water	1	0.302	0.582
Field	3	2.84	0.410
Water x Field	3	1.15	0.762

The response variable is habitat selectivity index (P_i). P_i has a binomial distribution. A logistic GLM was used to analyse the variation of P_i between treatments within years.

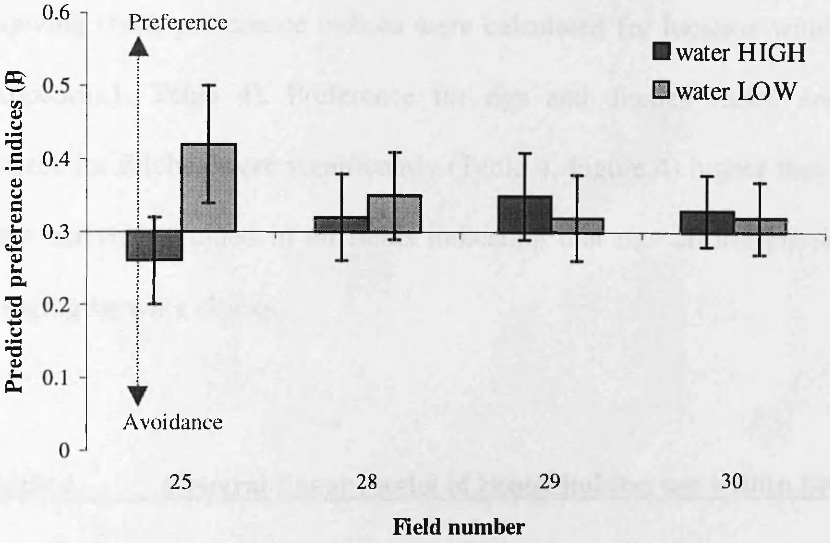


Figure 3 **Habitat preference indices of lapwing broods for WATER treatments within 'actual range'.**

The predicted values and standard errors shown control for terms remaining in the model (Table 3).

Lapwing chick preference indices were calculated for location within treatment (rig/ditch) (Appendix1, Table 4). Preference for rigs and ditches varied considerably. Preference indices for ditches were significantly (Table 4, Figure 4) higher than rigs in all fields. Rigs were actively avoided in all fields indicating that rigs do not provide suitable habitat for foraging lapwing chicks.

Table 4 General linear model of brood habitat use within fields.

Minimal Model

Term	d.f.	Deviance	*P*-value
NULL	98	80.68	
Location	1	77.84	0.001
Field	4	9.56	0.048
Terms dropped			
Field x Location	4	6.05	0.195

The response variable is habitat selectivity index (P_i). P_i has a binomial distribution. A logistic GLM was used to analyse the variation of P_i between treatments within years.

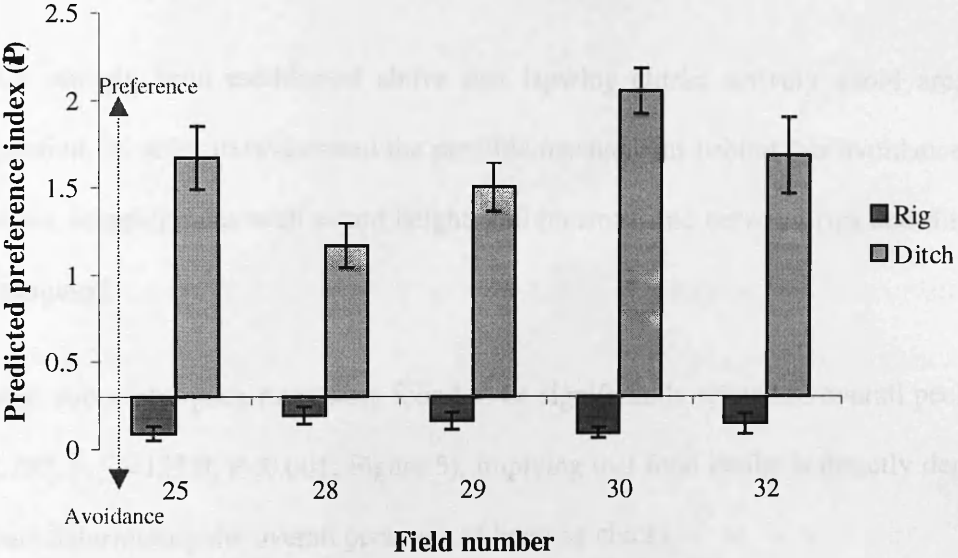


Figure 4 **Treatment preference indices of lapwing broods within fields.**

The predicted values and standard errors shown control for terms remaining in the model (Table 3).

5.3.2 Chick foraging rates

It has already been established above that lapwing chicks actively avoid areas of long vegetation. In order to understand the possible mechanisms behind this avoidance, variation in chick foraging rates with sward height, soil moisture and between rigs and ditches, were investigated.

Firstly, successful peck rates were found to be significantly related to overall peck rates ($R^2 = 0.797$, $F_{1,35}=137.9$, $P<0.001$; Figure 5), implying that food intake is directly dependent on factors determining the overall peck rate of lapwing chicks.

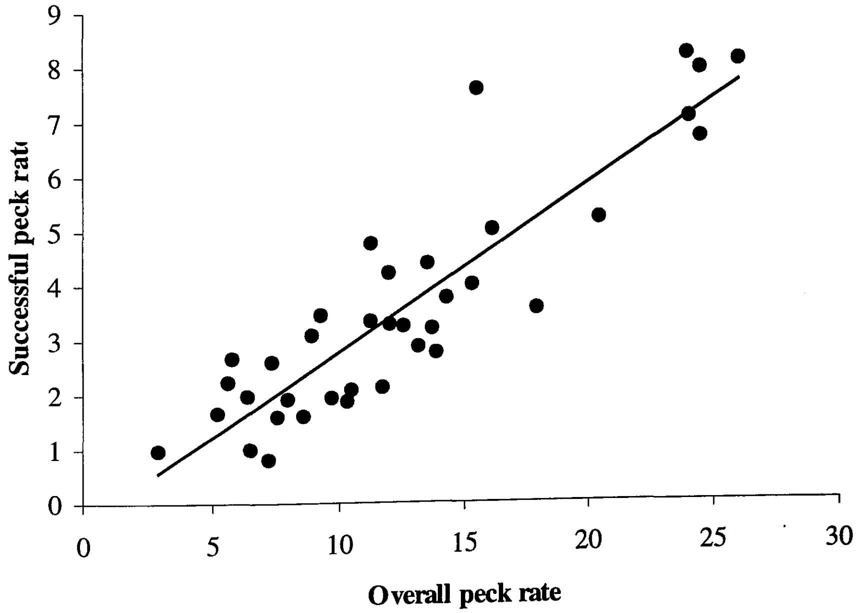


Figure 5 **Relationship between overall peck rate and successful peck rate.**

As 'overall' and 'successful' peck were significantly related (Figure 5) the effects of sward height and soil moisture were only investigated on overall peck rates.

The rate at which chicks fed and the number of prey caught per minute varied significantly with sward height and location within field (Table 8). Foraging rates were significantly reduced as sward height increased (Figure 6). Lapwing chicks have relatively short legs and are not well adapted to long vegetation (Galbraith 1988c). It is probable therefore that food intake is compromised by restricted mobility.

Foraging rates were considerably greater on ditches than on rigs (Figures 7). Surface invertebrate abundance is also significantly greater on ditches than rigs (Chapter 3). Therefore variation in foraging rates between rigs and ditches is likely to be a direct consequence of increased food availability and accessibility. As water levels in ditches retreat over the season, areas of bare soil become available providing unrestricted access to an abundant food supply.

Soil moisture was not found to be a predictor of foraging rates (Table 8) as assumed in other studies (Milsom *et al.* 2002, Baines 1990).

Table 8 Generalised linear mixed model of foraging rates (overall).

Minimal Model

Term	d.f.	Wald statistic (χ^2)	*P*-value
Sward height	1	20.38	<0.001
Rig/Ditch	1	14.58	0.002
Terms dropped			
Soil moisture	1	0.04	0.835

The response variable is number of pecks min. Number of pecks is Poisson distributed. A generalised linear mixed model (GLMM) was used to analyse the effects of sward height, soil moisture and location (rig/ditch) on foraging rates.

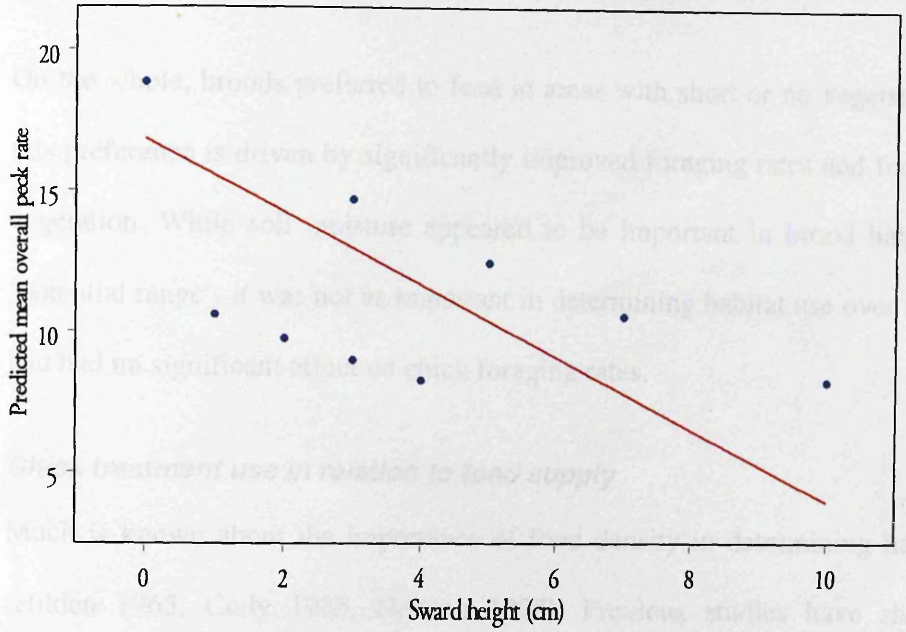


Figure 6 **Variation in overall peck rate with sward height (cm).**

The predicted values shown controls for terms remaining in the model (Table 8).

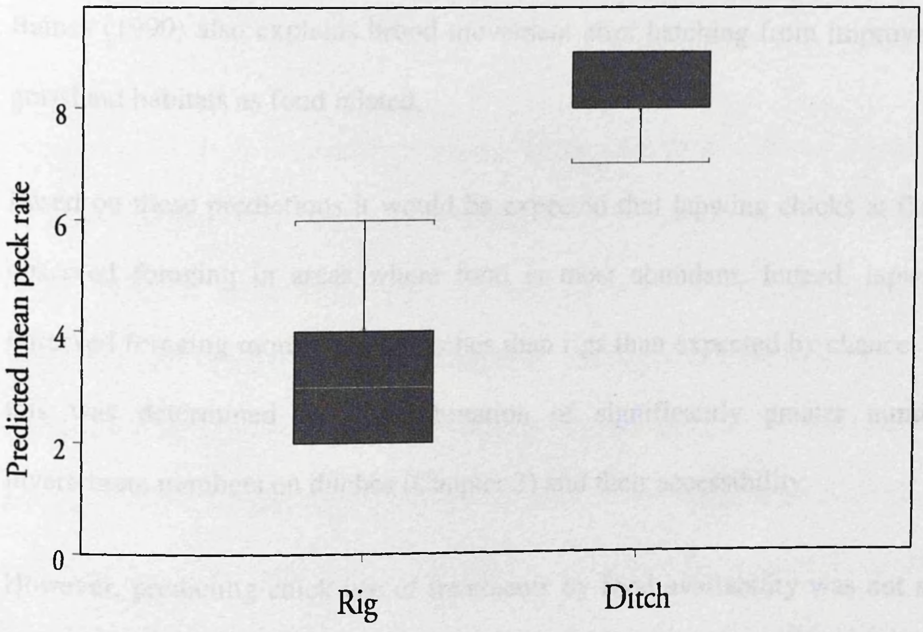


Figure 7 **Variation in overall peck rate between rigs (1) and ditches (2).**

The predicted values shown controls for terms remaining in the model (Table 8).

5.4 Discussion

On the whole, broods preferred to feed in areas with short or no vegetation. It appears that this preference is driven by significantly improved foraging rates and food intake in shorter vegetation. While soil moisture appeared to be important in brood habitat use over their 'potential range', it was not as important in determining habitat use over their 'actual range' and had no significant effect on chick foraging rates.

Chick treatment use in relation to food supply

Much is known about the importance of food density in determining habitat use by birds (Hilden 1965, Cody 1985, Newton 1998). Previous studies have shown how habitat selection by lapwing broods is largely determined by food supply. For example Galbraith (1988b) and Johansson & Blomqvist (1996) explained that brood movement from natal arable fields was driven by a more abundant food supply on adjacent grassland fields. Baines (1990) also explains brood movement after hatching from improved to unimproved grassland habitats as food related.

Based on these predictions it would be expected that lapwing chicks at Gruinart should be observed foraging in areas where food is most abundant. Indeed, lapwing chicks were observed foraging more often in ditches than rigs than expected by chance, and it likely that this was determined by a combination of significantly greater numbers of surface invertebrate numbers on ditches (Chapter 3) and their accessibility.

However, predicting chick use of treatments by food availability was not so clear, as food abundance did not always reflect where chicks were observed. Food abundance between treatments varied considerably (see Figure 10, Chapter 3). In particular higher numbers of surface invertebrates (important in chick diet) were sometimes observed on treatments with long sward.

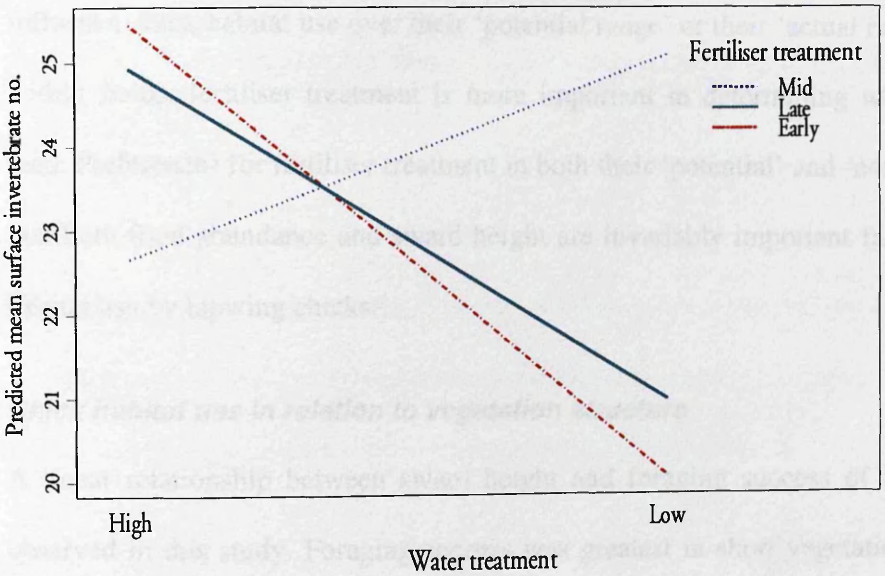


Figure 10 **(taken from chapter 3) Variation in surface invertebrate number with water and fertiliser treatment.**

Differences in food availability between water treatments differed significantly depending on sward height. This trend was reflected in chick use of treatments over their 'potential range'. In LOW water treatments chick preference for fertiliser treatments closely reflected surface invertebrate responses to fertiliser treatment, where LOW EARLY treatments were avoided and marginal preference for LOW LATE treatments was observed. When water was HIGH, however, chicks were observed on MID fertilised treatments more than expected and observed less than expected on EARLY treatments in relation to surface invertebrate abundance. Treatment preference in relation to earthworm biomass was similar. Earthworm biomass was greatest when water was LOW and fertiliser was applied EARLY, treatments that were actively avoided by lapwing chicks. When water was HIGH, earthworms were most abundant in LATE fertilised treatments, treatments that were most preferred by chicks.

Chick preference for fertiliser treatment in their 'actual range' closely reflected the trend observed on their 'potential range' where short grass was selected over long. Selection for water treatments on the other hand differed between ranges. Water level did not appear to influence chick habitat use over their 'potential range' or their 'actual range' suggesting that within fields, fertiliser treatment is more important in determining where lapwing chicks feed. Preferences for fertiliser treatment in both their 'potential' and 'actual' ranges suggests that both food abundance and sward height are invariably important factors in determining habitat use by lapwing chicks.

Chick habitat use in relation to vegetation structure

A linear relationship between sward height and foraging success of lapwing chicks was observed in this study. Foraging success was greatest in short vegetation than long, which explains preference for treatments with short sward over long. Recent studies on the foraging success of passerines propose that depressed prey detectability in tall vegetation contributes to low food intake rates (Whittingham & Markland 2002). However it is more likely that a combination of restricted mobility (Galbraith 1988a) and reduced visibility in tall vegetation are responsible for poor foraging efficiency in lapwing chicks.

Milsom *et al.* (2002) suggested that soil wetness is important in creating habitat for foraging lapwing broods, however no variation in lapwing chick foraging success was observed with soil moisture in this study. Milsom *et al.* (2002) considered that soil wetness might reduce vegetation cover thus improving detectability of prey items but this was not proven. In this study soil moisture on rigs did not affect sward height on rigs (chapter 3) and therefore was not a predictor of variation in foraging success or water treatment preference within fields.

Foraging success on ditches was much greater than rigs, highlighting their importance as foraging habitats for lapwing chicks. As the season progressed water levels in ditches dropped, creating conditions of moist soil with little or no vegetation. Chick mobility in ditches is therefore easier allowing greater detectability of abundant surface invertebrates. These factors can explain the considerable variation in preference indices between rigs and ditches.

To conclude, areas of short (LATE fertilised treatments) or no vegetation (ditches) are preferred foraging habitats for lapwing chicks on two counts. Firstly they provide an abundant surface food supply and secondly they allow chicks to move without restriction to catch their prey and increase prey detectability.

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APPENDIX 1

Table 1 Habitat selectivity indices of lapwing broods for all treatments 'potential range'.

Year	Treatment			Available area (ha^{-1})	Proportion of available area (A_i)	Mean proportion of brood encounters in treatments ± s.e. (U_i)	Mean Preference index per treatment ± s.e. (P_i)
		WATER	**FERTILISER**				
	1.	HIGH	EARLY	6.96	0.111	0.060 ± 0.210	0.17±0.59
	2.	HIGH	MID	8.67	0.138	0.080 ± 0.180	0.20±0.45
2000	**3.**	HIGH	LATE	9.35	0.149	0.410 ± 0.420	0.86±0.89
(n=30)	**4.**	LOW	EARLY	10.7	0.170	0.155 ± 0.330	0.28±0.60
	5.	LOW	MID	10.1	0.161	0.260 ± 0.106	0.06±0.23
	6.	LOW	LATE	16.8	0.268	0.266 ± 0.383	0.32±0.44
	1.	HIGH	EARLY	6.96	0.111	0.043 ± 0.168	0.12 ± 0.49
	2.	HIGH	MID	8.67	0.138	0.185 ± 0.234	0.47 ± 0.59
2001	**3.**	HIGH	LATE	9.35	0.149	0.173 ± 0.295	0.39 ± 0.63
(n=20)	**4.**	LOW	EARLY	10.7	0.170	0.064 ± 0.193	0.12 ± 0.36
	5.	LOW	MID	10.1	0.161	0.100 ± 0.183	0.22 ± 0.40
	6.	LOW	LATE	16.8	0.268	0.431 ± 0.368	0.52 ± 0.43

Table 2 Habitat selectivity indices of lapwing broods for FERTILISER treatments.

Field number (number of broods)	**Fertiliser treatment**	**Available area (ha-1)**	**Proportion of available area (Ai)**	**Proportion of brood observations (Ui)**	**Preference index (Pi)**
25 (9)	Early	1.5	0.22	0.44 ± 0.8	0.09
	Mid	2.7	0.41	4.1 ± 5.1	0.37
	Late	2.4	0.36	5.3 ± 4.6	0.52
28 (12)	Early	1.56	0.10	0.09 ± 0.25	0.39
	Mid	3.12	0.20	0.34 ± 0.26	0.65
	Late	10.92	0.70	0.55 ± 0.29	0.28
29 (13)	Early	2.56	0.33	0.34 ± 0.39	0.39
	Mid	3.84	0.50	0.30 ± 0.35	0.23
	Late	1.28	0.16	0.35 ± 0.39	0.82
30 (17)	Early	3.42	0.39	0.33 ± 0.37	0.32
	Mid	1.96	0.22	0.23 ± 0.27	0.41
	Late	3.43	0.28	0.43 ± 0.39	0.56
32 (5)	Early	5.64	0.42	0.26 ± 0.42	0.24
	Mid	3.76	0.28	0.23 ± 0.37	0.32
	Late	3.76	0.28	0.50 ± 0.47	0.64

Table 3 Habitat selectivity indices of lapwing broods for WATER treatments.

Field	Water treatment	Available area (ha-1)	Proportion of available area (Ai)	Proportion of brood observations (Ui)	Preference index (Pi)
25	High	4.01	0.60	0.42 ± 0.39	0.26
	Low	2.61	0.40	0.57 ± 0.39	0.49
28	High	7.8	0.50	0.48 ± 0.32	0.35
	Low	7.8	0.50	0.51 ± 0.32	0.36
29	High	5.12	0.57	0.60 ± 0.28	0.36
	Low	3.84	0.42	0.40 ± 0.29	0.35
30	High	5.14	0.50	0.51 ± 0.37	0.36
	Low	5.09	0.50	0.48 ± 0.37	0.34

Table 4 Habitat selectivity indices of lapwing broods within fields.

Field	Location within field	Available area (ha-1)	Proportion of available area (Ai)	Proportion of brood observations (Ui)	Preference index (Pi)
25	Rig	5.62	0.84	0.24 ± 0.18	0.11
	Ditch	1	0.15	0.76 ± 0.19	0.64
28	Rig	13.2	0.84	0.43 ± 0.23	0.19
	Ditch	2.4	0.15	0.57 ± 0.24	1.30
29	Rig	7.84	0.87	0.41 ± 0.26	0.17
	Ditch	1.12	0.13	0.59 ± 0.26	1.55
31	Rig	9.05	0.88	0.22 ± 0.29	0.10
	Ditch	1.18	0.12	0.80 ± 0.29	2.12
32	Rig	11.48	0.87	0.34 ± 0.22	0.15
	Ditch	1.68	0.13	0.67 ± 0.20	1.72

Chapter 6

Grassland management, life history and lapwing breeding success.

Abstract

The importance of egg size and chick body condition in determining chick survival in avian species is well documented. Previous studies have established the importance of several life history traits and development factors in lapwing chick survival. Other studies have demonstrated how variation in food supply between habitat types can influence chick survival. In this chapter, the effects of two commonly used grassland management practices, fertilising and drainage, on lapwing life history (egg size, clutch size and survival) and development (chick body condition), with particular reference to the to the importance of food supply are examined using a farm-scale factorial experiment. The experiment took the form of a 2 x 3 factorial design with 2 water (high, low) and 3 fertiliser treatments (application early, mid and late season) generating 6 treatment combinations. No significant variation in clutch size or egg size in relation to treatment was observed. No effect of egg size on chick body condition was observed but both water and fertiliser treatments significantly affected chick body condition. These trends were explained by variation in surface invertebrate number between treatments. No effect of body condition on survival of broods to day 5 was observed, however water and fertiliser treatment significantly predicted chick survival thereafter. Both body condition and water and fertiliser treatment affected chick survival from day 5 to day 10. This chapter demonstrates how changes in grassland management practices can affect body condition in lapwing chicks through changes in food supply, thereby affecting their survival.

6.1 Introduction

Recent changes in agricultural practices have been blamed for declines in farmland bird populations in Britain (Fuller *et al.* 1995, Chamberlain *et al* 2000). It has been suggested that a reduction in both invertebrate and plant food availability has had a major effect on breeding success of many species (Benton *et al.* 2002, Robinson & Sutherland 2002). For example, reductions in invertebrate food supply through herbicide application to arable crops are thought to be responsible for reduced chick survival of the grey partridge *Perdix perdix* (Potts 1986). The mechanisms driving farmland bird declines are still poorly understood, in particular how changes in management practices may affect reproductive success indirectly through changes in food supply (Vickery *et al.* 2001, Chamberlain & Fuller 2001).

Intensification of grassland management has been suggested as one of the major factors contributing to the decline of breeding lapwings in Britain (O'Brien and Smith 1992, Wilson *et al.* 2001), however the mechanisms underlying the decline on grassland habitats has not been as well documented as arable habitats. Much is known about differences in invertebrate abundances and diversity between arable and grassland habitats and the resultant impact on the breeding success of farmland birds (Southwood & Cross 1969, Galbraith 1988b). On the other hand very little is known about the effects of grassland improvement on invertebrate abundance and availability and the potential effects on chick survival (Baines 1990, Vickery *et al.* 2001).

Life history traits of animals, such as adult size and fecundity rate, all show a wide variation which is determined by natural selection and reflects adaptation of that animal to its environment (Roff 2002). In birds, a wide range of life histories occur, from short lived, mostly small-bodied species to long-lived, mostly large-bodied species. Body size correlates with most avian life history traits such as longevity, age of first breeding, breeding cycle and fecundity (Newton 1998). It is widely accepted that food limitation can induce much of the variation in life history traits of birds within species by influencing clutch size, egg size, chick growth rates and ultimately fledging success (Lack 1947, Martin 1987, Martin 1995, Perrins 1995, Brinkhof & Cavé 1997, Bukaciński *et al.* 1998, Clifford and Anderson 2001). In lapwings previous studies have outlined the potential importance of food availability in determining chick survival (Galbraith 1988b, Baines 1990), while other studies have highlighted how life history traits (Blomqvist & Johansson 1995, Galbraith 1988b) determine breeding success and chick survival. However, the impact of food limitation through agricultural improvement on lapwing life history traits and the resultant implications for lapwing breeding success have never been investigated.

A wide range of clutch size variation exists among bird species. Much of this variation between species can be explained by life history i.e. clutch size will be limited to the number of eggs that can be incubated successfully or in altricial species how many young parents can provision (Lack 1947, Godfray *at al.* 1991). There is evidence to suggest that some of the variation in clutch size within species can be explained by other factors such as predation (Kuleza, 1990) and food supply prior to egg laying (Martin 1995, Clifford and Anderson (2001). Clutch size in lapwings, like all wader species, is a relatively invariable feature of reproduction and is truncated at the modal number of 4 eggs (Arnold 1999, Ward 2000). Despite this, differences in clutch size between habitat types have been observed in previous studies. Analysis of BTO nest-record cards from England and Wales (1962 - 1985) by Shrubb (1990) found significantly larger clutches in tillage than grassland. Differences were also observed within grassland habitats with smaller clutches being observed on improved grassland than unimproved grassland. Shrubb (1990) suggested that food availability was probably the cause of variation between grassland habitat types.

Wader chicks are precocial and as such their eggs are large and contain large yolk reserves (Carey *et al.* 1980). Indeed this egg size trait amongst precocial species may also contribute to clutch size limitation where there is a trade off between egg size and clutch size. Egg size is important in lapwings, as chicks that hatch from large eggs are heavier and larger at hatching, grow faster and survive better than those from small eggs (Galbraith 1988a, Blomqvist *et al.* 1997, Kirby & Tyler 1999). Magrath (1992) suggests the reason why egg size has a greater effect in precocial than altrical species is their dependence on nutrient reserves during the first few days after hatching while learning to feed. Indeed Galbraith (1988a) found that egg size enhanced chick survival to fledging through an effect in the first 10 days after hatching. In lapwings intrinsic factors such as female body mass, wing length and condition, are known to correlate with egg volume, as are extrinsic factors such as food availability prior to breeding (Galbraith 1988a, Blomqvist & Johansson 1995).

The role of condition in determining chick survival in lapwings and other wader species is well documented (Galbraith 1988 a & b, Beintema & Visser 1989, Johansson & Blomqvist 1997, Grant 1991, Pearce-Higgins & Yalden 2002). Previous studies have shown how body condition in lapwing chicks can be determined indirectly by food supply through maternal condition and egg size (Galbraith 1988a, Beintema 1994). Galbraith (1988c) suggests that condition in lapwing chicks can be influenced directly by habitat types through differences in food abundance between them, but this has not been investigated in detail.

In this chapter, experimental treatment effects will be examined at various stages of lapwing life history including clutch size, egg size, chick condition and finally survival. The results will be interpreted in relation to how variation in food supply between treatments (see Chapter 3) determines lapwing life history traits and how predator activity varies between fields thereby influencing lapwing breeding success.

6.2 Methods

6.2.1 Clutch size & egg volume

In 2001, clutch sizes from 39 nests selected at random throughout the season were recorded from each treatment type. The length and breadth of 133 eggs from these 39 nests were measured to the nearest 0.1mm using dial callipers. Egg volumes were calculated using the equation:

Egg volume (cm^3) = $0.425 * L * B^2$ (Galbraith 1988a)

Where, L= egg length and B= egg breadth.

6.2.2 Chick condition

Chick mass (gm) and bill length (mm) were measured using a 'Pesola' spring balance and dial callipers respectively from chicks of known age. As nests were monitored daily, hatching dates were recorded therefore allowing accurate determination of chick age. Condition indices for chicks of known age were derived from the relationship between standard mass (expected mass) and observed chick mass:

Condition index (CI) = observed mass (OW) / standard mass (EW) (Beintema 1994),

Standard masses were calculated from the relationship between mean chick mass and chick age (Appendix 1).

Mean chick condition indices were then calculated for each brood using standardised body masses. At Gruinart lapwing chicks remain close to the nest site for 3-4 days after hatching. Treatment effects in relation to where chicks hatched were investigated. Separate analyses were undertaken on broods aged between 3-4 days old and all broods.

6.2.3 Brood survival

After hatching chicks were ringed using BTO metal rings and colour rings to allow individual identification on re-location. Numbers of chicks per brood were monitored every 3 days for survival and their location noted to monitor movement within and between fields. Brood survival estimates were derived using the modified Kaplan Meier procedure described in Flint *et al.* (1995). This estimator controls for the assumption that individuals within broods have independent survival probabilities. Two brood survival estimates were calculated. Firstly, survival estimates for broods from **hatching to day 5** were derived, as natal treatment effects are more detectable at this stage before broods are moved to other potential feeding areas. Secondly, survival estimates for brood from **hatching to day 10** were derived. Numbers of chicks monitored after day 10 (due to either migration or mortality) were too few to detect treatment effects accurately.

Between-field variation encompasses a range of factors, the most important of which in this section is predation. Predator pressure was quantified from daily observations of predator activity within each field over the study period (see Chapter 4 methods & Appendix 1: Figure 1, Table 1).

6.2.4 Data analysis

Generalised linear models (GLMs) in S-plus were used to test the effects of treatment on clutch size, chick condition and brood survival. GLMs allow the analysis of non-gaussian error distributions through the use of linearising link functions (McCullagh & Nelder 1983). Minimal models were arrived at by stepwise deletion (McCullagh & Nelder 1983). Model residuals are checked for normality. Predicted fits were used to display results controlling for other terms remaining in the model. Rig and ditch were nested in field to control for repeated measures. The effects of treatment on egg volume were investigated using restricted maximum likelihood techniques (REML) performed in Genstat 5. This technique allows repeated measures on the same nest by fitting nest identity as a random effect.

6.3 Results

6.3.1 Clutch size & egg volume

In this section the hypothesis that water and fertiliser treatments predict clutch size and egg volume is tested.

Clutch size over the study period ranged from 3 to 4 eggs per clutch. Water and fertiliser treatments did not influence clutch size of lapwings (Table 1). There were no significant effects of field, location within field, field age or clutch type (first or replacement clutch) on clutch size.

Table 1 Generalised linear model of clutch size.

Minimal Model

Term	d.f.	Deviance	*P*-value
NULL	37	8.37	
Terms dropped			
Water	1	0.004	0.894
Fertiliser	2	0.17	0.696
Field age	1	0.29	0.280
Field	6	0.01	0.653
Field (Rig/Ditch)	7	0.99	0.791
Clutch type	1	0.50	0.162

The response variable was clutch size of lapwings. The response variable appeared to be poisson distributed. The effects of treatment and field age were analysed using a log-linear GLM. The dispersion parameter calculated was too large (<2), therefore a quasi-likelihood GLM was applied with the appropriate "log" link and "mu" variance functions for the Poisson family. Field (Rig/Ditch) was included to control for between and within field variation Clutch type distinguishes between first and replacement clutches. Model residuals appeared Normal.

Mean egg volume per clutch ranged from 20.28 cm^3 to 25.44 cm^3. Variation in egg volume in lapwings is likely to be influenced by intrinsic factors such as female condition and extrinsic factors such as food availability (Galbraith 1988a, Blomqvist & Johansson 1995). Invertebrate response to treatments (Chapter 3) did not occur until after the measured nests were initiated, therefore an egg volume response to treatment was not anticipated. As expected, water and fertiliser treatments did not significantly affect lapwing egg volumes (Table 4). No differences in egg volume were observed between fields and within fields. Egg volumes in first clutches did not differ significantly from replacement clutches.

Table 2 Linear mixed model of egg volume.

Minimal Model

Term	d.f.	Wald statistic (χ^2)	*P-value*
Terms dropped			
Water	1	0.05	0.822
Fertiliser	2	0.66	0.567
Field age	1	1.42	0.234
Clutch type	1	0.10	0.751

The response variable is egg volume cm^{-3}. Egg volume distribution tested normal. A linear mixed model, restricted maximum likelihood technique (REML) was used to analyse the effects of treatment, field age and clutch type (first or replacement) on egg volume. REML allows repeated measures of egg volume from the same nest, by fitting individual nest as a random effect. Field (Rig/Ditch) and nest age were added as random variables to control for between and within field variation and egg volume differences that might arise due to nest age. Random effects tested non-significant.

6.3.2 Chick condition

In this section the following hypotheses are tested, **1.** life history traits (egg volume) predict the body condition of broods aged 3-4 days and **2.** water and fertiliser treatments predict the body condition of broods aged 3-4 days.

The relationship between lapwing chick condition at hatching and subsequent survival is well documented (Galbraith 1988a, Beintema 1994). Chick condition can be determined both intrinsically through maternal size and extrinsically through factors such as food supply (Galbraith 1988a, Blomqvist & Johansson 1995). In this study the relationship between mean egg volume per clutch and mean chick condition per brood of 23 broods was not found to be significant ($R^2=0.049$, $F_{1,21}=0.964$, $P=0.337$; Figure 1). This result suggests that extrinsic factors such as food supply may be more influential in determining chick condition.

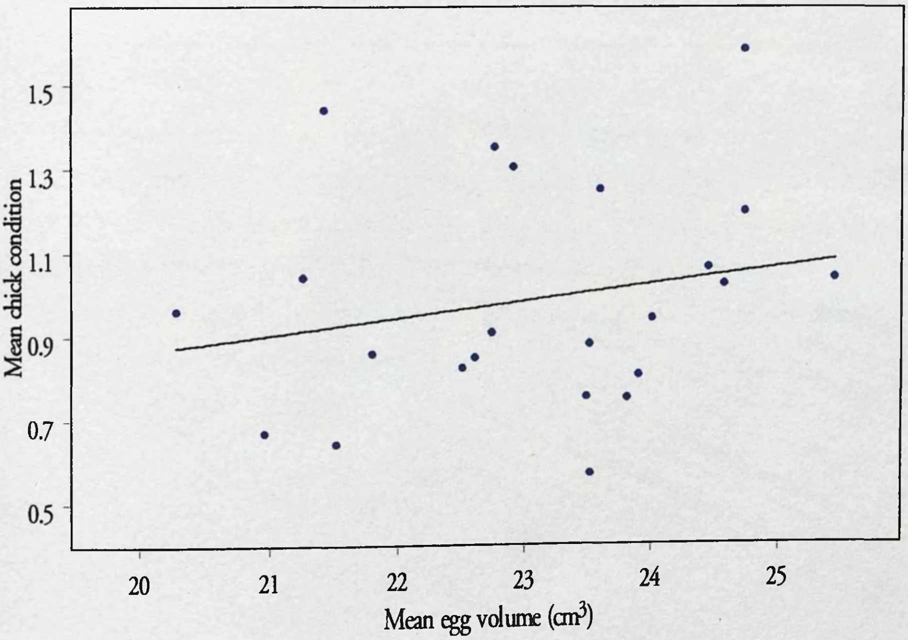

Figure 1 **Relationship between mean egg volume and mean condition of chicks ranging from 3-10 days.**

Body condition of young broods (3-4 days) were significantly affected by natal treatments as shown by the water x fertiliser interaction (Table 3, Figure 2). In HIGH water treatments, chicks that hatched on EARLY and LATE fertilised treatments were in significantly better condition than chicks that hatched on MID treatments. When water treatment was LOW, chicks that hatched on MID and LATE fertilised treatments were in better condition than those that hatched on EARLY treatments. These results may reflect the response of surface invertebrates to water and fertiliser treatments (Chapter 3: Table 6, Figure 11) as their responses to treatments were similar. This suggests that chick condition may be closely linked to food supply, in particular surface invertebrates.

Chick condition of young broods did not vary significantly with year, field age or between first and replacement clutches (Table 3). Condition of young broods hatched before fertiliser application did not vary significantly from those which hatched after fertiliser application.

Table 3 General linear model of mean chick condition (broods aged 3-4 days).

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	43	2.31	
Water	1	0.022	0.439
Fertiliser	2	0.059	0.449
Field	6	0.533	0.051
Field (Rig/Ditch)	6	0.370	0.158
Water x Fertiliser	2	0.37	0.014
Terms dropped			
Fertiliser presence	1	0.020	0.468
Clutch type	1	0.024	0.417
Field age	1	0.006	0.824
Year	1	0.001	0.656

The response variable was mean brood condition of lapwing broods. The response variable appeared to be normally distributed. The effects of treatment and field age were analysed using gaussian GLM. Field and Rig/Ditch were included to control for between and within field variation Clutch type was included to investigate for differences in chick condition between first and replacement clutches. Fertiliser presence (1/0) was included to investigatel for variation in condition of broods hatched before and after fertiliser application. Model residuals appeared Normal.

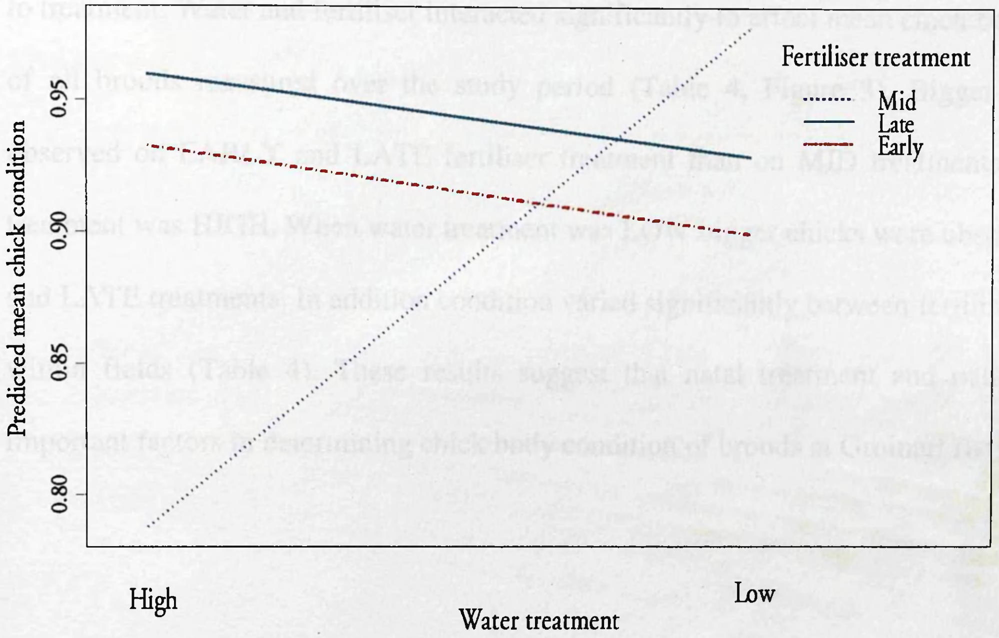

Figure 2 **Variation in mean chick condition (0-3days) per brood with water and fertiliser treatment**

The predicted values shown control for terms remaining in the model (Table 3).

Next, mean body condition in broods of all ages were analysed to investigate the response to treatment. Water and fertiliser interacted significantly to affect mean chick body condition of all broods measured over the study period (Table 4, Figure 3). Bigger chicks were observed on EARLY and LATE fertiliser treatment than on MID treatments when water treatment was HIGH. When water treatment was LOW bigger chicks were observed on MID and LATE treatments. In addition condition varied significantly between fertiliser treatments within fields (Table 4). These results suggest that natal treatment and natal field were important factors in determining chick body condition of broods at Gruinart flats.

Table 5 General linear model of mean chick condition (all broods).

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	93	4.9	
Water	1	0.002	0.815
Fertiliser	2	0.03	0.635
Field	6	0.43	0.11
Field (Rig/Ditch)	7	0.477	0.133
Water x Fertiliser	2	0.40	0.009
Field x Fertiliser	10	0.91	0.020
Terms dropped			
Fertiliser presence	1	0.005	0.701
Clutch type	1	0.02	0.430
Field Age	1	0.02	0.444
Year	1	0.01	0.509

The response variable was mean chick condition of lapwing broods. The response variable appeared to be normally distributed. The effects of treatment and field age were analysed using a gaussian GLM. Field (Rig/Ditch) was included to control for between and within field variation Clutch type was included to investigate for differences in chick condition between first and replacement clutches. Fertiliser presence (1/0) was included to investigate for variation in condition of broods hatched before and after fertiliser application. Model residuals appeared Normal.

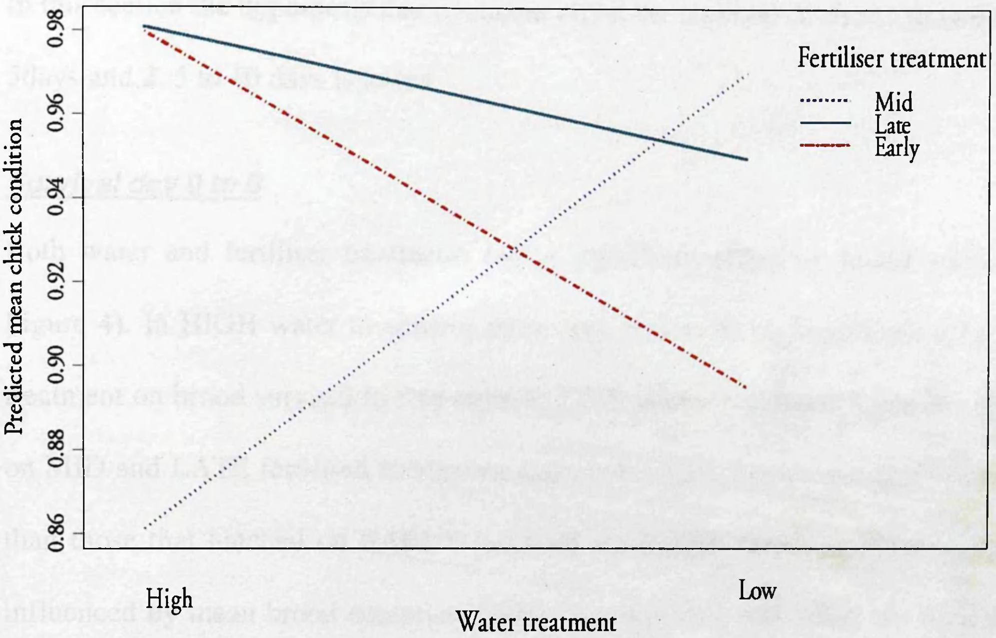

Figure 3 **Variation in mean chick condition (all broods) per brood with water and fertiliser treatment.**

The predicted values shown control for terms remaining in the model (Table 4).

6.3.3 Brood survival

In this section the hypothesis that treatment affect the survival of chicks to two stages **1.** 0 to 5days and **2.** 5 to 10 days is tested.

Survival day 0 to 5

Both water and fertiliser treatments had a significant effect on brood survival (Table 5, Figure 4). In HIGH water treatments there appeared to be no significant effect of fertiliser treatment on brood survival to five days. In LOW water treatments however, chicks hatched on MID and LATE fertilised treatments appeared to have higher survival estimates to day 5 than those that hatched on EARLY fertilised treatments. Chick survival to day 5 was not influenced by mean brood condition (Table 5) suggesting that either the food abundance or food availability responses to treatments might be important in determining chick survival.

Fertiliser treatment also interacted significantly with clutch type to affect brood survival to day 5 (Table 5, Figure 5). Survival of first clutches was greater than replacement clutches in all fertiliser treatments and appeared to be significantly greater in LATE fertilised treatments. Survival estimates of first clutches to day 5 responded negatively to fertiliser input. This may be attributable to variation in food abundance (see Chapter 3) or restricted foraging rates in taller sward (see Chapter 5).

Variation in brood survival was also dependent on the inferred level of predator activity within natal fields (Appendix 2, Figure 1). In fields 28 and 29, where predator activity is highest (Figure 6) brood survival to day 5 appears to be greater in EARLY and MID fertilised treatments than LATE fertilised treatments. In fields 32 and 31, where predator activity is lowest (Figure 6) broods hatched on LATE treatments appear to have a higher chance of survival to day 5 than those hatched on MID or LATE treatments. This result suggests that cover provided by EARLY fertilised treatments benefits chicks when predation pressure is high, and the absence of cover under LATE treatments results in higher mortality rates amongst broods.

Table 5 Generalised linear model of brood survival (0-5 days).

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	83	257.22	
Fertiliser treatment	2	1.29	0.752
Water treatment	1	0.54	0.626
Clutch type	1	14.45	0.014
Field	6	22.67	0.148
Field (Rig/Ditch)	6	8.32	0.721
Water x Fertiliser	2	20.43	0.015
Clutch type x Fertiliser	2	20.60	0.015
Field x Fertiliser	9	46.97	0.029
Terms dropped			
Fertiliser presence	1	2.30	0.305
Year	1	4.17	0.169
Field Age	1	5.04	0.141
Condition index	1	6.59	0.087

The response variable has a binomial distribution. The effects of treatment, field age and brood condition were analysed using a logistic regression GLM. Fields were ranked in order of their predator activity (Figure 7). Field (Rig/Ditch) was included to control for between and within field variation. The dispersion parameter calculated for the logistic regression model was too large (>2). A quasi-likelihood GLM was applied with the appropriate "logit" link and "mu (1-mu)" variance functions. Clutch type was included to investigate for differences in chick survival between first and replacement clutches. Fertiliser presence (1/0) was included to investigate for variation in survival of broods hatched before and after fertiliser application. Model residuals appeared Normal.

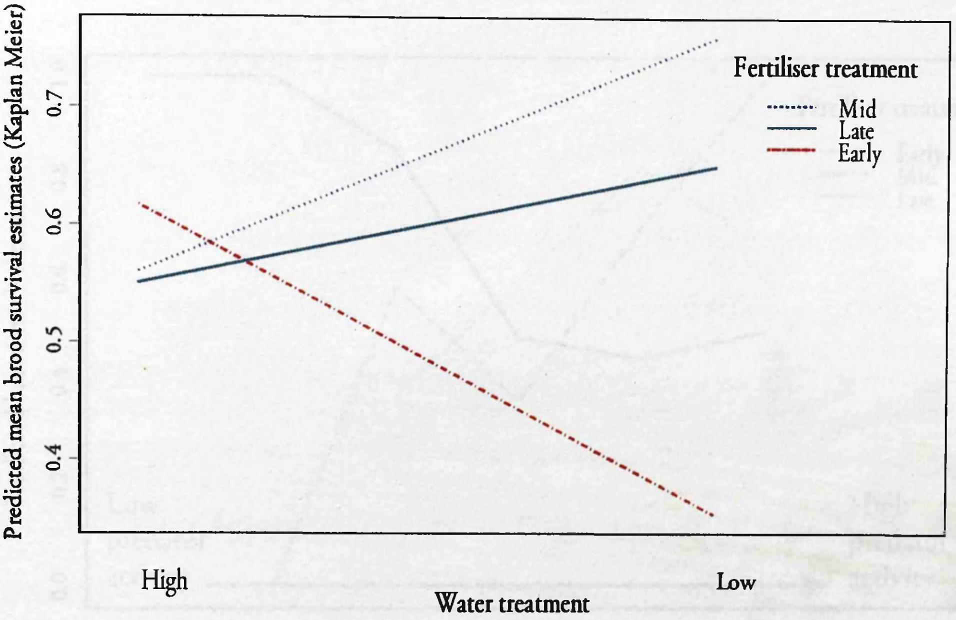

Figure 4 **Variation in brood survival estimates (0 – 5 days) with water and fertiliser treatment.**
The predicted values shown control for terms remaining in the minimal model. (Table 5).

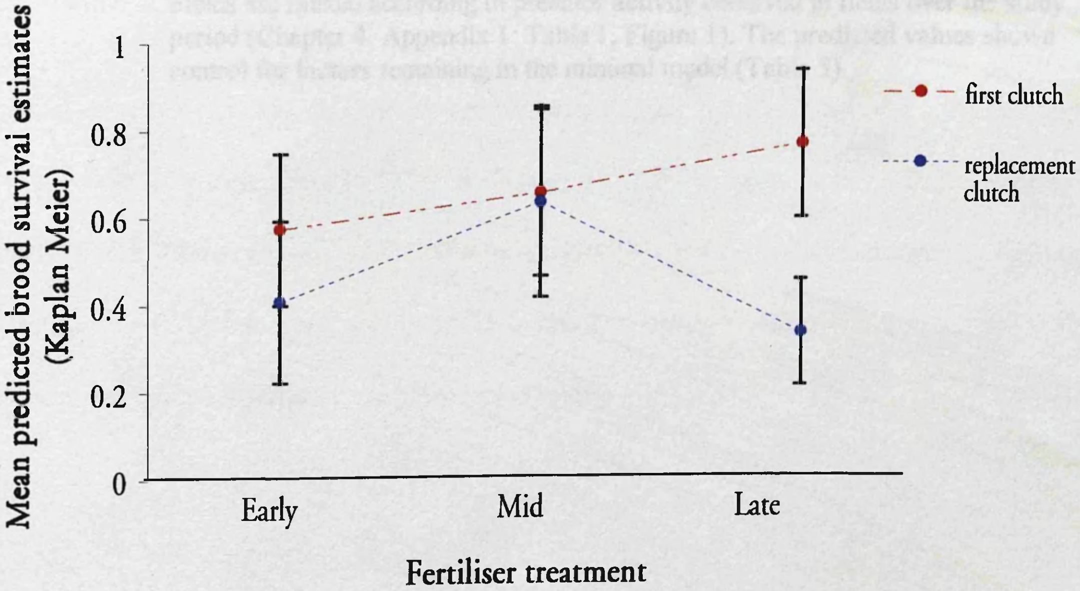

Figure 5 **Variation in brood survival estimates (0 – 5 days) between first and replacement clutches within fertiliser treatments.**
The predicted values shown control for terms remaining in the minimal model. (Table 5).

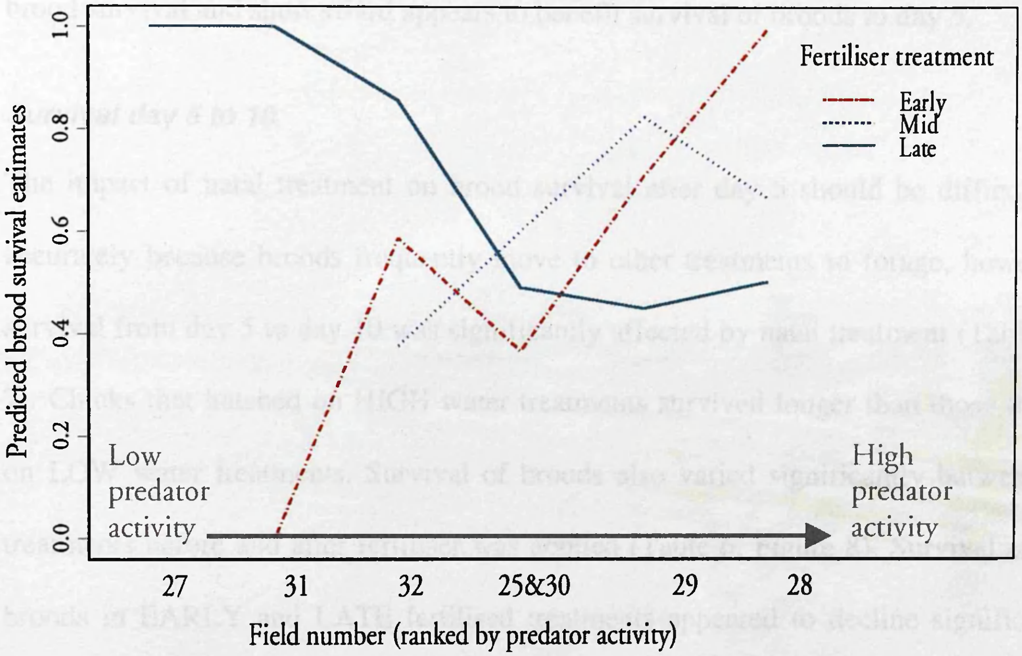

Figure 6 **Variation in brood survival (0 – 5 days) between fertiliser treatments within fields.**

Fields are ranked according to predator activity observed in fields over the study period (Chapter 4, Appendix 1: Table 1, Figure 1). The predicted values shown control for factors remaining in the minimal model (Table 5).

However when predation pressure is lower, tall sward appears to have an adverse effect on brood survival and short sward appears to benefit survival of broods to day 5.

Survival day 5 to 10

The impact of natal treatment on brood survival after day 5 should be difficult to assess accurately because broods frequently move to other treatments to forage, however, brood survival from day 5 to day 10 was significantly affected by natal treatment (Table 6, Figure 7). Chicks that hatched on HIGH water treatments survived longer than those that hatched on LOW water treatments. Survival of broods also varied significantly between fertiliser treatments before and after fertiliser was applied (Table 6, Figure 8). Survival estimates of broods in EARLY and LATE fertilised treatments appeared to decline significantly after fertiliser was applied while survival of broods hatched in MID fertilised treatments did not appear to change after fertiliser application. This indicates fertilising may have an adverse effect on brood survival from day 5 to 10 depending on timing of fertiliser.

Survival of replacement broods were significantly greater than first broods which contrasts with survival of young chicks (Table 6, Figure 9). Survival estimates varied significantly between fields (Table 6), however predator activity was not found to explain this variation. In contrast with survival of young chicks, chick condition interacted significantly with treatment to predict chick survival from day 5 to day 10 (Table 6).

Table 6 Generalised linear model of brood survival (5 - 10 days).

Minimal model

Term	d.f.	Deviance	*P*-value
NULL	57	124.98	
Fertiliser treatment	2	1.93	0.225
Water treatment	1	23.20	<0.001
Fertiliser presence	1	6.99	0.002
Condition Index	1	0.69	0.297
Field Age	1	3.57	0.022
Clutch Type	1	2.69	0.045
Field	6	20.98	<0.001
Field (Rig / Ditch)	6	13.27	0.008
Water x Fertiliser Treatment	2	4.89	0.029
Water x Fertiliser presence	1	9.21	<0.001
Water x Condition Index	1	9.11	<0.001
Fertiliser treatment x Condition Index	1	16.64	<0.001
Fertiliser treatment x fertiliser presence	1	13.69	<0.001
Terms dropped			
Year	1	1.017	0.743

The response variable has a binomial distribution. The effects of treatment, field age and mean brood condition were analysed using a logistic regression GLM. Field (Rig/Ditch) was included to control for between and within field variation. Clutch type was included to investigate for differences in chick survival between first and replacement clutches. Fertiliser presence (1/0) was included to investigate for variation in survival of broods hatched before and after fertiliser application. Model residuals appeared Normal.

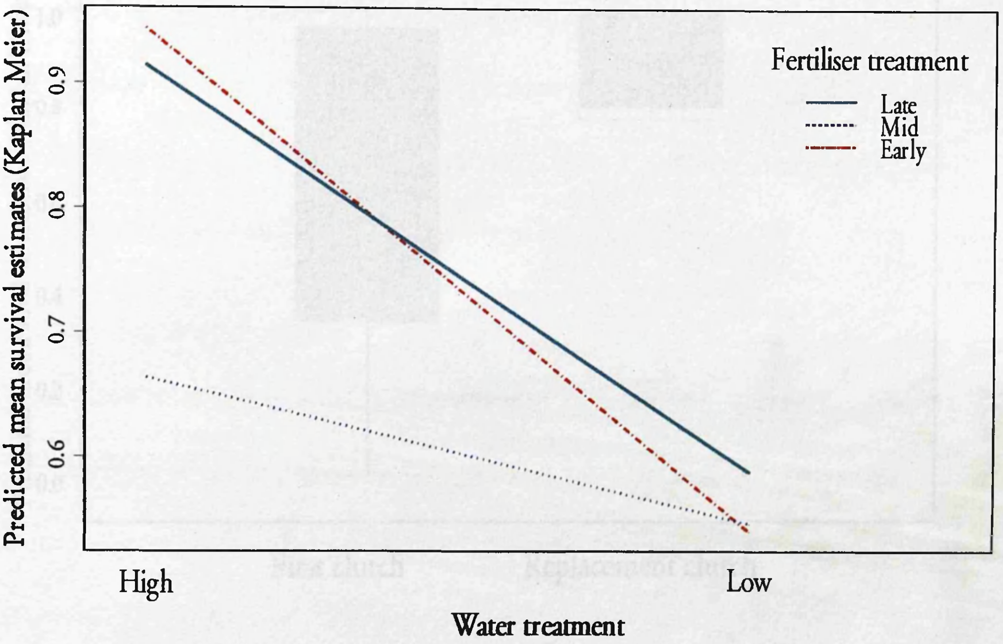

Figure 7 **Variation in brood survival estimates (5 – 10 days) between water and fertiliser treatments.**
The predicted values shown control for terms remaining in the minimal model. (Table 6).

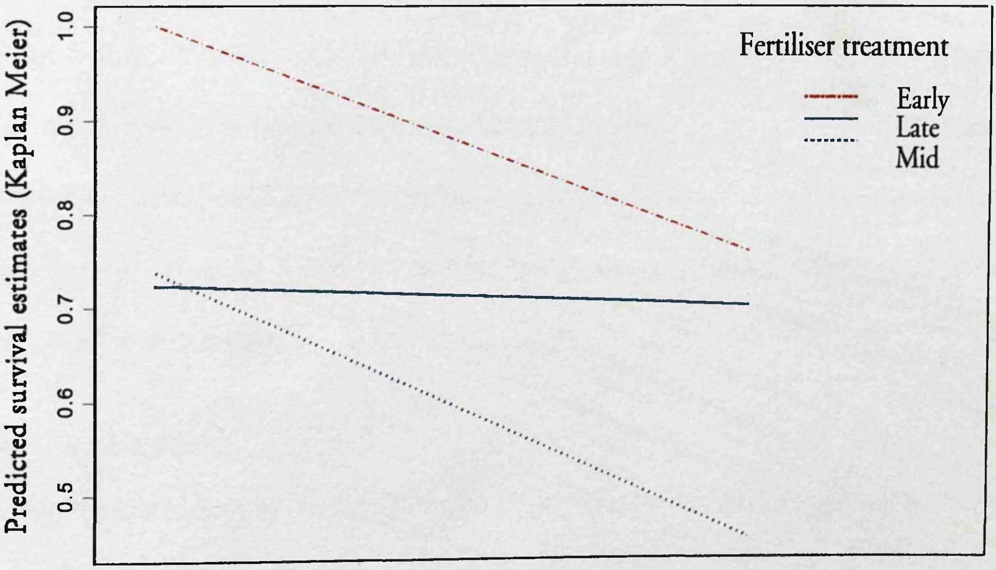

Figure 8 **Variation in brood survival estimates (5 – 10 days) between fertiliser treatments before and after fertiliser application.**
The predicted values shown control for terms remaining in the minimal model. (Table 6).

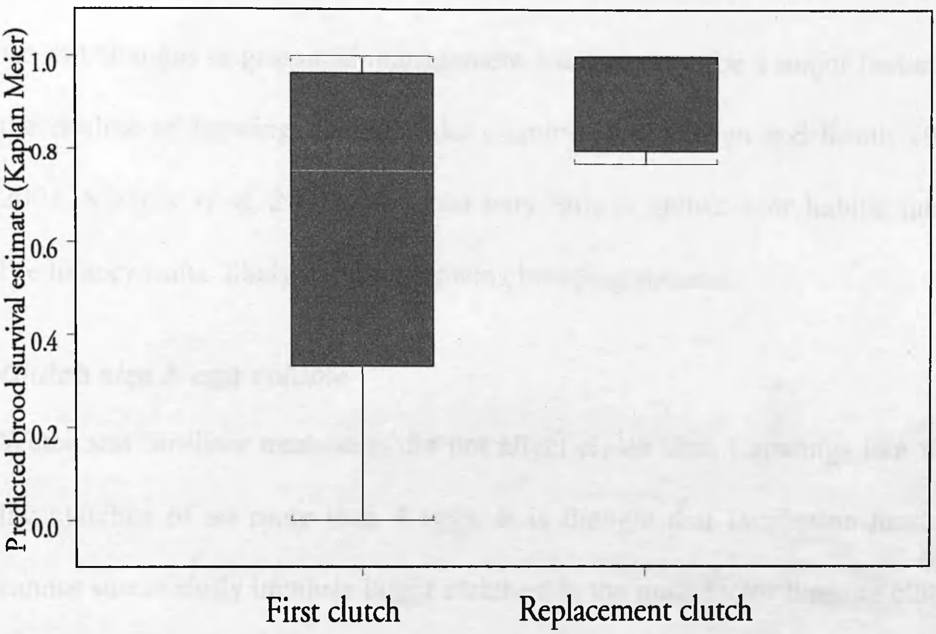

Figure 9 **Variation in brood survival estimates (5 – 10 days) between first and replacement clutches**
The predicted values shown control for terms remaining in the minimal model. (Table 6).

6.4 Discussion

Recent changes in grassland management are thought to be a major factor in contributing to the decline of lapwings in the wider countryside (O'Brien and Smith 1992, Wilson *et al.* 2001, Vickery *et al.* 2001). However very little is known how habitat quality affects those life history traits likely to affect lapwing breeding success.

Clutch size & egg volume

Water and fertiliser treatments did not affect clutch size. Lapwings like most other waders lay clutches of no more than 4 eggs. It is thought that incubation-limitation (i.e. waders cannot successfully incubate larger clutches) is the main factor limiting clutch size in waders (Arnold 1999, but see Wallander & Andersson 2002). Therefore, the effects of habitat quality or in this case the effects of treatment are more likely to be expressed in egg volume rather than clutch size (Galbraith 1988a), however this was not the case in this study. In addition, variation in egg size between females was not found to be significant. Treatment effects on food supply were not observed until all clutches measured were initiated (see Chapters 3 & 4); therefore differences in clutch size and egg volume due to treatment were not expected. Effects of treatment in clutches initiated later in the season when variations in food supply were detected were too few to analyse. Differences in egg volume between first and replacement clutches found in other studies (Galbraith 1988a, Parish *et al* 2001) were not observed in this study.

Chick body condition

Body condition of lapwing chicks and other wader species can be determined in two ways 1. by intrinsic factors such as maternal condition and egg size or 2. by extrinsic factors such as food supply and weather conditions (Galbraith 1988 a, b & c, Grant 1991 Bientema 1994, Blomqvist & Johansson 1995, Parish *et al.* 2001, Pearce-Higgins & Yalden 2002). Body condition in precocial chicks is important in determining survival, where survival rates of big chicks are greater than those of small chicks (Galbraith 1988b, Pearce-Higgins & Yalden 2002). Previous studies have found a relationship between egg volume and chick condition (Galbraith 1988a). In this study, however the relationship between mean egg volume per clutch and mean body condition of broods was not significant suggesting that extrinsic factors such as food supply might be more important in determining body condition of chicks. In addition treatment effects may have been detected with a larger sample size, adding more power to the analysis or by measuring chicks within a day after hatching. Both water and fertiliser treatments interacted significantly to affect body condition of chicks aged between 3 and 4 days and all broods. Chick condition responses to treatments were similar to surface invertebrate responses to water and fertiliser treatment (Figure 10 a & b), indicating that food availability at hatching is important in determining chick body condition. The effect of treatment on condition at hatching appears to have been sustained as body condition of all broods (both young and old combined) was also significantly affected by food supply at hatching.

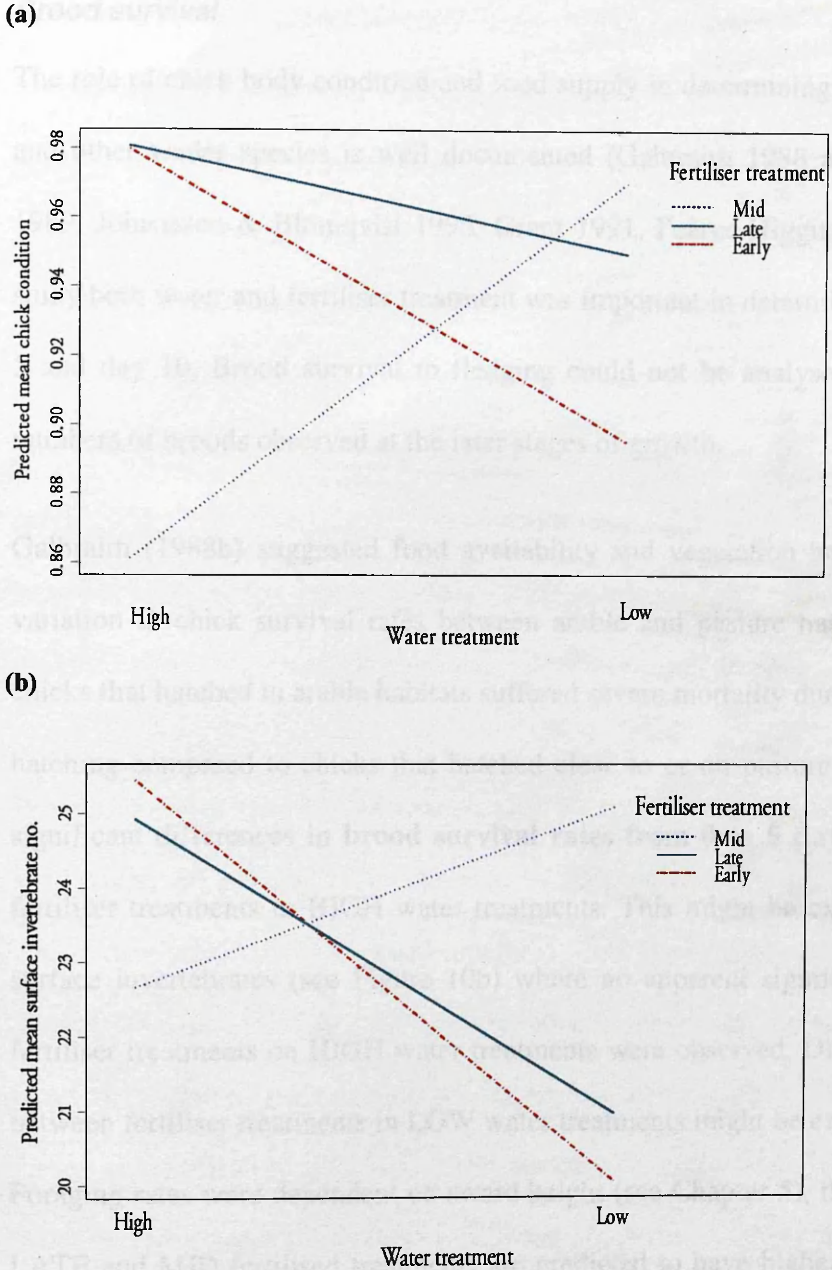

Figure 10 **Effect of water and fertiliser interaction on (a) chick body condition (all broods) and (b) surface invertebrate number.**

Brood survival

The role of chick body condition and food supply in determining chick survival in lapwings and other wader species is well documented (Galbraith 1988 a & b, Beintema & Visser 1989, Johansson & Blomqvist 1996, Grant 1991, Pearce-Higgins & Yalden 2002). In this study both water and fertiliser treatment was important in determining brood survival to day 5 and day 10. Brood survival to fledging could not be analysed accurately due to small numbers of broods observed at the later stages of growth.

Galbraith (1988b) suggested food availability and vegetation height were responsible for variation in chick survival rates between arable and pasture habitat types. He found that chicks that hatched in arable habitats suffered severe mortality during the first few days after hatching compared to chicks that hatched close to or on pasture habitats. In this study no significant differences in **brood survival rates from 0 to 5 days** were apparent between fertiliser treatments in HIGH water treatments. This might be explained by availability of surface invertebrates (see Figure 10b) where no apparent significant differences between fertiliser treatments on HIGH water treatments were observed. Differences in survival rates between fertiliser treatments in LOW water treatments might be explained by foraging rates. Foraging rates were dependent on sward height (see Chapter 5), therefore chicks feeding in LATE and MID fertilised treatments are predicted to have higher food intake, resulting in higher survival rates, than in EARLY fertilised treatments where the sward is significantly longer (see Chapter 3). Therefore, when soil moisture is HIGH food abundance is the most important predictor of chick survival and when soil moisture is LOW, a short sward enabling increased food intake is important in determining brood survival rates.

Previous studies that have considered the interaction effects of habitat structure and lapwing predation have focussed on predation at the nest stage (Baines 1990, Galbraith 1988b). In these studies nest predation rates were lower on habitats with tall or more uniform vegetation than those with short or heterogeneous vegetation structure. In this study we identified that brood survival in an individual field was dependent on vegetation height and amount of predator activity observed within that field boundry. It appeared that chicks that hatched in fields with low predator activity benefited from being able to forage in areas of short sward, however their survival decreased as predator activity increased. Chicks hatched on treatments with longer vegetation benefited from extra cover and survived better when predator activity was high. These results highlight both the potential importance of vegetation cover for young lapwing chicks when predator levels are high and a potential trade-off which results when providing suitable foraging habitat.

Previous authors have shown how survival rates between first and replacement clutches can vary (Galbraith 1988a). In this study brood survival rates (to day 5) were also dependent on clutch type (first or replacement clutches). The apparent linear negative response of first broods to sward height also indicates the importance of food abundance and availability. It is likely that survival rates of first broods are predicted by their food intake, where foraging rates are significantly greater in short sward than long sward (Chapter 5). Explaining the brood survival rates of replacement broods between fertiliser treatments is not as clear. Replacement broods hatched in EARLY and MID treatments appear to benefit from cover. It appears that replacement broods hatched on LATE fertilised treatments may also be more vulnerable to predation through a combination of less cover from predators and poorer body condition.

Brood survival from day 5 to day 10 was also dependent on soil moisture and sward height although the observed response varied slightly from the observed response in broods to day 5. Survival estimates of older broods on HIGH water treatments were higher than

LOW water treatments particularly in EARLY and LATE fertilised treatments. Older chicks appeared to be more sensitive to differences in soil moisture than sward height in contrast with young broods where differences in survival estimates between water treatments were not as obvious. This trend is again consistent with variation observed in surface invertebrate numbers between treatments where higher numbers of surface invertebrates were observed in treatments with LATE and EARLY fertiliser application and HIGH water levels (Figure 10b). Fertiliser application appeared to have a negative effect on brood survival however this was dependant on timing of that application. Broods hatched on EARLY and LATE treatments were most sensitive to fertiliser application showing an negative response.

In contrast with young broods, survival estimates to day 10 were significantly predicted by chick condition. While survival estimates of chicks to day 5 appear to have been predicted by food supply alone the results suggest that the influence of food availability on chick body condition, a life history trait, is important in predicting the survival of chicks to a later stage in their development. In comparison, Galbraith (1988a) found that egg size enhanced chick survival through effect in the first 10 days after hatching. Food supply is therefore important in determining body condition and this effect is sustained to predict chick survival later in development (5 to 10days).

Survival estimates of replacement broods from 5 to 10 days was significantly higher than first broods. This result contrasted with young broods (0 to 5 days) where survival estimates of first broods and did not differ significantly from replacement broods, except in LATE fertilised treatments, where survival of first broods was greater. It is possible as first broods become more mobile in day 5 to 10 they are more susceptible to predation than replacement broods where more adequate cover is available.

To conclude, both water and fertiliser treatments were found to effect lapwing chick condition and survival. The role of body condition as a predictor of chick survival is well documented, however this study demonstrates the importance of extrinsic factors in determining lapwing body condition and its subsequent effect on chick survival.

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APPENDIX I

(a)

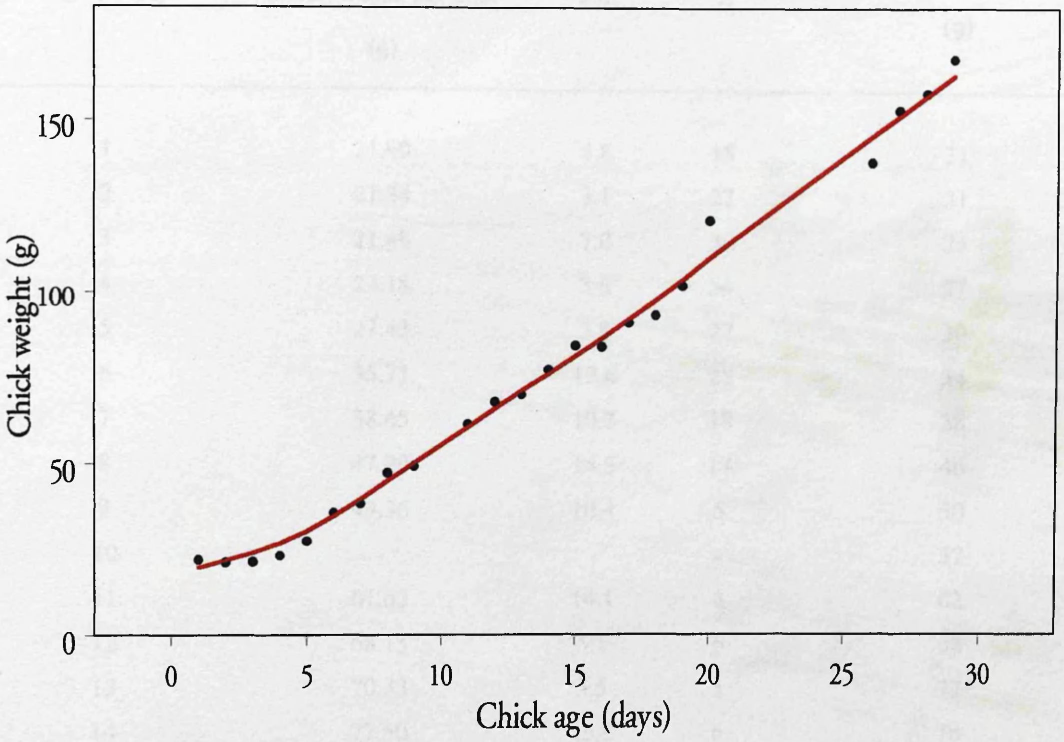

Figure 1 **Relationship between chick age and chick weight.**

Each point represents the expected weight (average weight) of chicks of each age. A Friedman super smoothed line was fitted to standardise expected weights for all chick ages.

(b)

Table 1 Standardised body weights of lapwing chicks at Loch Gruinart.

Age (days)	Expected weight (mean weight per age) (g)	s.d.	n	Standardised values for expected weight (g)
1	21.99	4.8	18	21
2	21.34	3.1	27	21
3	21.48	7.0	30	25
4	23.18	3.6	54	27
5	27.43	5.8	27	30
6	35.71	12.6	28	34
7	38.45	10.3	18	38
8	47.29	14.5	17	46
9	49.36	10.4	5	50
10	-	-	-	57
11	61.62	14.1	8	62
12	68.15	5.1	6	68
13	70.33	5.5	3	72
14	77.50	15.8	6	78
15	84.50	3.5	4	85
16	84.20	11.0	5	88
17	91.30	24.2	11	93
18	93.50	11.0	4	98
19	102	-	2	103
20	121	-	1	113
21	-	-	-	118
22	-	-	-	125
23	-	-	-	132
24	-	-	-	137
25	-	-	-	143
26	138	19.85	3	150
27	153	5.8	5	156
28	158	-	1	162
29	168	-	1	167

Chapter 7

General discussion

The relationship between farmland birds and agricultural intensification has previously been tested in many ways including on a community level, where associations between farmland bird declines parallel declines in both plant and invertebrate food supply on farmland (Wilson *et al.* 1999, Benton *et al.* 2002). Secondly, many autecological studies have demonstrated negative behavioural (e.g. habitat use) and demographic (e.g. hatching success and chick survival) responses of farmland birds to agricultural intensification (Donald *et al.* 2002, Baillie, *et al.* 1997, Green 1984). However, the use of field experiments in identifying the mechanisms of population declines with changes in management has been limited and they have proved to be powerful in understanding and quantifying the impact of a particular component of agricultural change (Potts 1986, Green & Stowe 1993).

The aim of this thesis was to investigate the relationship between farming practice, invertebrate food supplies and the life history of a bird of conservation importance, in order to assess the likely mechanistic effect of farming practice on population biology. The model system we chose was to assess the effects of lowland grassland management on lapwing food supply and lapwing breeding success using a farm-scale experiment. The experiment has highlighted that the impacts of farming methods on the breeding success of a farmland bird and its invertebrate food supply are complex and multifactorial and has indicated that there is no one single farming practice that will reverse farmland bird declines. The experiment found links between vegetation structure and nest success, between chick food supply and chick survival, between vegetation structure and foraging success all of which are likely to affect other species which depend on grassland habitats for breeding such as redshank, oystercatcher, snipe and skylark.

In this chapter the results are discussed with reference to long term trends in lapwing productivity at the study site (see Chapter 2. Options to manage lowland grassland habitat for breeding lapwings are also compared.

Invertebrate abundance and lapwing breeding success

Earthworm biomass

Earthworms are an important component of adult lapwing chick diet and are so likely to be an important determinant of the adults' performance. While other studies have found significant independent responses of earthworm abundance with fertiliser application (Edwards 1984) and soil moisture (Ausden *et al.* 2001), in this study the interaction effects of both fertiliser and soil moisture were presented. Treatments with low soil moisture and early fertiliser application provided best conditions for earthworm biomass (Chapter 3, Figure 7). It is possible that the slow release of nutrients from fertiliser pellets in LOW water treatments had a beneficial affect on earthworms while the application of nutrients in HIGH treatments appears to deter earthworms, possibly brought about by an increase in biological oxygen demand or acidification in soil water (Andrews & Rebane 1994). Within-field variation in earthworm biomass is consistent with between-treatment variations where biomass is highest on rigs, which have a lower soil moisture and higher fertiliser content than ditches.

Earthworm biomass and distribution between treatments did not predict nest density, chick foraging behaviour or chick survival in lapwings. There is evidence from previous studies to suggest that lapwings benefit most from earthworm abundance during the pre-breeding season, for example, pre-breeding lapwing flocks were found foraging in fields with a high earthworm density (Galbraith 1989a, Baines 1990, McKeever unpublished data). Other studies have documented the importance of earthworms in determining egg size in lapwings (Galbraith 1988c, Blomqvist & Johansson 1995). The statistical model including earthworms as a predictor variable predicts that lowering water levels and applying fertiliser early in the season will benefit pre-breeding lapwings by increasing earthworm abundance, however, applying fertiliser early in the season has a negative effect on lapwing chick foraging behaviour and survival (Chapters 5 and 6) and lowering water levels has a negative effect on surface invertebrates and chick survival. Therefore, trade-offs are likely to occur in providing adult lapwings with an abundant pre-breeding food source. However, it is not necessary for lapwing nesting fields to be good feeding sites for adults, provided that productive foraging areas are available nearby (Hudson *et al.* 1994). This suggests the importance of a heterogeneous farmland habitat. Lapwings require fields close to nesting and chick rearing areas which are well drained and have fertiliser applied early to provide them with an abundant food supply. The importance of earthworm abundance to pre-breeding lapwings has been well documented (Galbraith 1988c, Blomqvist & Johansson 1995), however the proximity of an abundant food source throughout the breeding season is likely to have implications in nest survival, chick survival and adult survival, where adults can be more attentive if their preferred food source is close by.

The response of earthworms to water and fertiliser treatment may have implications for other breeding species that forage on grasslands. Species such as breeding curlew, redshank, oystercatcher and snipe are also likely to be affected by changes in earthworm abundance brought about by grassland improvement. Previous studies have highlighted the importance of grassland as a foraging habitat for these species during the breeding season (Berg 1992b, Green & Cadbury 1987); they are therefore susceptible to changes in earthworm food supply brought about by grassland improvement.

Surface invertebrates

Surface invertebrates are an important source of lapwing chick food (Hudson *et al.* 1994).

While previous studies have demonstrated the effects of agricultural intensification on the surface invertebrate populations of arable farmland habitats (Robinson & Sutherland 2002, Wilson *et al.* 1999), very little is still known of the effects of grassland management on surface invertebrate abundance (Vickery *et al.* 2001).

Higher numbers of surface invertebrates, including predominantly beetles and spiders, which are important in chick diets (Galbraith 1989b, Baines 1990, Beintema *et al.* 1991, Johansson & Blomqvist 1996), were observed on ditches than rigs (Chapter 3, Figure 13). This variation in surface invertebrate number within fields (i.e. between rigs and ditches) was suggested as a possible mechanism for differences in nest density between rigs and ditches at Gruinart Flats between 1995 and 1999 (Rout 1999; Chapter 2, Figure 4). In more general terms, we might expect to find more insects in wet areas in fields which do not have a rig and ditch structure. Proximity to suitable chick rearing areas can be important in determining lapwing chick survival (Galbraith 1988a); where nesting close to an abundant food source has advantages, especially in as dense a population as Gruinart Flats, where movements between territories can be hazardous from attacks by neighbouring adults. In the factorial experiment, surface invertebrates were most abundant in treatments with high soil moisture and in treatments with low soil moisture when fertiliser was applied in early May (Chapter 3, Figure 11). This response was replicated when numbers of spiders were analysed. These responses in surface invertebrate and spider number occurred long after nesting was initiated and therefore did not predict nest density nor hatching success but were found to be important only in affecting chick growth, condition and survival.

Lapwing chicks were not observed foraging in all treatments with the highest number of surface invertebrates as expected from the surface invertebrate model (Chapter 3, Figure 11). While lapwing chicks were observed foraging on ditches and on LATE fertilised, HIGH water treatments (Chapter 5, Figure 4) chicks appeared to avoid EARLY fertilised, HIGH water treatments despite those treatments having high numbers of surface invertebrates. Galbraith (1988a) suggested that restricted mobility contributes to the avoidance of long vegetation by lapwing chicks, making it more difficult for them to detect and access their prey. This was confirmed in this study as foraging rates of lapwing chicks declined with an increase in sward height (Chapter 5, Figure 6) highlighting the importance of prey availability. Foraging rates of lapwing chicks on ditches were greater than rigs (Chapter 5, Figure 7) highlighting the importance of both prey availability and abundance as a mechanism in determining habitat preference. In a study of skylark foraging habitat use in relation to arthropod abundance and vegetation structure, Odderskaer *et al.* (1997) found skylarks preferred areas with short vegetation even though these areas contained lower food densities than the main crop. Vickery *et al.* (1997) found higher densities of redshank in fields with short sward and attributed this to ease of prey detectability in shorter sward. This evidence suggests that foraging locations are selected on the basis of both vegetation structure and food supply.

It is widely accepted that food limitation can underlie much of the variation in life history traits of birds by influencing clutch size, egg size, fledging success and later survival (Lack 1947, Martin 1987, Martin 1995, Perrins 1995, Brinkhof & Cavé 1997, Bukaciński *et al.* 1998, Clifford and Anderson 2001). Previous studies have demonstrated how reductions in surface invertebrate food supply brought about by agricultural practices have affected the breeding success of both passerine and non-passerine species. For example, Southwood & Cross (1969) and Potts (1986) demonstrated how grey partridge chick survival is closely liked to the abundance of sawfly larvae, their preferred prey, which is affected by the use of pesticides. Studies on skylark in the UK (Wilson *et al.* 1997) and yellowhammer in Denmark (Petersen *et al.* 1997) suggest that the higher breeding success of these species on organically managed farmland than intensively managed farmland is, in part, attributable to the increased number of arthropods found on organically managed farmland.

While food supply has previously been noted to be important in determining egg size, as well as chick condition and survival in lapwings (Galbraith 1988b, Baines 1990, Blomqvist & Johansson 1995), no effects of treatment were observed on clutch size and egg size. In studies where variation in clutch size and egg volume has occurred, these differences were only observed between habitat types (Shrubb 1990, Galbraith 1988a), suggesting that variation within habitats is more difficult to detect. This is especially the case within the experimental design used here, in that the experimental unit was a much smaller size than the area that an adult lapwing could forage in. Thus the placement of the nest was not necessarily an indicator of adult foraging areas, and hence we did not expect, a priori, a relationship between the food available in the experimental unit where a nest was located and the egg size.

Lapwing chicks tended to remain in close proximity to the nest site in the first 3-4 days after hatching, making the effects of natal treatments more likely to be detected at this stage in chick development, before becoming increasingly mobile and foraging elsewhere. Egg volume had no effect on chick body condition as observed in other studies (Galbraith 1988a, Blomqvist *et al.* 1997, Kirby & Tyler 1999). However, variation in surface invertebrate number between treatments closely matched variation in chick body condition and chick survival between treatments implying that surface invertebrate responses to treatments affected chick body condition. Even so, variation in surface invertebrates did not predict body condition of young chicks or their survival to day 5, but did explain variation in chick condition of older broods and the survival of chicks from day 5 to 10. This suggests that the benefits of an abundant food source are not detectable in chick body condition and survival until later in their development. The fact that natal treatment effects are detected later in chick development is testament to the importance of providing suitable habitat for both the early nesting stage and chick rearing. Previous studies have discussed the negative impacts of chicks hatching in habitats unsuitable for foraging, in particular arable habitats where food is limited and rapid vegetation growth can inhibit movement within those habitats (Galbraith 1988b, Blomqvist & Johansson 1995).

To conclude, the importance of an abundant food source on hatching is important, particularly in predicting chick condition and survival in lapwing chicks. From a management perspective the surface invertebrate model predicts that maintaining high water levels throughout the season and applying fertiliser early or late in the season will benefit lapwing chick survival by increasing numbers of surface invertebrates. However, chicks avoid long sward despite an abundant food source, as mobility and detectability of food is restricted, decreasing foraging rates. Therefore, by maintaining high water levels and maintaining a short sward during the chick-rearing period by withholding fertiliser application until early June increases the chance of chick survival as a result of providing good foraging habitat.

Changes in habitat structure and lapwing breeding success

The previous section has considered the effects of grassland management on lapwing breeding success in relation to food supply. In this section the effects of manipulating sward structure and water levels on breeding success are discussed.

Nest Survival

The main causes of lapwing nest failure on agricultural land are disturbance, such as trampling by livestock (Beintema & Müskens 1987, Shrubb 1990) and destruction from farm machinery (Kruk *et al.* 1996). Baines (1990) suggested that differences in sward structure between improved and unimproved pasture in the English uplands might contribute to increased lapwing nest mortality due detection by predators, however this has never been tested. The role of vegetation structure in providing good nesting habitat for other ground nesting species in farmland habitats is well documented. For example, corncrakes tend to nest in tall, dense vegetation in order to avoid detection from predators (Green & Stowe 1993), while skylarks prefer nesting in more open habitat allowing early detection of predators (Henderson 2001).

In the absence of disturbance from agricultural practices in this study, sward height was found to have a significant impact on hatching success whilst soil moisture had no effect (Chapter 4). Early cover benefits nest survival when the threat from predators is low. When the threat from predators is high, however, lapwings benefit from nesting in short sward, allowing adults to detect approaching predators more easily than in longer grass. This assumes that lapwings are more tolerant of longer sward when threat from predators is low but not when predator activity is high, when early detection is apparently important in defending nests. Predation-risk indices did not explain differences in hatching success between fields in the period 1995 –1999 at Gruinart Flats (Chapter 2). As fertiliser was only applied once during the season over that period, variation in hatching success with sward height was not detected. The nest survival experiment model predicts that fertilising early or late in the season can benefit nest survival, but this is dependent on predator activity, suggesting that a heterogeneous sward structure would provide an appropriate range of conditions for nesting lapwings, as it is also for skylarks (Donald *et al.* 2002).

Predation is a well-known cause of lapwing chick mortality (Baines 1990, Galbraith 1988b, Rout 1999). Variation in vegetation height has been suggested as a possible mechanism for variation in predator mortality among lapwing chicks (Galbraith 1988b), however this has never been tested. While variation in food supply between treatments predicted chick survival (0 – 5 days), predator activity within fields was also important. Chicks hatched in fields where predator activity was low benefited from a short sward, allowing adults to watch over their broods efficiently (Galbraith 1988b), whilst chicks hatching in fields with high predation benefited from cover (long sward) from predators (Chapter 6). This response was not observed in the survival of older chicks in the experiment but analysis of long-term data from the site suggests that field proximity to buzzard nest sites is important in determining chick survival to fledging (Chapter 2). However, the long-term data also suggests that while predators are an important factor in determining chick survival between fields this has not affected chick productivity over time, where increases in fledging rates were observed over the 1995 – 1999 period. As with nest survival, the chick survival model predicts that providing a heterogeneous sward structure will benefit chicks from predators, and this will trade-off against providing suitable chick foraging habitat. This view is in accordance with a recent review undertaken by Benton *et al.* (in press) who have demonstrated the importance of heterogeneity in the farmland landscape both at a between-field scale and a within-field scale in maintaining farmland biodiversity.

Management recommendations

To conclude, taking both the results of the experiment and Chapter 2 into consideration, the following recommendations to manage Gruinart Flats for lapwings is proposed.

Option 1:

This option solely focuses on the breeding requirements of lapwings and does not consider goose management and farming requirements.

- **Apply NO fertiliser and maintain HIGH water levels in ditches throughout the season.**

In the absence of fertiliser at Gruinart Flats grazing by barnacle geese is likely to be reduced (Percival 1993) thereby increasing the diversity of sward height and suppressing rapid sward growth throughout the lapwing breeding season. This measure benefits nesting lapwings and provides adequate cover for lapwing chicks in addition to providing good chick foraging areas. In a study of the management of grazing marshes for wintering geese and breeding waders, Vickery *et al.* (1997) found that fields that had been lightly grazed by geese in winter were more attractive to breeding waders the following summer. However, we recommend removal of fertiliser from the system as a short-term management recommendation while more research is carried out to monitor the effects of no nutrient input over time on the abundance of both sub-surface and surface invertebrate populations.

Removing fertiliser from the system at Gruinart Flats brings into question the validity of reseeding. Reseeding is used along with fertilisers to promote grass growth for silage production and to attract geese on to the reserve (Percival 1993). Reseeding is also useful in controlling the spread of *Juncus* (Evans 1985), however other methods can be used to control *Juncus* such as topping and weed-wiping (RSPB Loch Gruinart Management Plan).

More research is required to monitor the effects of reseeding without fertilising on the invertebrate communities and sward structure.

Option 2:

This approach takes into consideration other species which use the site, such as corncrake and barnacle geese in addition to the farming operation.

- **Fertilise EARLY (late April) on part of each field i.e. every second rig and LATE in season (end May) on remaining rigs and maintain HIGH water levels throughout the season.**

In the case of barnacle geese, providing suitable over-wintering habitat is integral with maintaining the in-hand farming operation on the reserve in that both benefit from fertilising. The presence of fertiliser is known to significantly increase the time that barnacle geese spend grazing a pasture (Percival 1993), which if removed will reduce the effectiveness of Gruinart Flats as a refuge for geese. In addition, removing fertiliser from the system will reduce the silage crop required to feed cattle over winter and reduce cattle grazing in the autumn. Therefore option 2 recommends applying fertiliser both EARLY in the season and LATE in the season to provide the heterogeneous sward required for nest and chick survival while maintaining the goose management and silage production requirements of the reserve. McFarlane (2001) found that manipulating the timing of fertiliser and water levels in the previous spring had no effect on the foraging behaviour or distribution of barnacle geese in the following winter. Therefore managing Gruinart Flats for lapwings using option 2 is unlikely to compromise the value of the site for over-wintering geese in contrast to Vickery *et al.* (1997) who suggest that there is a conflict between managing grassland for geese and breeding waders.

Fertiliser input also benefits breeding corncrakes that use the site by providing cover later in the season. Little is known about the effects of both fertiliser and water treatment on the breeding success of redshank, which also breed in high numbers on the site. Norris (1998) explained the decline of redshank nesting on saltmarshes on the decrease of sward diversity brought about by increased grazing by cattle. This suggests that a more diverse sward as a result of two fertiliser applications will provide a more suitable nesting habitat for nesting redshank.

To conclude, this study has demonstrated the effectiveness of a formal farm-scale factorial experiment in addressing the mechanisms of farming practices on the food supply, behaviour, life history and productivity of a declining farmland bird species.

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