Foraging Behaviour of the European Starling *Sturnus vulgaris*. A Case Study to Explore the Potential Implications of Climate Change on Ground-probing Birds

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A thesis submitted for the degree of Doctor of Philosophy, December 2012,
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Abstract

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It is well established that farmland bird population declines are strongly linked to the land use and management changes associated with increased agricultural intensification. In future, climate change is predicted to be an increasingly important driver of bird population changes. A substantial number of studies have investigated the large scale impacts of climate change on species' distribution and abundance. However, few have examined in detail specific ecological impacts of climate change on bird demographics that would allow predictions of the effects of climate on bird populations.

Here I show that below-ground prey form a key part of the diet, of my study species, the Starling *Sturnus vulgaris,* on UK grassland in both the breeding and non-breeding season. I then show that soil moisture mediates intake rates of below-ground prey using field experiments on wild-caught Starlings. Intermediate soils provided the best foraging opportunities with both saturated and dry soils being suboptimal

I then linked delivery of below-ground prey to reproductive success. A study of adult provisioning of nestlings (n= 42 nests), over a four year period, established that the delivery of below-ground prey, specifically Tipulidae larvae, was mediated by changes in soil moisture and linked to Starling reproductive success via changes in fledgling survival.

Analysis of fledgling success at a range of sites (n=132) provided evidence that an increase in the mean spring (April-June) soil moisture deficit over a twenty year period was a significant driver of Starling population dynamics in Britain; even after controlling for temporal changes in starling populations (likely to be linked to agricultural intensification). I conclude by discussing different management options to alter soil moisture levels on grassland to benefit both ground-probing birds and the impacts on a range of other ecosystem services (e.g. reducing flood risk).

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Chapter 1: General Introduction

1.1 Main study species: European Starling *Sturnus vulgaris*

The European Starling *Sturnus vulgaris* L. (hereon referred to as the Starling) is a medium sized passerine (c. 75-80g) with glossy black plumage and an iridescent mauve/green sheen (Cramp& Perrins 1994, Feare 1984) found throughout most of the Western Palaearctic. The British breeding population is resident and numbers approximately eight to ten million individuals (1994 – 2000) (Robinson *et al*. 2002, 2005). It is augmented in winter by the arrival of millions of migrants from northern and eastern populations (Baillie *et al*. 2002, Cramp & Perrins 1994, Robinson *et al*. 2002, 2005). Starlings are gregarious birds that feed in small flocks numbering tens to hundreds, foraging on the ground in areas of short grass or other open vegetation (Brownsmith 1977) searching for their prey by pushing their closed bill into the top few centimetres of the soil (probing) then widening the hole by opening the bill during repeated stabs into the hole (rooting) (Feare 1984). Reasonably dated descriptive studies have reported that Starlings will preferentially consume soil and ground-dwelling invertebrates, but switch to soft fruit and seeds when their preferred prey, leatherjackets (tipulid larvae) and earthworms, are not available (Dunnet 1956), particularly in the autumn (Tinbergen 1981). Tipulid numbers are variable from year to year, making trends difficult to discern (Wilson *et al*. 1999). However, soil invertebrate biomass particularly that of tipulids is generally highest in areas of permanent pasture, where soil disturbance is minimal (Paoletti 1999, Robinson *et al*. 2005). Foraging birds are strongly associated with areas of grassland pasture, primarily those with high densities of invertebrates (Whitehead *et al*. 1995, Feare 1984).

Starlings are semi-colonial, hole-nesting passerines (Feare 1984). They are known to be highly site faithful, returning to the same general area each year to breed (Feare 1984). Adults generally do not breed until they are two years old, but in many populations, large numbers of non-breeding individuals, especially males, are found throughout the breeding season (Stewart 1973, Sandell & Diemer 1999). Although these floaters do not defend a nest site, they often remain within a specific area possibly to gain information on the location of potential future breeding sites (Tobler & Smith 2004). Starlings demonstrate a high degree of breeding synchrony (Feare 1984), but with some variation both between different populations (Pinxten *et al*. 1990, Smith *et al*. 1994), and within the same population (Feare 1984, Smith & Sandell 1998). In the UK, the mean laying date of Starlings advanced between 1968 and 2008, from the 27th to the 22nd April (http://www.bto.org/birdtrends2010/wcrstarl.shtml#population). Starlings lay 4-6 eggs and fledging occurs at around 21 days. Parents continue to feed the young for two weeks until they are independent. A second clutch may be laid 40 to 50 days after the first clutch (Crick *et al*. 2002).

A breeding colony will feed communally within a home range. Parent Starlings feeding nestlings are central place foragers (Orians & Pearson 1979, Kacelnik 1984) and mostly limit their foraging to areas within 500 m of their nest (Feare 1984). The foraging day consists of up to 250 round trips to and from the nest site after a load of food has been collected for the young (Tinbergen 1981). Distance to foraging grounds affects load size; as distance increases so does the food load transported by the provisioning adult (Kacelnik 1984). Prey type, size and percentage in the diet is influenced by age, due to changes in prey availability, developmental requirements of nestlings and nestling demand (Dunnet 1955, Westerterp 1973, Feare 1984), and brood size (Tinbergen & Drent 1980, Tinbergen 1981).Parents feed small and normal-sized broods different prey species with different consequences for the nestlings (Tinbergen 1981).

Soon after becoming independent of their parents, first brood juveniles join communal roosts, leaving the parents to rear a second brood (Feare 1984). It has been suggested that the synchronisation of breeding is to allow the immediate formation of juvenile flocks after fledging (Dunnet 1955). Post-breeding dispersals lead to geographical and sometimes habitat separation between juveniles and adults and may reduce competition between the age groups for scarce food resources in summer (Feare 1984). Invertebrates continue to be eaten in summer but where soft fruits are available they become an important food source, especially for juveniles. In Britain, large flocks of juveniles from nearby colonies, sometimes numbering thousands, appear on upland heather and rough grazing moors and on coastal salt marshes from late June through August-September (Feare & Douville de Franssu 1992**).** In winter, Starlings are omnivorous, eating invertebrates, grain and stock feed and they also scavenge food scraps and feed at refuse tips and within wintering areas, behaviour of Starlings can vary from philopatry (Feare & Wadsworth 1981) to movements ranging over many kilometres within short time periods (up to 50km) (Summers & Cross 1987). Regular flight lines are used between feeding sites and roosts.

Currently, Starlings are Red-listed in the UK owing to their breeding population size experiencing a severe ‘longer- term’ decline since 1969 (i.e. since the first Birds of Conservation Concern review) and declining by more than 50% during the past 25 years (Gregory *et al*. 2002, 2004; Eaton *et al*. 2009).Populations across northern and western Europe have been declining at an unprecedented rate since the 1980s (Baillie *et al*. 2002, Robinson *et al*. 2002, PECBMS 2011). In the UK, European Starling numbers have decreased throughout all of the main habitats they reside in (woodland, farmland and urban), especially woodland (Robinson *et al*. 2002, 2005). The declines have been greatest in the south and west of Britain and trends on farmland, which holds half of Britain’s Starlings, differ with respect to farm type, with the steepest declines in regions of pastoral and mixed arable-pastoral farming (Robinson *et al*. 2002, 2005). As the population has dropped, the numbers of fledglings per breeding attempt has increased; clutches are now larger and rates of nest loss have fallen. It is thought that this decline in the overall population is a result of decreasing survival rates, particularly of first-year overwintering birds (Freeman *et al*. 2002, 2007, MacLeod *et al*. 2008). Despite the range of studies already targeting Starlings there is no clear evidence of why their populations are currently declining. This thesis will examine a previously neglected issue: the role of soil conditions (specifically soil moisture) on Starling populations.

A range of species are also likely to be affected in similar ways to Starlings because they also probe the ground for food. For example, there is a range of bird species that feed predominantly on soil invertebrates that are also associated with lowland grasslands and have been experiencing similar population declines (e.g. waders such as Common Snipe *Gallinago gallinago L.* - Green 1986; Common Redshank *Tringa totanus L.* and Northern Lapwing *Vanellus vanellus L.* - Baines 1990, Ausden *et al*. 2003, Tucker 1992; European Golden Plover *Pluvialis apricaria L*. - Pearce-Higgins & Yalden 2003, Fuller &Youngman 1979; corvids such as Chough *Pyrrhocorax pyrrhocorax L.* -

McCracken *et al*. 1992 and passerines such as Song Thrush *Turdus philomelos* L. - Peach *et al*. 2004 a, b). Decline of bird species associated with lowland farmland is a major conservation concern and is largely attributed to the land use and management changes associated with agricultural intensification (e.g. Chamberlain *et al*. 2000, Donald *et al.* 2001, Gregory *et. al*. 2004). In the future, there are further substantial effects predicted from climate change on species' distribution and abundance (Parmesan & Yohe 2003, Root *et al.* 2003, Thomas *et al.* 2004, Hickling *et al*. 2006).

1.2 Agricultural Intensification and Farmland Bird Declines

Although I am not specifically exploring changes in soil conditions due to agricultural intensification (e.g. land drainage) it is important to place my study in context of wider changes on farmland over recent decades. I outline these briefly below and describe how changes have influenced farmland birds that live predominantly on grassland.

Agricultural intensification in Britain since the second World War (WWII) has been paralleled with a reduction in biodiversity and a decline in abundance across many taxa (Robinson & Sutherland 2002). There is much evidence to suggest a causal link between changing agricultural practices and farmland bird declines on both arable and pastoral farming systems (e.g. Krebs *et al*. 1999, Wilson *et al*. 1999, Chamberlain *et al*. 2000, Donald *et al*. 2001, Vickery *et al*. 2001, Newton 2004). Grassland accounts for over 65% of the area of agricultural land in Britain, occupying approximately seven million hectares, and most is agriculturally improved or semi-improved. The mechanisms by which changes in management have affected ground-probing bird populations are diverse. Population effects could arise from reduced breeding productivity (Siriwardena *et al*. 2000), reduced survival (Siriwardena *et al*.1998) or a combination of the two. In terms of reduced foraging opportunities there are known links to the loss of permanent pasture and the intensification of livestock management (Robinson *et al.* 2005). Widespread land drainage over the last 200 years has resulted in a reduction in the quantity of grassland through conversion of wetland habitats to arable farmland. Subsequent intensive management of the remaining grassland resource means that it is of limited quality for ground-probing birds through reductions in suitable nesting habitat, direct effects of trampling on nests/chicks, soil degradation and compaction and reduced abundance, availability and access to invertebrate prey. The management and productivity of improved grassland has been transformed during the period of agricultural intensification by an increase in use of fertilisers and insecticides (Chamberlain *et al*. 1999, Chamberlain *et al*. 2000), changes in stocking densities and by changes in crop type, from hay to silage (Fuller & Gough 1999, Fuller 1987, Stoate 1996). Specifically, access and abundance to soil dwelling invertebrate prey is reduced through the use of fertilizers that increase soil moisture deficit, thus increasing soil penetration resistance (indication of the difficulty a bird might be expected to have when probing the soil to forage) through increased evapotranspiration (Garwood 1988) and the widespread spraying of grass fields to control Diptera spp. larvae (Campbell & Cooke 1997, Garthwaite *et al.* 1997, Vickery *et al.* 2001). Changes in sward structure through the decline in cattle and subsequent increase in sheep numbers (Chamberlain *et al.* 2000, Fuller & Gough 1999, Devereux *et al*. 2004), the increased use of fertilizer (Paoletti 1999) and the change in crop type from hay to silage (Stoate 1996) affect nest site selection and breeding success (Wilson *et al*. 2005). Sward changes also affect physiological demands of thermoregulation and locomotion (Walsberg 1985), access and abundance of food (e.g. Wilson *et al*.1999) and perceived predation risk (Butler & Gillings 2004, Devereux *et al*. 2006, Whittingham & Evans 2004).

1.3 Climate Change

Climate change is likely to have a significant impact on the availability of suitable feeding habitat for species that probe the ground for their food as a result of both drought in the spring/summer and waterlogged soils in the autumn/winter (Hulme *et al*. 2002, Huntley *et al*. 2007). Soil conditions are likely to affect both below-ground invertebrate populations and access to them by their predators (i.e. ground-probing birds). Dry soil conditions can result in the death of invertebrate larvae, depending on the time of year (McCracken *et al*. 1995), and, for example, force earthworms (Lumbricidae spp.) to descend deeper into the soil, thus reducing prey availability. Conversely, prolonged flooding results in invertebrate prey that are accessible but at low abundance because excessive water-logging reduces populations (McCracken *et al.* 1995, Plum 2005). Under the high emissions scenario, annual moisture content of soils is liable to decrease by 10-20% across the UK by the 2080s, with 20- 50% reductions in average summer soil moisture content occurring in southeast England compared with a 0-20% in the northwest. Winter soil moisture contents are expected to increase by around 4% in parts of Wales and southwest England, and by 4-10% in Scotland. However, higher temperatures in winter are expected to result in reductions of winter soil moisture content (up to 10%), particularly in the southeast, rather than increases (Bisgrove & Hadley 2002). There is already some evidence linking soil moisture changes with population declines. For example, the timing and spatial distribution of Song Thrush population decline is consistent with the pattern of land drainage in Britain (Peach *et al*. 2004b). Although this does not imply causation, it is important to determine how changes in soil moisture caused by climate change may alter population levels of species of conservation concern in order to inform land management policy.

A number of studies have investigated the large scale impacts of climate change on species' distribution and abundance (e.g. Thomas *et al*. 2004). However, few have examined in detail specific ecological impacts of climate change on bird demographics that would allow predictions of the effects of climate on bird populations (e.g. Great Tit *Parus major* Cresswell & McCleery 2003, Golden Plover Pearce-Higgins *et al*. 2010). Here I use the Starling as study species to explore the links between changes in soil moisture and population changes in ground-probing birds. Starlings are ideally suited as a model species for studying ground-probing birds for a number of reasons. They can be kept in captivity and are hole-nesting: both of which permit detailed studies via captive experiments and nest cameras respectively (see Chapters 2-4). They inhabit and forage on farmland grassland, thus enabling us to assess the mechanisms by which climate change may affect farmland birds. They forage on soil and surface invertebrates in common with other grassland species (e.g. thrushes *Turdus* spp.) and feed in a similar manner to other guilds (e.g. waders).

1.4 Aims of thesis

1. Examine the effects of experimentally manipulated soil moisture on Starling foraging success (Chapter 2).
2. Confirm the importance of below-ground prey, specifically Tipulidae larvae, in the diet of nestling Starlings on farmland (Chapter 3).
3. Determine the effects of natural variation in soil moisture on nestling Starling diet composition and Tipulidae larvae provisioning on fledging success (Chapter 4).
4. Examine the correlative effects of changes in soil moisture deficit on Starling breeding populations over a long term period (1981-2000) over a wide spatial scale (Chapter 5).
5. Review management options that could alter habitat quality for farmland birds that rely on probing the ground for their food and link these to ecosystem service provision (e.g. flood mitigation) (Chapter 6).

1.5 Thesis outline

Chapter 2 examines the effect of soil penetration resistance on the foraging behaviour and success of Starlings. There was a strong negative correlation between penetration resistance and soil moisture content. Trial field plots were manipulated to produce a range of soil moisture levels by protecting them from direct rainfall and water flow for different periods of time. Foraging observations were conducted on trios of captive Starlings, one focal and two companions, in a purpose-built wire mesh bottomless cage.

Chapter 3 established the importance of below-ground prey, specifically Tipulidae larvae, in the diet of nestling Starlings on farmland. This chapter also examined the effects of brood size variation and nestling age on diet composition through the observation of parental food provisioning at four breeding colonies at John Krebs Field Station, Wytham, Oxfordshire, UK, over a four year period, using nestbox video recorders. Findings from this chapter were published in Bird Study in 2012.

Chapter 4 related nestling food provisioning, specifically provisioning of Tipulidae larvae, and fledgling survival at one colony to natural variations in soil moisture content in the area surrounding the nest sites. Soil moisture content data were supplied by the Environmental Change Network from an automatic weather station situated at the field station. Soil moisture was found to alter fledgling survival with intermediate levels of soil moisture linked to higher reproductive output.

Chapter 5 examined the effect of decreases in soil moisture on Starling populations at a national scale, using Met Office soil moisture deficit data and British Trust for Ornithology Common Bird Census data. The chapter firstly investigated changes in soil moisture deficit (the amount of water in millimetres needed to bring the soil moisture content back to field capacity) since the 1980s and then explored the correlative effects of soil moisture deficit changes on Starling breeding populations. This chapter provides evidence linking long-term changes in soil moisture to Starling population changes and provides the first evidence of a direct link between climate change and Starling population declines.

In Chapter 6, I investigated the evidence linking soil moisture, foraging by grassland birds and their macro-invertebrate prey and population changes with soil moisture change. This evidence was then used to assess the potential linkage between ecosystem services (e.g. flood mitigation) and habitat management for grassland birds that derive the majority of prey from below-ground soil invertebrates. Data were limited, particularly for non-wading species; therefore the study focused mainly on waders. Findings were presented at the BOU’s Lowland Farmland Birds 3: Delivering Solutions in an Uncertain World Conference in 2009 and published in Ibis: The International Journal of Avian Science in 2010.

I conclude with Chapter 7 which sums up the main finding of the thesis and provides suggestions for future research.

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Chapter 2: The Effects of Experimentally Manipulated Variations in Soil Moisture on Starling Foraging Success in the Autumn and Winter

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Short title: Soil moisture and foraging success

2.0 Abstract

Capsule Starling intake rates of below-ground prey were highest on soils with intermediate soil moisture levels, with lower levels on saturated and drier soils.

Aims To examine the effects of experimentally manipulated soil moisture on Starling foraging success.

Methods We observed the foraging success of 25 wild-caught captive Starlings on outdoor grassland enclosures at a range of soil moisture levels during the autumn and winter.

Results On saturated soils, the number and percentage of probes to the ground (roots) that resulted in prey capture had a curvilinear relationship with decreasing soil moisture. The number and percentage of successful roots initially increased as the soil became less saturated then decreased as the soil continued to dry.

Conclusion A trade-off exists between soil moisture, prey abundance and accessibility: saturated soils are easy to access but have less prey.

2.1 Introduction

In the UK, a major conservation concern is the decline of bird species associated with lowland farmland. The decline is largely attributed to the land use and management changes associated with agricultural intensification (e.g. Chamberlain *et al*. 2000, Donald *et al.* 2001, Gregory *et. al*. 2004). In the future, there are further substantial effects predicted from climate change on species' distribution and abundance (Parmesan & Yohe 2003, Root *et al.* 2003, Thomas *et al.* 2004, Hickling *et al*. 2006). Extinction risks will be higher if locations of suitable climate do not coincide with other essential resources, such as food (Thomas *et al*. 2004, Huntley *et al*. 2007).

A number of bird species associated with lowland farmland grassland feed predominantly on soil-dwelling invertebrates (e.g. waders such as Common Snipe *Gallinago gallinago L.* - Green 1986; Common Redshank *Tringa totanus L.* and Northern Lapwing *Vanellus vanellus L.* - Baines 1990, Ausden *et al*. 2003; European Golden Plover *Pluvialis apricaria L*. - Pearce-Higgins & Yalden 2003; corvids such as Chough *Pyrrhocorax pyrrhocorax L. -* McCracken *et al*. 1992 and passerines such as Song Thrush *Turdus philomelos* L. - Peach *et al*. 2004 a, b and European Starlings *Sturnus vulgaris* - Dunnet 1955, Tinbergen 1981, Rhymer *et al*. 2012). For most soils, raised ground water levels keep the soil surface moist; decreasing penetration resistance (the difficulty a bird may be expected to have when probing the ground) (Gerard 1967, Green *et al*. 2000) and increasing the abundance and accessibility of soil-dwelling invertebrates (e.g. earthworms) in the top layer (e.g. Milsom *et al.* 2000). Climate change is likely to have a significant regional impact on ground water levels and the availability of suitable feeding habitat for these species (Hulme *et al*. 2002), as a result of both drought in the spring/summer and waterlogged soils in the autumn/winter. Under the high emissions scenario, annual moisture content of soils is liable to decrease by 10-20% across the UK by the 2080s, with 20- 50% reductions in average summer soil moisture content occurring in southeast England compared with a 0-20% in the northwest. Winter soil moisture contents are expected to increase by around 4% in parts of Wales and southwest England, and by 4-10% in Scotland. However, higher temperatures in winter are expected to result in reductions of winter soil moisture content (up to 10%), particularly in the southeast, rather than increases (Bisgrove & Hadley 2002). There is already some evidence linking soil moisture with population declines. For example, the timing and spatial distribution of Song Thrush population decline is consistent with the pattern of land drainage in Britain (Peach *et al*. 2004b). Although this does not imply causation, it is important to determine how changes in soil moisture caused by climate change may alter population levels of species of conservation concern in order to inform land management policy.

Here we focus on a model species, the Starling, that has undergone substantial declines in the UK (Robinson *et al*. 2002, 2005) and Europe (PECBMS 2010) since the 1980s. Currently, Starlings are Red-listed in the UK owing to their breeding population size experiencing a severe ‘longer- term’ decline since 1969 (i.e. since the first Birds of Conservation Concern review) and declining by more than 50% during the past 25 years (Gregory *et al*. 2002, 2004; Eaton *et al*. 2009). It is thought that this decline is a result of decreasing survival rates, particularly of first-year birds (Freeman *et al.* 2002, 2007).

This study tests the hypothesis that soil moisture is an important factor limiting Starling foraging efficiency, mediated by its effect on accessibility and abundance of soil-dwelling invertebrate prey in the top layer of soil. Starlings forage on a wide range of different prey, but subsurface prey is important throughout the year (Dunnet 1956, Tinbergen 1981). If we are to understand how soil moisture affects ground-probing birds we need to understand how conditions at different times of year affect foraging. Here we investigated the impacts of manipulating soil moisture in outdoor grassland enclosures during the autumn and winter period.

2.2 Methods

2.2.1 Study site

This study took place at Heddon Banks Farm (54°59'34''N, 01°47'26''W), Heddon on the Wall, Northumberland, UK between October 2010 and January 2011. The experiment was performed on a horse-grazed pasture (2.6km^2 (260 hectares)) regularly used by foraging European Starlings (hereafter called Starlings). The study compared the foraging behaviour and success of wild-caught captive Starlings foraging on grassland plots that had been manipulated to have a range of soil moisture levels.

A randomized block design was used to establish seventy-five plots (each measuring1.5m x 3m) within the study site. To create a range of soil moisture levels on the seventy-five plots there were three levels of treatment: (i) twenty-five plots were unprotected from direct rainfall or from water draining from the upslope (ii) twenty-five plots were protected from direct rainfall for between 14 and 21 days and also had a water drain inserted along the top side from day 1 (iii) similarly twenty-five plots were protected from water drainage from day 1 and from direct rainfall for 28 days or more. Plots were protected from direct rainfall and water drainage in two ways (Fig 2.1). Firstly, a section of the plot was covered with a polythene cloche (0.5 m x 0.5 m x 2m) to protect the area from direct rainfall. Cloches were positioned at a 90° angle to the top of the field so that one of the two openings faced to the southwest. This reduced damage to the cloches as winds came most often from a south-westerly direction. To encourage airflow, and reduce humidity, a gap of 5cm was left between the grass and the base of the polythene cover. Secondly, to prevent water draining through the trial plots a plastic barrier was placed 20cm below ground level along the top side (up the slope) of each treatment plot (0.5m from the edge).

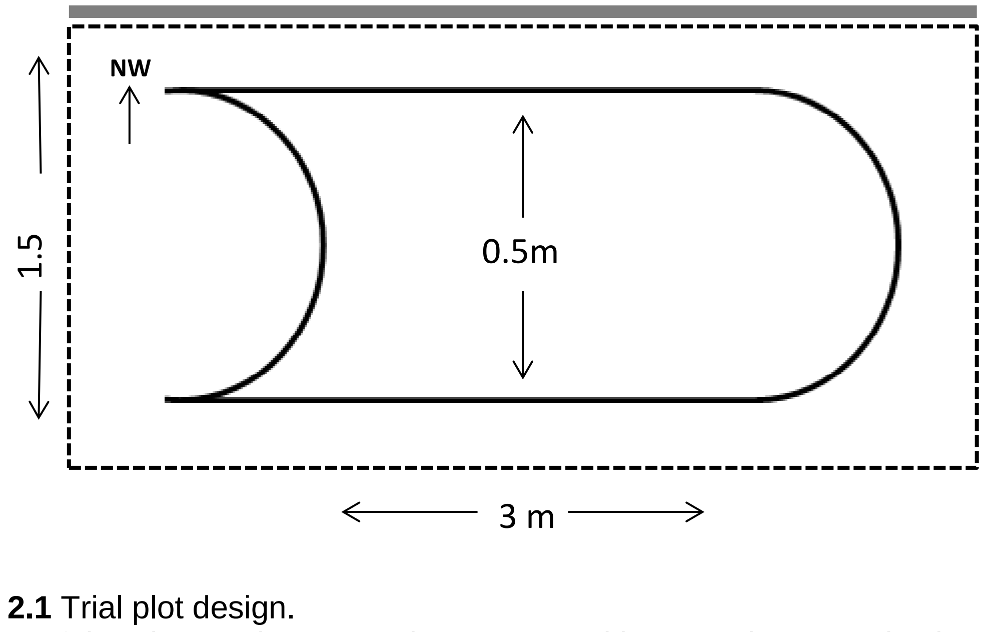

Figure 2.1 Trial plot design.
A section of the trial plot (1.5m x 3m) was covered in a polythene cloche (0.5m x 0.5m x 2m) positioned so that one of the two openings faced southwest. To prevent water draining through the trial plots a plastic barrier was placed 20cm below ground level along the top side of each treatment plot (0.5m from the edge). The cloche is shown as a solid black line. The outline of the plot area is shown as a dashed black line and the plastic barrier is shown as a thick grey line

The study site had a 12.4° slope (1:4.7 gradient, 21.3% grade). To control for the potential effects of water retention at the bottom of the field, the study site was divided into three blocks (1: top, 2: middle and 3: bottom) (Fig. 2.2). Ten replicates of each treatment were assigned to the top and middle blocks and five replicates of each treatment were assigned to the bottom block in a randomized block design. In total, the top and middle blocks contained 30 trial plots each. The bottom block contained 15 trial plots.

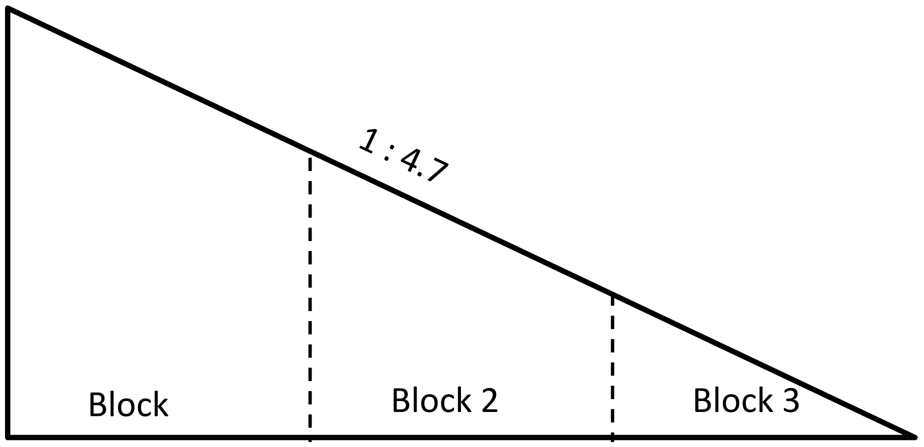

Figure 2.2 Schematic diagram of the study site at Heddon Banks Farm, Heddon on the Wall, Northumberland, UK showing the gradient of the field and the partitioning of the site into three blocks (1: top, 2: middle, 3: bottom). Block 1 contained 30 trial plots, Block 2 contained 30 trial plots and Block 3 contained 15 plots.

2.2.2 Experimental set-up

Twenty-five Starlings from a nearby population (55°05'03''N, 01°28'12''W) were captured under Natural England licence using whoosh nets. They were housed indoors in 0.9 m x 0.7 m x 0.6 m cages (at Close House). Each cage housed a maximum of three birds and all groups were in auditory and visual contact with each other. The ambient temperature and lighting within the enclosure reflected external conditions. Birds received a diet of *ad libitum* turkey starter crumb and softbill pellets, and a 2.5 cm^3 daily ration of mealworms *Tenebrio molitor* was provided after each days trial were completed (Devereux *et al*. 2006). Water for drinking and bathing was available at all times. Starlings were aged and sexed using morphological traits e.g. throat feather length (Smith *et al.* 2005, Devereux *et al.* 2006) and colour ringed with a unique colour-coded combination for identification. They were released at the capture site following completion of all trials (mean time in captivity = 45 days, maximum = 89 days).

Each of the twenty-five birds was randomly selected to be a focal bird (6 adult females, 6 first winter females, 9 adult males, 4 first winter males) (Appendix 2.A). Each focal bird was assigned to an individual block (top: 10 birds, middle: 10 birds, bottom: 5 birds). A randomized block design was used for measuring foraging behaviour, with each bird undergoing one replicate of each of the three treatments in a random order within a block. Each treatment plot was used only once. Each focal bird had the same two companions, selected at random, present for each trial to ensure that the focal bird's foraging rate was not influenced by individual differences in its companion's rates, because foraging rates are mediated by the rates of other flock members (Fernández-Juricic & Kacelink 2004). To avoid pseudoreplication, the combination of companion birds was different for each focal bird. Each bird experienced five trials in total, three as a focal and two as a companion.

Foraging trials were conducted in a purpose-built wire mesh bottomless cage that was divided into two sections (A and B) both measuring 0.5m x 0.5m x 0.5m (Fig. 2.3). Before a trial began, the cage would be placed on the treated area of the trial plot. Within section A, five measurements of penetration resistance and sward height (cm) were made, one at the centre and at each corner. There is a strong negative correlation between soil surface strength (penetration resistance) and soil moisture content (Vaz *et al*. 2011). For most soils, this is associated with the water table depth from the surface (Armstrong 2000). Raised water levels keep the surface soil moist reducing the surface strength. Soil surface penetrability is an indirect measure of soil moisture that provides an indication of the difficulty a bird might be expected to have when probing the soil to forage (Armstrong 2000). Penetration resistance was measured using a hand-held soil penetrometer (Model 16 – T0171, Controls Testing Equipment Ltd., UK) on a scale of 0 to 5 KgF, with five indicating the most force required to penetrate the soil. A JVC Everio digital camcorder on a tripod was placed 3m in front of the cage and used to record the trials.

Figure 2.3 Wire-mesh bottomless cage used for conducting foraging trials at Heddon Banks Farm, Heddon on the Wall, Northumberland, UK.
The cage was divided into section A (left) and B (right). The focal bird was released into section A and the two companions were released into section B.

Up to three focal birds were tested (in a random order) per day, with trials carried out between 8:30 and 15:00. Observations were not made in adverse weather such as rain or windy conditions or when the ground was covered in frost or snow. On average, each bird was used in a trial once every 10 (± 0.87) days, the number of rest days ranged between 1 and 28. No bird experienced more than one trial per day, as a focal or companion. Individual birds were transported to the field site in cotton bags. The focal bird was released into section A and the two companions were released into section B. The birds were left to forage for 10 min and the trials lasted 20min from the first probe by the focal bird. The behaviour of the focal bird was recorded by the digital video camera. If the focal bird failed to forage in the 10min following release into the cage the trial was abandoned. Birds were returned to their indoor cages after completing a trial.

Earthworm (Lumbricidae spp.) abundance was measured throughout the study period. The average beak length of an adult Starling was taken to be 25mm (Feare 1984). However, soil moisture has been linked to earthworm abundance in the top 5–10 cm of soils (Gerard 1967, Green *et al*. 2000, Peach *et al*. 2004a) and is likely to influence movement throughout the top layer of soil. In each block (top, middle and bottom) six soil samples were taken every 7 days, two soil samples from each treatment. A bulb planter (100mm x100mm) was used to take soil samples and a single soil core was taken from the centre of section B of the bottomless wire cage prior to the start of a trial. The penetration resistance of the soil and the number and wet mass (g) of earthworms contained within the core was recorded.

2.2.3 Data collection

It took 22 trial days to complete the study. From 25 birds, 20 hours and 58 minutes of digital video recordings were collected and analysed from 62 trials. Foraging behaviour data was extracted from the digital video recordings using an event recorder. Each recording was analysed frame by frame and a number of variables were recorded: video date, video duration, number of probes, number of roots and number of roots that resulted in prey captured (Table 2.1). The time of day, temperature, mean penetration resistance, mean sward height, area of bare soil and identity of prey items (when possible) were also recorded. Random data were cross-checked (CMR) and the recording of foraging variables was found to be consistent in all cases.

Variable	**Description**
Probe	Initial investigative stab into the soil
Root ‘gape’ [a]	Secondary stab into the soil followed by opening of the bill. The number of roots gives an indication of search intensity [b]
Prey capture	Secondary stab that results in prey capture

[a] Tinbergen 1981
[b] Devereux 2006

Table 2.1 Description of the foraging variables used in this study

We had two main aims. First, describe the effects of variation in soil moisture on the foraging behaviour of Starlings (e.g. number of probes made into the ground known as ‘rooting’). Soil surface penetrability is an indirect measure of soil moisture that provides an indication of the difficulty a bird might be expected to have when probing/rooting the soil to forage (Armstrong 2000). Typically, as soil moisture increases penetration resistance decreases (Francis *et al*. 1987, Tekeste *et al*. 2008). We expected the root rate to increase with decreasing soil penetration resistance (increased soil moisture), as found in studies of Common Snipe (Green 1988). Second, determine the effects of variations in soil moisture on the success rate i.e. the number of roots per trial that resulted in prey capture.

Starlings are predominantly ground foraging birds (Feare 1984), although they eat a wide range of foods (Tinbergen 1981). During the autumn/winter, earthworms increase in importance as a below-ground food source as their preferred prey Tipulidae larvae ‘disappear’ as a result of pupation and/or because the new population are too small to be detected (Feare 1984, McCracken 1990). Dry soils support fewer soil invertebrates (Milsom *et al*. 2000), as the top layer of soil dries earthworms descend deeper into the soil and become less available to foraging birds. Waterlogged soils, although easier to probe, have a lower abundance of invertebrate prey (McCracken *et al.* 1995, Ausden *et al*. 2001, Plum & Filser 2005). We expect accessibility to prey to increase with an increase in soil moisture, up to a point. Therefore, we predicted that Starlings will increase their root rate (A) with decreased penetration resistance (increased soil moisture) and that the number (B) and percentage(C) of roots that resulted in prey capture (accessibility) will change in a curvilinear fashion, increasing with increased soil moisture at first and then decreasing when the soil becomes waterlogged. These hypotheses were tested with Generalized Linear Mixed Models (GLMMs) as follows:

A. Total number of roots across each trial as the response variable with a poisson error structure and log link function.

Total number of roots = penetration resistance + treatment + block + temperature + Julian date + time of day + 1|bird ID + 1|observation

B. Total number of roots that resulted in prey capture as the response variable with a poisson error structure and log link function.

Total number of roots that resulted in prey capture = penetration resistance + treatment + block + temperature + Julian date + time of day 1|bird ID + 1|observation

C. Percentage of roots that resulted in prey capture as the response variable with a binomial error structure and a logit link function.

Percentage of roots that resulted in prey capture = penetration resistance + treatment + block + temperature + Julian date + time of day + 1|bird ID + 1|observation

All tests were performed using the program LMER in the lme4 package v.0.999375-42 (Bates *et al*. 2012) for R version 2.14.1 (R Development Core Team 2011). Models were generalized linear mixed-effects models (GLMMs) fit using the Laplace method for estimating parameters. Individual bird identity ‘Bird ID’ was modelled as a random effect (in the models above 1|bird ID represents the random effect) to acknowledge the hierarchical design of the dataset and to control for possible temporal and spatial effects. Type of treatment (1 – 3) and block (top, middle or bottom field) were included as fixed factors. In addition, we included an individual-level random effect (1|observation) to control for overdispersion (Bates *et al*. 2012). Squared terms were dropped from the models if on their own they did not explain a significant amount of deviance. Treatment and penetration resistance were positively correlated ($P < 0.001$), meaning that penetration resistance increased the longer the ground was protected from rainfall and water drainage. Julian date increased with days in captivity ($P < 0.001$) and time of day ($P < 0.001$), but was negatively correlated with temperature ($P < 0.001$), meaning that the Starlings spent longer in captivity, trials took place later in the day and temperature decreased as the study progressed. Julian date shared less information with temperature than days in captivity and therefore was used in the models as a proxy for the number of days birds had been held in captivity. To check the robustness of models A, B and C and whether the variables were interchangeable, GLMMs were run with the penetration resistance, treatment, Julian date, temperature and time of day independently (referred to as ‘penetration resistance without treatment’, ‘treatment without penetration resistance’, ‘temperature without Julian date’, ‘Julian date without temperature’ and ‘Julian date without time of day’ (Appendices 2.D, E and F).

2.3 Results

Sixty-two trials were completed; treatment 1(15), treatment 2(25), treatment 3 (22) (Appendix 2.A). Twenty-six were completed in the top block, twenty-three in the middle block and thirteen in the bottom block. Fifteen birds completed all three trials, seven completed two trials and three only completed one (Appendix 2.A). Birds did not complete the three trials if they began to show stereotypical behaviour, specifically somersaulting, when released into the outdoor cage.

Birds displaying stereotypical behaviour were immediately excluded from any further trials and released at the original capture site before the end of the study period. Mean sward height across the 62 trials was 3.49cm ± 0.05 (± se) and mean air temperature was 5.8°c ± 0.48 (± se). There was no significant difference in sward height (GLM: $F_{3, 2} = 2.13$, $P = 0.13$) or air temperature (GLM: $F_{3, 2} = 1.72$, $P = 0.19$) between treatments.

The mean penetration resistance across all plots was 1.82 ± 0.11 (± se). There was a significant difference in penetration resistance between treatments (GLM: $F_{3, 2} = 72.05$, $P < 0.001$), but not between blocks (GLM: $F_{3, 2} = 0.41$, $P = 0.67$) (Appendix 2.B). The mean probe rate was 323.3 ± 37.6 (± se), root rate was 22.9 ± 3.87 (± se), success rate was 3.07 ± 0.43 (± se), number of roots that were successful was 22 ± 1.87 (± se) and percentage of roots that were successful was 20.21 ± 2.76 (± se) per twenty minute trial. There were no significant differences in probe rate (GLM: $F_{3, 2} = 0.83$, $P = 0.44$), root rate (GLM: $F_{3, 2} = 1.15$, $P = 0.32$), success rate (GLM: $F_{3, 2} = 0.10$, $P = 0.91$) or percentage of roots that were successful (GLM: $F_{3, 2 =}$ 1.61, $P = 0.21$) between treatments.

The mean number of earthworms per sample (786 cm^3) was 0.82 ± 0.10 (± se) and the mean earthworm wet mass was 0.55 ± 0.07 (± se) (Appendix 2.C). There was no significant difference in the number (GLM: $F_{3, 2}= 2.27$, $P = 0.11$) or mass (GLM:$F_{3, 2}= 1.79$, $P = 0.17$) of earthworms between treatments.

A. After block had been taken into account, there was no effect of penetration resistance within treatments ($P = 0.46$) on the number of roots per trial (Appendix 2.D). Although penetration resistance and treatment were significantly positively correlated they were not interchangeable. There was no effect of treatment on rooting rate (ANOVA: $P =0.49$) (Appendix 2.D). The number of roots tended to increase as the soil initially dried out and then declined as the soil became too dry, along a scale from 0.5 KgF (waterlogged) to 3.5 KgF (Fig. 2.4), but the relationship with natural variation in penetration resistance was not significant (penetration resistance without treatment: $P = 0.80$). The total number of roots was not affected by temperature ($P = 0.11$), Julian date ($P = 0.29$) or time of day ($P = 0.09$). Julian date and time of day were significantly positively correlated, but were not interchangeable within the full model. However, Julian date and temperature were interchangeable. When Julian date was dropped from the model the positive relationship with temperature became significant (P = 0.01). When temperature was dropped from the model the negative relationship with Julian date became significant (P=0.02).

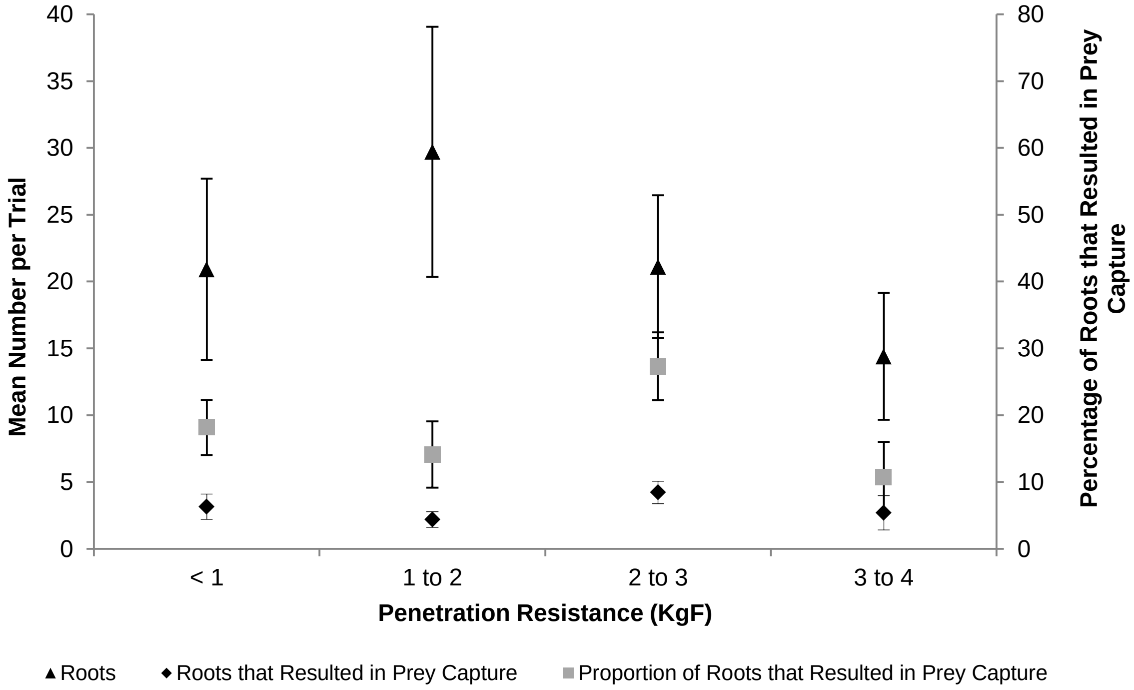

Figure 2.4 Mean number of roots (± se), roots that resulted in prey capture (± se) and percentage of roots that resulted in prey capture (± se) in relation to natural variations in penetration resistance at Heddon Banks Farm, Heddon on the Wall, Northumberland, UK. Penetration resistance is known to be strongly correlated with soil moisture (see methods). Neither the number of roots per trial (penetration resistance without treatment: P = 0.80) or the number of roots that resulted in prey capture (P = 0.10) were correlated with penetration resistance. However, the percentage of roots that resulted in prey capture were positively correlated with penetration resistance (P = 0.04).

B. After block had been taken into account, there was a significant positive relationship between the total number of roots per trial that resulted in prey capture and penetration resistance within treatments (P = 0.002) (Appendix 2.E). The amount of time the ground was protected from direct rainfall and water drainage (treatment) had a significant effect on the number of roots that resulted in prey capture overall (ANOVA: P = 0.03) (Appendix 2.E.a). As the soil became less waterlogged the number of roots that resulted in prey capture tended to increase, particularly on treatment 2 (Fig. 2.5). The number of roots that resulted in prey capture were highest on treatment 1(unprotected) (parameter estimate: 0.60), followed by treatment 2 (protected 14 - 21 days) (parameter estimate: -0.93) then 3 (protected for 28 days or more) (parameter estimate: -1.97). Although penetration resistance and treatment were significantly positively correlated they were not interchangeable. There was no independent effect between treatments (treatment without penetration resistance: Treatment 2: P = 0.91, Treatment 3: P = 0.91). The number of roots that resulted in prey capture tended to increase as the soil dried out and then declined as the soil became too dry, along a scale from 0.5 KgF (waterlogged) to 3.5 KgF (Fig 2.4), but the relationship with natural variation in penetration resistance was not significant (penetration resistance without treatment: P = 0.10). Temperature had no effect on the number of roots that resulted in prey capture (P = 0.29), neither did time of day (P = 0.12). The number of roots that resulted in prey capture decreased with advancing Julian date (days in captivity) (P = 0.004). Julian date and time of day were significantly positively correlated but were not interchangeable within the full model. Neither were Julian date and temperature.

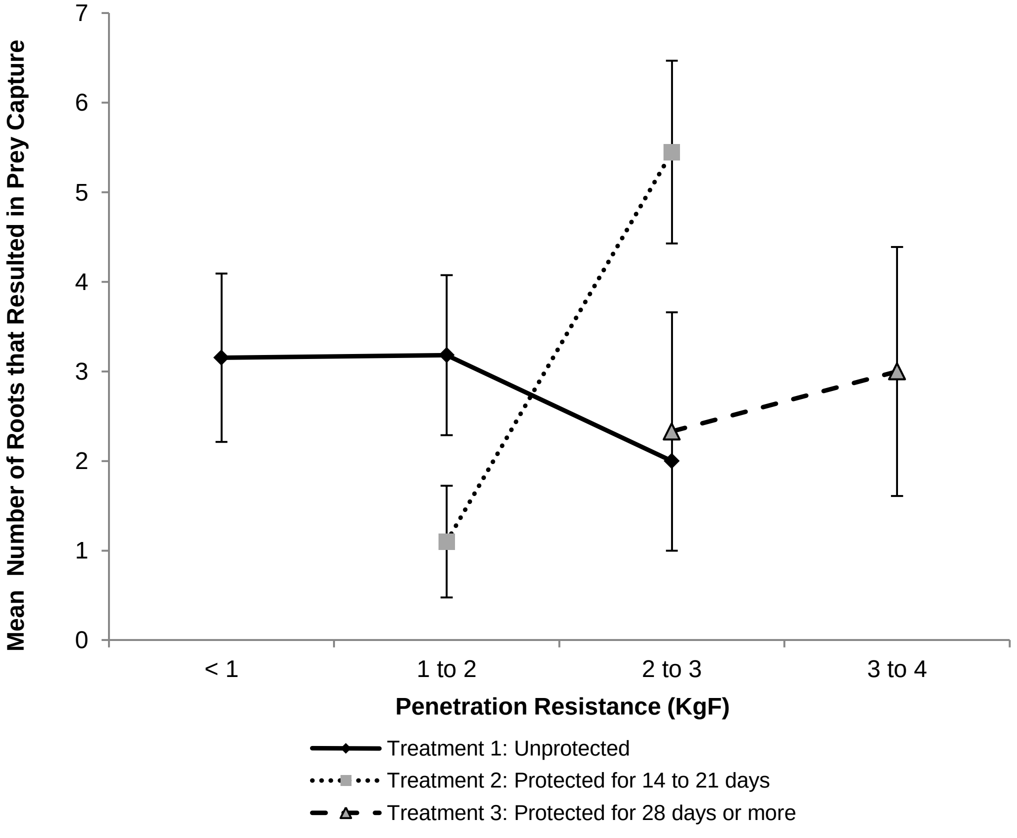

Figure 2.5 Mean number of roots per trial that resulted in prey capture (± se) in relation to penetration resistance within each type of treatment at Heddon Banks Farm, Northumberland, UK. There was a significant positive relationship between the total number of roots per trial that resulted in prey capture and penetration resistance within treatments (P = 0.002).

C. After block had been taken into account, there was a significant positive relationship between the percentage of roots per trial that resulted in prey capture and penetration resistance within treatments (P < 0.001) (Appendix 2.F). As the soil became less waterlogged the percentage of roots that resulted in prey capture tended to increase (Fig.2.6). The percentage of roots that resulted in prey capture were highest on treatment 2 (protected 14 – 21 days) (parameter estimate: -1.17), followed by treatment 1(unprotected) (parameter estimate: -1.34) then treatment 3 (protected for 28 days or more) (parameter estimate: -2.09). There was no independent effect between treatments (treatment without penetration resistance: Treatment 2: P = 0.95, Treatment 3: P = 0.67). Overall, the amount of time the ground was protected from direct rainfall and water drainage (treatment) did not have a significant effect on the number of roots that resulted in prey capture (ANOVA: P = 0.06). Natural variation in penetration resistance had an independent positive effect on the percentage of roots that resulted in prey capture (penetration resistance without treatment: P = 0.04). The relationship was curvilinear, increasing as the soil dried out and then decreasing as the soil became too dry, along a scale from 0.5 KgF (waterlogged) to 3.5 KgF (Fig 2.4), but not significantly so. Temperature had a significant negative relationship on the percentage of roots that resulted in prey capture (P = 0.002). The number of roots that resulted in prey capture decreased with advancing Julian date (days in captivity) (P = 0.01). There was no effect of time of day (P = 0.66). Julian date and time of day were significantly positively correlated but were not interchangeable within the full model. Julian date and temperature were interchangeable. When temperature was dropped from the model Julian date was no longer significant (P = 0.30).

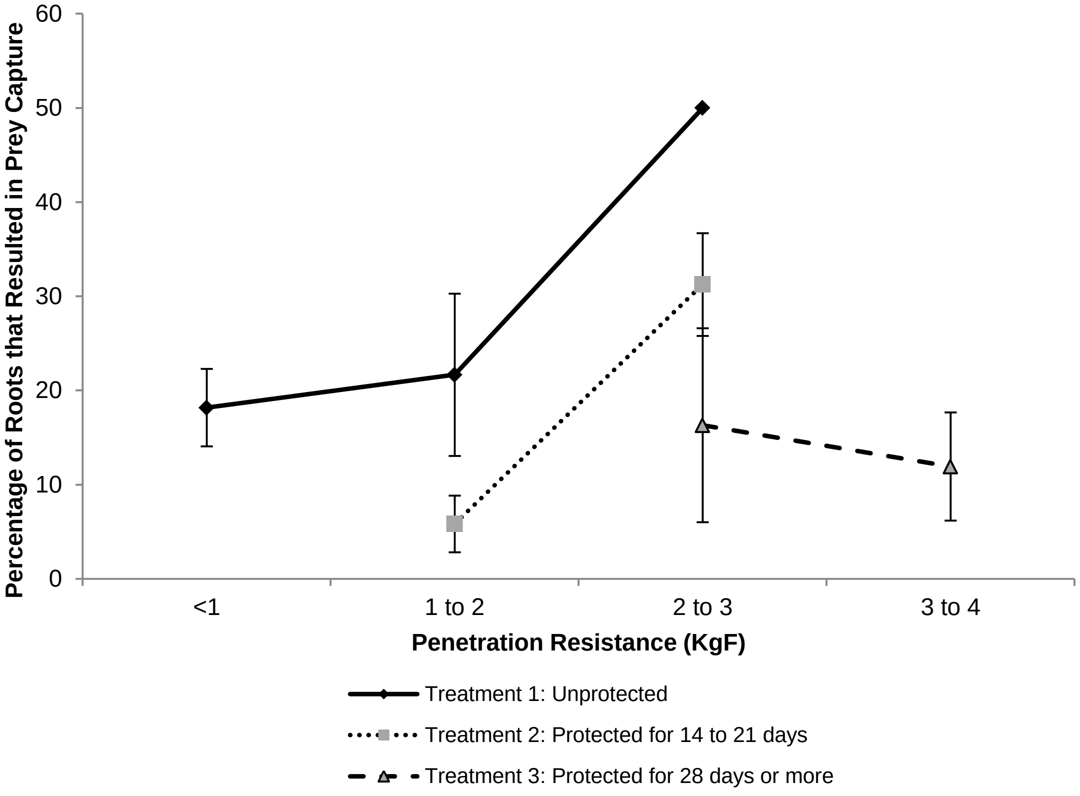

Figure 2.6 The percentage of roots per trial that resulted in prey capture (± se) in relation to penetration resistance within each type of treatment at Heddon Banks Farm, Northumberland, UK. There was a significant positive relationship between the total number of roots per trial that resulted in prey capture and penetration resistance within treatments ($P < 0.001$).

2.4 Discussion

Both the number and percentage of successful roots per trial increased as soil moisture decreased. This is counter to the a priori prediction that both would decrease with increased penetration resistance. This can be explained by the fact that the soil at the study site was saturated (average rainfall at the beginning of the trial period (http://www.metoffice.gov.uk/climate/uk/2010/november/averages.html) and a period of snow cover mid-way through resulted in the study area being waterlogged in parts and the soil being generally saturated), prior to undergoing treatments. For example, plots that had been protected from rainfall and water flow for more than 28 days recorded a maximum of 3.5 KgF, on a scale of 0 to 5 (5 being the driest / hardest). On most soils, increased soil moisture will increase accessibility to below-ground prey i.e. decrease penetration resistance (e.g. Green *et al*. 2000), however, prolonged water logging will reduce the abundance of invertebrate prey in the top soil (McCracken et al. 1995, Ausden et al. 2001, Plum & Filser 2005). Earthworm (Lumbricidae spp.) numbers and biomass at the study site demonstrate that this is likely to be the case at our study site (Fig. 2.7). Within treatments, the number and percentage of roots that are successful increased with penetration resistance. Specifically, the percentage of roots that were successful was highest on treatment plots that had intermediate penetration resistance of between 1 and 3 KgF (protected for 14-21 days).

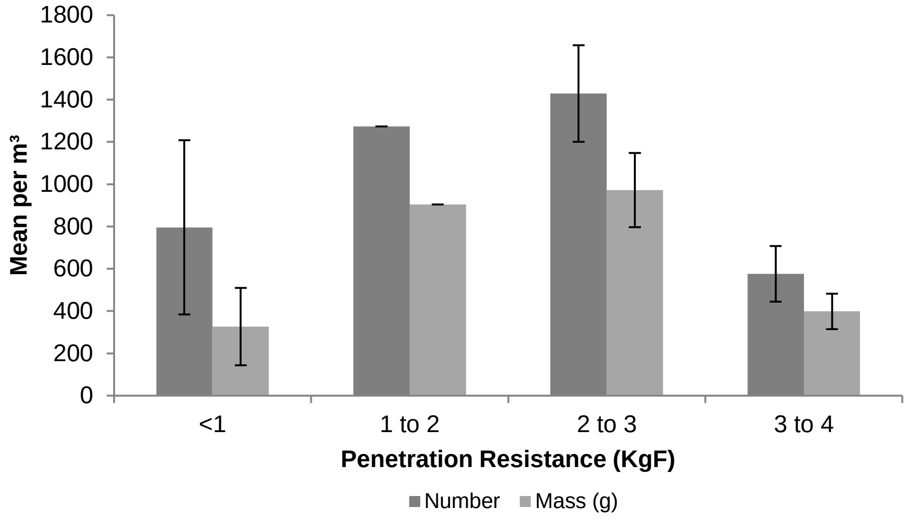

Figure 2.7 The mean number and mass of earthworms (Lumbricidae spp.) (± se) per m^3 at Heddon Banks Farm, Heddon on the Wall, Northumberland, UK in relation to soil penetration resistance.

In terms of natural variation in penetration resistance, the percentage of roots that were successful also increased as the soil dried to between 2 and 3 KgF and then declined as penetration resistance continued to increase. From these results, it can be concluded that optimal conditions for both invertebrate survival and foraging therefore require a trade-off between soil conditions (e.g. Smart *et al*. 2008). Prolonged water logging results in invertebrate prey that are accessible but at low abundance. Conversely, as the soil dries prey will become increasingly less accessible as (i) penetration resistance increases and (ii) earthworms descend deeper into the soil. At this study site, mean earthworm numbers and biomass declined at penetration resistance of between 3 and 4. Soils at these values are still relatively moist, on a scale of 0 to 5 KgF where five is the driest, and therefore a higher number and biomass would be expected. Trial plots with a penetration resistance between 3 and 4 were predominantly under treatment three and had been covered and protected from water flow for over 28 days but it is unclear why they had lower earthworm numbers and biomass.

During the autumn and winter, temperature had a significant positive effect on the number of roots per trial. There was no correlation between penetration resistance and temperature (P = 0.70) and therefore this may have been as a result of the effect of air temperature on the birds themselves. At low temperatures individuals will reduce energy expenditure (e.g. Grubb 1975) and maximize prey intake profitability (e.g. Pyke 1984, Stephens & Krebs 1986). At lower temperatures intake rate was higher. However, temperature increased over the course of the trials and therefore a decrease in success may be a result of time in captivity (e.g. Butler *et al*. 2006). It is important to note that because temperature was controlled for in models penetration resistance (soil moisture) explained a significant amount of deviance in addition to that explained by temperature.

Our results are consistent with the idea that soil moisture is an important factor limiting Starling foraging success. If we are to understand how soil moisture affects ground-probing birds more fully we also need to understand how conditions at different times of year affect foraging. It is probable that the curvilinear relationship between penetration resistance and foraging success described here will also be observed on drier soils in the spring/summer and may influence reproductive success. This information is critical to determining management of habitats to enhance below-ground prey abundance and accessibility (e.g. Devereux *et al*. 2004, Whittingham & Devereux 2008) and will be explored in the following chapters.

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Appendix 2.A

The identification numbers, sex and age of Starlings used in field trials. The identification numbers of the two companions birds used in each trial. The treatment block in which each focal bird carried out all three trials and the number of trials each bird completed.

Focal Bird ID	Sex	Age	Companions	Block	Treatments completed
1	M	A	25 & 8	2	2
2	M	A	17 & 18	3	1,2,3
3	M	A	4 & 21	1	1,2,3
4	M	A	11 & 24	1	1,2,3
5	M	A	13 & 23	1	1,2,3
6	M	A	7 & 3	2	1,2,3
7	F	A	16 & 25	1	1,2,3
8	F	A	26 & 18	1	2,3
9	M	FW	23 & 11	3	2,3
10	M	FW	11 & 14	1	2
11	M	A	20 & 13	2	2,3
12	F	FW	6 &14	1	1,2,3
13	F	FW	5 & 12	3	1,2,3
14	M	A	8 & 9	3	1,2,3
15	F	FW	1 & 17	2	2,3
16	F	FW	16 & 4	2	2
17	F	A	10 & 19	2	2,3
18	F	FW	20 & 15	2	1,2,3
19	F	A	12 & 5	3	2,3
20	F	A	3 & 22	1	2,3
21	M	FW	7 & 24	2	1,2,3
22	F	FW	6 & 9	1	1,2,3
23	M	FW	2 & 26	1	1,2,3
24	M	A	2 &15	2	1,2,3
25	F	A	22 & 10	2	1,2,3

M = Male, F= Female, A = Adult, FW = First winter

Appendix 2.B

Mean penetration resistance (Mean PR), probe rate, root rate, success rate and the percentage of successful roots per 20 minute trial in relation to treatment type and block. Treatment type refers to the amount of time a trial plot was protected from direct rainfall and water flow: (1) unprotected (2) 14 – 21 days and (3) 28 days or more. Block refers to sections of the study site: (1) top, (2) middle and (3) bottom. Results are quoted in the form of mean (± se).

	Treatment 1 (n = 15)	**Treatment 2 (n = 25)**	**Treatment 3 (n = 22)**
***Block 1* (n=26)**			
Mean PR	0.98 ± 0.13	1.92 ± 0.13	2.86 ± 0.16
Probe rate	218.80 ± 52	452.90 ± 92.5	297 ± 140
Root rate	14.18 ± 3.64	34.50 ± 10.60	12 ± 5.72
Success rate	2.10 ± 0.60	3.90 ± 1.22	2.25 ± 1.29
Percentage of roots that were successful	21.68 ± 9.11	18.08 ± 5.07	18.10 ± 11.30
Block 2 (n=23)			
Mean PR	0.92 ±0.11	1.93 ± 0.14	3 ± 0.15
Probe rate	459 ± 113	416 ± 125	239.60 ± 79
Root rate	34.30 ± 11.6	37 ± 19.2	15.20 ± 4.31
Success rate	5.10 ± 1.14	3.50 ± 1.32	4.40 ± 1.94
Percentage of roots that were successful	21.31 ± 3.35	24.10 ± 10.60	22.52 ± 9.35
Block 3 (n=13)			
Mean PR	1.43 ± 0.41	1.96 ± 0.40	2.93 ± 0.28
Probe rate	237 ± 105	119 ± 30	98 ± 76
Root rate	11.75 ± 7.42	3.75 ± 0.63	23 ± 23
Success rate	1 ± 0.41	1 ± 0.41	0.50 ± 0.5
Percentage of roots that were successful	18.20 ± 11.5	23.80 ± 10.30	2.17 ± 0
Overall			
Mean PR	1.06 ± 0.11	1.93 ± 0.10	2.91 ± 0.10
Probe rate	317.6 ± 56.5	378.6 ± 65.6	251.5 ± 78.5
Root rate	21.84 ± 5.31	29.82 ± 8.59	14.53 ± 4.06
Success rate	3.12 ± 0.62	3.23 ± 0.75	2.73 ± 0.96
Percentage of roots that were successful	20.98 ± 4.43	21.16 ± 4.42	17.11 ± 6.12

Appendix 2.C

The mean number and mass of earthworms (Lumbricidae spp.) per sample (783 cm^3) at Heddon Banks Farm, Heddon on the Wall, Northumberland, UK in relation to treatment type and block. Treatment type refers to the amount of time a trial plot was protected from direct rainfall and water drainage: (1) unprotected (2) 14 – 21 days and (3) 28 days or more. Block refers to sections of the study site: (1) top, (2) middle and (3) bottom. Results are quoted in the form of mean (± se).

	Treatment 1 (n = 36)	**Treatment 2 (n = 36)**	**Treatment 3 (n = 36)**
Block 1 **(n=36)**			
Mean number	0.73 ± 0.38	0.92 ± 0.40	0.17 ± 0.11
Mean biomass (g)	0.46 ± 0.25	0.58 ± 0.26	0.15 ± 10.10
Block 2 **(n=36)**			
Mean number	1.27 ± 0.30	0.50 ± 0.34	0.40 ± 0.16
Mean biomass (g)	0.86 ± 0.28	0.30 ± 0.21	0.35 ± 0.14
Block 3 **(n=36)**			
Mean number	0.79 ± 0.19	1.43 ± 0.31	0.93 ± 0.22
Mean biomass (g)	0.48 ± 0.10	1.04 ± 0.29	0.56 ± 0.12
Overall			
Mean number	0.92 ± 0.17	1.00 ± 0.21	0.53 ± 0.12
Mean biomass (g)	0.59 ± 0.12	0.68 ± 0.16	0.37 ± 0.07

Appendix 2.D

Results of a generalized linear mixed-effects model (GLMM) of the total number of times wild-caught captive Starlings root the ground for invertebrate prey during a twenty minute observation period (*n* = 62) as a function of the mean penetration resistance and ground treatment, accounting for variations in Julian date, temperature and time of day. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	***se***	**z**	***P***
Full model [a]				
Intercept	0.94	0.32	2.97	0.003
Penetration resistance	0.13	0.18	0.74	0.46
Treatment 2	-0.13	0.25	-0.50	0.62
Treatment 3	-0.48	0.43	-1.10	0.27
Block 2	0.22	0.18	1.25	0.21
Block 3	-0.48	0.28	-1.71	0.09
Temperature	0.17	0.10	1.61	0.11
Julian date	-0.14	0.13	-1.07	0.29
Time of day	0.17	0.10	1.70	0.09
Penetration resistance without treatment [b]				
Intercept	0.85	0.28	3.00	0.003
Penetration resistance	-0.03	0.10	-0.26	0.80
Block 2	0.22	0.18	1.24	0.22
Block 3	-0.43	0.28	-1.56	0.12
Temperature	0.19	0.10	1.88	0.06
Julian date	-0.13	0.13	-0.99	0.32
Time of day	0.14	0.10	1.46	0.14
Treatment without penetration resistance [c]				
Intercept	0.87	0.30	2.88	0.004
Treatment 2	-0.00	0.19	-0.01	0.99
Treatment 3	-0.21	0.24	-0.88	0.38
Block 2	0.21	0.18	1.19	0.23
Block 3	-0.45	0.28	-1.64	0.10
Temperature	0.19	0.10	1.94	0.05
Julian date	-0.10	0.12	-0.86	0.39
Time of day	0.16	0.10	1.59	0.11
Temperature without Julian date [d]				
Intercept	1.01	0.31	3.20	0.001
Penetration resistance	0.06	0.17	0.37	0.71
Treatment 2	-0.08	0.25	-0.30	0.76
Treatment 3	-0.42	0.44	-0.97	0.33
Block 2	0.19	0.18	1.08	0.28
Block 3	-0.51	0.28	-1.86	0.06
Temperature	0.23	0.09	2.63	0.01
Time of day	0.14	0.10	1.43	0.15
Julian date without temperature [e]				
Intercept	0.92	0.33	2.84	0.01
Penetration resistance	0.23	0.18	1.29	0.20
Treatment 2	-0.16	0.26	-0.63	0.53
Treatment 3	-0.62	0.44	-1.41	0.16
Block 2	0.26	0.18	1.41	0.16
Block 3	-0.40	0.28	-1.41	0.16
Julian date	-0.25	0.11	-2.25	0.02
Time of day	0.18	0.10	1.80	0.07

Julian date without time of day [f]				
Intercept	1.33	0.22	6.04	< 0.001
Penetration resistance	0.07	0.18	0.42	0.67
Treatment 2	-0.09	0.25	-0.37	0.71
Treatment 3	-0.32	0.42	-0.75	0.45
Block 2	0.22	0.18	1.23	0.22
Block 3	-0.42	0.28	-1.52	0.13
Temperature	0.18	0.11	1.72	0.09
Julian date	-0.07	0.12	-0.57	0.57

[a] AIC: 122.3, Random effects (variance): bird = 1.39 , individual level = 1.36.

[b] AIC: 119.7, Random effects (variance): bird = 0.00 , individual level = 0.14.

[c] AIC: 120.9, Random effects (variance): bird = 4.86 , individual level = 1.38..

[d] AIC: 121.5, Random effects (variance): bird = 0.02 , individual level = 0.14.

[e] AIC: 122.8, Random effects (variance): bird = 0.01 , individual level = 0.16.

[f] AIC: 123.2, Random effects (variance): bird = 0.02 , individual level = 0.01.

Appendix 2.E

Results of a generalized linear mixed-effects model (GLMM) of the total number of times wild-caught captive Starlings successfully root the ground for invertebrate prey during a twenty minute observation period (*n* = 62) as a function of the mean penetration resistance and ground treatment, accounting for variations in Julian date, temperature and time of day. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	***se***	**z**	***P***
Full model [a]				
Intercept	0.60	0.54	1.11	0.27
Penetration resistance	1.01	0.32	3.15	0.002
Treatment 2	-0.93	0.45	-2.06	0.04
Treatment 3	-1.97	0.74	-2.67	0.01
Block 2	0.75	0.30	2.47	0.01
Block 3	-1.14	0.54	-2.11	0.04
Temperature	-0.19	0.18	-1.05	0.29
Julian date	-0.69	0.24	-2.89	0.004
Time of day	0.26	0.17	1.56	0.12
Penetration resistance without treatment [b]				
Intercept	-0.03	0.51	-0.06	0.95
Penetration resistance	0.30	0.18	1.64	0.10
Block 2	0.73	0.32	2.28	0.02
Block 3	-0.83	0.53	-1.57	0.12
Temperature	-0.09	0.19	-0.48	0.63
Julian date	-0.60	0.24	-2.49	0.01
Time of day	0.18	0.17	1.06	0.29
Treatment without penetration resistance [c]				
Intercept	0.02	0.57	0.03	0.98
Treatment 2	-0.04	0.36	0.12	0.91
Treatment 3	-0.05	0.45	-0.12	0.91
Block 2	0.64	0.33	1.95	0.05
Block 3	-0.85	0.55	-1.55	0.12
Temperature	0.00	0.19	0.02	0.98
Julian date	-0.41	0.23	-1.79	0.07
Time of day	0.17	0.18	0.95	0.34
Temperature without Julian date [d]				
Intercept	0.95	0.57	1.67	0.09
Penetration resistance	0.64	0.31	2.06	0.04
Treatment 2	-0.67	0.47	-1.42	0.16
Treatment 3	-1.72	0.80	-2.16	0.03
Block 2	0.59	0.33	1.82	0.07
Block 3	-1.24	0.55	-2.27	0.02
Temperature	0.10	0.17	0.59	0.56
Time of day	0.10	0.17	0.55	0.58
Julian date without temperature [e]				
Intercept	0.59	0.54	1.08	0.28
Penetration resistance	0.90	0.31	2.96	0.003
Treatment 2	-0.89	0.46	-1.95	0.05
Treatment 3	-1.81	0.73	-2.50	0.01
Block 2	0.71	0.30	2.33	0.02
Block 3	-1.20	0.54	-2.23	0.03
Julian date	-0.57	0.21	-2.75	0.01
Time of day	0.25	0.17	1.48	0.14

Julian date without time of day [f]				
Intercept	1.20	0.37	3.23	0.001
Penetration resistance	0.91	0.31	2.90	0.004
Treatment 2	-0.87	0.46	-1.91	0.06
Treatment 3	-1.76	0.73	-2.41	0.02
Block 2	0.73	0.31	2.40	0.02
Block 3	-1.12	0.55	-2.04	0.04
Temperature	-0.17	0.18	-0.94	0.35
Julian date	-0.57	0.22	-2.54	0.01

[a] AIC: 154.17, Random effects (variance): bird = 0.00 , individual level = 0.69.

[b] AIC: 156.6, Random effects (variance): bird = 0.00 , individual level = 0.81.

[c] AIC: 161, Random effects (variance): bird = 0.01 , individual level = 0.90.

[d] AIC: 159.4, Random effects (variance): bird = 0.02 , individual level = 0.84.

[e] AIC: 153.6, Random effects (variance): bird = 0.01 , individual level = 0.72.

[f] AIC: 153.6, Random effects (variance): bird = 0.00 , individual level = 0.69.

Appendix 2.F

Results of a generalized linear mixed-effects model (GLMM) of the percentage of roots that result in prey capture by wild-caught captive Starlings during a twenty minute observation period (*n* = 62) as a function of the mean penetration resistance and ground treatment, accounting for variations in Julian date, temperature and time of day. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	***se***	**z**	***P***
Full model [a]				
Intercept	-1.34	0.66	-2.05	0.04
Penetration resistance	1.24	0.39	3.21	0.001
Treatment 2	-1.17	0.54	-2.15	0.03
Treatment 3	-2.09	0.90	-2.32	0.02
Block 2	0.45	0.36	1.25	0.21
Block 3	-0.05	0.62	-0.09	0.93
Temperature	-0.71	0.23	-3.09	0.002
Julian date	-0.79	0.31	-2.54	0.01
Time of day	0.09	0.20	0.43	0.66
Penetration resistance without treatment [b]				
Intercept	-2.02	0.63	-3.23	0.001
Penetration resistance	0.47	0.23	2.06	0.04
Block 2	0.41	0.38	1.07	0.29
Block 3	0.17	0.62	0.27	0.78
Temperature	-0.61	0.24	-2.54	0.01
Julian date	-0.67	0.31	-2.15	0.03
Time of day	0.01	0.21	0.05	0.96
Treatment without penetration resistance [c]				
Intercept	-2.00	0.71	-2.82	0.01
Treatment 2	0.03	0.44	0.06	0.95
Treatment 3	0.25	0.58	0.43	0.67
Block 2	0.32	0.41	0.80	0.42
Block 3	0.10	0.65	0.15	0.88
Temperature	-0.43	0.24	-1.79	0.07
Julian date	-0.40	0.30	-1.34	0.18
Time of day	-0.01	0.23	-0.03	0.98
Temperature without Julian date [d]				
Intercept	-1.07	0.69	-1.54	0.12
Penetration resistance	0.82	0.37	2.24	0.03
Treatment 2	-0.86	0.56	-1.55	0.12
Treatment 3	-1.91	0.97	-1.97	0.05
Block 2	0.36	0.39	0.94	0.35
Block 3	-0.25	0.62	-0.41	0.68
Temperature	-0.35	0.20	-1.72	0.09
Time of day	-0.03	0.22	-0.13	0.89
Julian date without temperature [e]				
Intercept	-1.60	0.74	-2.15	0.03
Penetration resistance	0.85	0.41	2.10	0.04
Treatment 2	-1.02	0.61	-1.67	0.09
Treatment 3	-1.70	1.01	-1.69	0.09
Block 2	0.41	0.42	0.99	0.32
Block 3	-0.39	0.66	-0.60	0.55
Julian date	-0.29	0.28	-1.04	0.30
Time of day	0.15	0.24	0.62	0.53

Julian date without time of day [f]				
Intercept	-1.13	0.43	-2.61	0.01
Penetration resistance	1.21	0.38	3.21	0.001
Treatment 2	-1.15	0.54	-2.13	0.03
Treatment 3	-2.01	0.88	-2.29	0.02
Block 2	0.43	0.35	1.22	0.22
Block 3	-0.03	0.61	-0.05	0.96
Temperature	-0.71	0.23	-3.13	0.002
Julian date	-0.75	0.30	-2.54	0.01

[a] AIC: 140, Random effects (variance): bird = 0.00 , individual level = 0.83.

[b] AIC: 156.6, Random effects (variance): bird = 0.00, individual level = 1.73.

[c] AIC: 147.3, Random effects (variance): bird = 0.00, individual level = 1.27.

[d] AIC: 144.4, Random effects (variance): bird = 0.00 , individual level = 1.09.

[e] AIC: 146.3, Random effects (variance): bird = 0.00 , individual level = 1.27.

[f] AIC: 146.3, Random effects (variance): bird = 0.00 , individual level = 0.83.

Chapter 3: Diet of Starling *Sturnus vulgaris* Nestlings on Farmland: the Importance of Tipulidae Larvae

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Short title: Starling nestling diet on farmland

Dr Claire Devereux and Dr Matthew Denny collected the data (foraging videos) between 2005 and 2008, prior to the start of this studentship. Caroline Rhymer extracted and analysed the data from the foraging videos and wrote the manuscript. Dr Mark J. Whittingham acted in a supervisory capacity.

3.0 Abstract

Capsule Tipulidae larvae are a key resource for adult Starlings provisioning their young on lowland farmland.

Aims **(i)** To describe Starling nestling diet on lowland farmland. **(ii)** To examine the effects of brood size variation and nestling age on Starling parental food provisioning.

Methods Over 4 years, we observed parental food provisioning at 42 nests across 4 sites on lowland farmland in Oxfordshire, UK using nest box video recorders.

Results Tipulidae larvae were the most frequent prey item recorded in provisioning loads (52%), the next most frequent were winged insects (11%), then Coleoptera larvae (6%), Lepidoptera larvae (5%) and Lumbricidae (5%), with 21% of prey unidentified. Estimates of prey lengths, dry mass and total energy content also confirmed that Tipulidae larvae were the key prey source. Generalized linear mixed-effects models showed that larger broods received fewer Tipulidae larvae per nestling per day and that the percentage of Tipulidae larvae in the diet did not vary with brood size or nestling age.

Conclusion Our results support the idea that Tipulidae larvae are the primary dietary item for nestling Starlings on lowland farmland.

3.1 Introduction

Around the world, a range of grassland bird species probe the ground to obtain their food (e.g. waders such as Snipe *Gallinago gallinago* (Smart *et al*. 2008) and Lapwing *Vanellus vanellus* (Wilson *et al.* 2005); corvids such as Chough *Pyrrhocorax pyrrhocorax* (McCracken *et al*. 1992) and passerines such as Song Thrush *Turdus philomelos* (Peach *et al*. 2004 a, b)). Therefore, informed management of their preferred habitats is crucial to successful land management targeting these species. For conservationists aiming to manage grasslands to benefit populations of a target species, it is key to understand the relative importance of below-ground prey versus above ground prey (e.g. is access to soil-dwelling prey important?). Here we focus on a target species, the Starling *Sturnus vulgaris*, that has undergone substantial declines in the UK (Robinson *et al*. 2002, 2005) and Europe (PECBMS 2010) since the 1980s. Currently, Starlings are Red-listed in the UK owing to their breeding population size experiencing a severe 'longer- term' decline since 1969 (i.e. since the first Birds of Conservation Concern review) and declining by more than 50% during the past 25 years (Gregory *et al*. 2002, 2004, Eaton *et al*. 2009). It is thought that this decline is a result of decreasing survival rates, particularly of first-year birds (Freeman *et al.* 2002, 2007).

The Starling is known to probe the ground for food and also to feed on a range of above ground resources (e.g. Dunnet 1955) and variations in diet composition reflect the distribution of invertebrates on a regional and local scale (Feare 1984). Despite regional differences, provisioning adults make use of Coleopteran and Lepidopteran larvae in most areas worldwide (e.g. Coleman 1977, Russell 1971). However, soil-dwelling larval prey is usually taken most frequently (Feare 1984). Of these soil-dwelling prey, Tipulidae larvae have been found to be important in Holland (Kluijver 1933, Westerterp 1973, Tinbergen & Drent 1980, Tinbergen 1981), England (Wright & Cuthill 1990a, b, Wright *et al*.1998) and Scotland (Dunnet 1955), but their relative importance to farmland nesting Starlings has received little attention. Furthermore, although a number of studies have looked at the importance of Tipulidae larvae (see above), most were carried out more than 30 years ago, before the widespread spraying of grass fields to control Diptera spp. (Campbell & Cooke 1997, Garthwaite *et al.* 1997).

This study firstly describes the prey items used to provision nestling Starlings from 2005 to 2008 across four study areas. We then explore how increased brood size and nestling age (both placing increasing stress on parents) alter provisioning patterns, in particular, the percentage and quantity of Tipulidae larvae in the diet. Given past studies, we expect Tipulidae larvae to be a key part of the diet (e.g. Dunnet 1955).

3.2 Methods

3.2.1 Experimental set-up

Data were collected at the John Krebs Field Station (51°47'N, 01°19’W), Wytham, Oxfordshire, UK. Historically, the area surrounding the study site was conventional mixed farmland that underwent routine pesticide spraying. Since 2001, the site is extensively managed organic grassland under the Upper Thames Tributaries Environmentally Sensitive Area Scheme and Countryside Stewardship. Four nest box colonies close to the Field Station were studied (Fig.3.1), one of which was an existing site and the others were established in winter 2004/5. From these 53 nestboxes, 42 Starling pairs in 33 nestboxes providing food for their young were observed over a 4-year period (2005-2008) (Appendix 3.A). Capturing and colour-ringing breeding adults in 2005 resulted in high desertion rates. Therefore, the identity of individual Starlings making each nesting attempt was unknown. Due to the potential for pseudoreplication (multiple records from individuals and/or pairs across years which we were unable to control for) we also examined patterns in each year individually (e.g. Table 3.1 split by year).

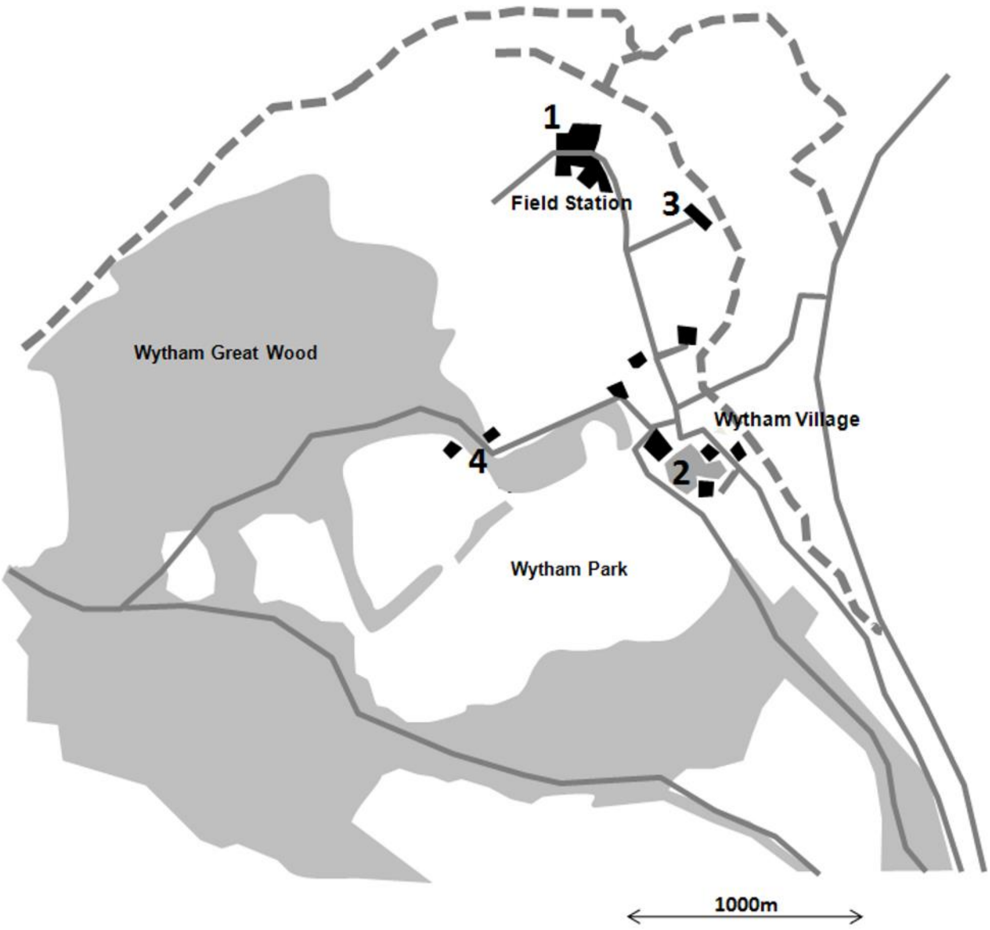

Figure 3.1 Location of Starling nestbox colonies 1, 2, 3 and 4 at John Krebs Field Station, Wytham, Oxfordshire, UK. Areas of grey represent woodland and areas of white represent farmland (predominantly pasture). Roads are shown as a solid dark grey line and waterways as dashed grey lines. Black shapes represent buildings.

	Tipulidae Larvae	**Lumbricidae**	**Winged Insects**	**Coleoptera Larvae**	**Lepidoptera Larvae**	**Unidentified**
2005 (n=5)	677 (49%)	93 (7%)	13 (1%)	79 (6%)	49 (4%)	460 (33%)
2006 (n=10)	680 (43%)	93 (6%)	35 (2%)	121 (8%)	185 (12%)	473 (29%)
2007 (n=17)	1788 (58%)	79 (3%)	689 (22%)	75 (2%)	116 (4%)	334 (11%)
2008 (n=10)	711 (52%)	89 (7%)	68 (5%)	140 (10%)	57 (4%)	295 (22%)
All years (n=42)	3856 (52%)	354 (5%)	805 (11%)	415 (6%)	407 (5%)	1562 (21%)

Table 3.1 Abundance of prey items delivered to nestlings by 42 Starling pairs at Wytham, Oxfordshire, UK. Data were collected from nestbox video cameras (see methods for further details). If a beak-load of food contained two Tipulidae larvae and one earthworm (Lumbricidae) then a count of two would be entered into the Tipulidae larvae column and one into the Lumbricidae column in the Table above. Tipulidae larvae were the key dietary prey item in each year of the study (n= number of nests).

Nestboxes were visited every 2-3 days from early April (pre-nest building) until mid-June and standard biometric and nest history data collected, with a particular note made of brood size and nestling age on days when filming occurred. Time-lapse video recorders were used to record the parental provisioning rates and the type and size of food items provided to nestlings in each nest. Each nest was videoed twice prior to fledging. The mean nestling age on the first day of observation was 11.05 ± 0.36, on the second observation day it was 14.81 ± 0.42. Cameras were fitted with motion-sensitive switches which recorded for a 10 second duration following any movement (continuous movement results in continuous recording). Cameras were attached to nestboxes after dusk, once foraging had ceased. They recorded for a 24 hour period and were powered by 12v battery. To aid with prey identification and estimation of prey size, a bird turner (clear tunnel) was permanently attached to the entrance of the nestboxes to ensure that birds always entered the nest facing in the direction of the camera.

3.2.2 Analysis

From the 42 nests, 807 hours of video recordings were collected and analysed from 84 video tape recordings. Random data were also cross-checked (30 video recordings) and both prey identification and size estimates were found to be consistent across observers in all cases. The total number of recording hours (shown in brackets) varied between years: 2005(118), 2006 (203), 2007 (262) and 2008 (224). On average, each nest was observed for 12.61 ± 0.45 hours during each 24 hour period. Each observation video was analysed frame by frame and a number of variables were recorded: video date and duration, the identity of prey items delivered (Chinery 2009), prey number (where possible to estimate) and the number of prey units in relation to adult beak length. The average adult beak length was taken to be 25mm (Feare 1984). A prey item that was the same length as the beak was therefore classed as measuring one unit.

3.2.3 Diet of nestling Starlings

Provisioning data recorded from nestbox foraging videos were analysed. From these data the percentage of the total number of prey items made up by each prey type delivered per nest per day was calculated. We also calculated the size and percentage of prey items, in relation to the total number of prey units in the nestling diet per nest per day. Neither is as good a score of information as biomass, but they give an indication of the key dietary requirements of the young. In addition, we were not able to record the abundance of the key dietary items in the surrounding areas to determine whether dietary items were taken at random or not.

Although it was not possible to measure biomass or energetic value of the prey items directly we were able to approximate these values: (i) volume of prey was expressed as the number of units of each prey item as a percentage of adult beak length and (ii) mean dry mass, mean kilojoules per item and mean ash content were calculated for each prey species from data in the literature (see Table 3.2).

Tipulidae Larvae Unknown species				**Lumbricidae** Unknown Species				**Winged Insects** Unknown species				**Coleoptera Larvae** Unknown species			**Lepidoptera Larvae** Unknown species				**Unidentified**
Mean Length (mm)	Mean Dry Mass (mg) (**a**)	Mean kJ per item (**e**)	Mean ash content (%) (**g**)	Mean Length (mm)	Mean Dry Mass (mg) (**b**)	Mean kJ per item (**e**)	Mean ash content (%) (**g**)	Mean Length (mm)	Mean Dry Mass (mg) (**c**)	Mean kJ per item (**e**)	Mean ash content (%) (**g**)	Mean Length (mm)	Mean Dry Mass (mg) (**d**)	Mean kJ per item (**f**)	Mean Length (mm)	Mean Dry Mass (mg) (**d**)	Mean kJ per item (**e**)	Mean ash content (%) (**g**)	Mean Length (mm)
27.53± 1.07	20.69 ± 0.72	0.39 ± 0.01	12	72.11 ± 8.01	51.3 ± 1.60	0.97± 0.03	19	11.29 ± 1.51	5.46 ± 1.37	0.12 ± 0.03	11	15.59± 1.17	0.01 ± 0.001	0.22 ± 0.03	30.39± 2.65	0.12 ± 0.02	2.75 ± 0.41	4	15.63± 1.17
58%	**77.87%**	**48%**	**73%**	**14%**	**17.76%**	**11%**	**11%**	**5%**	**4.31%**	**3%**	**13%**	**4%**	**0.01%**	**3%**	**7%**	**0.05%**	**35%**	**3%**	**12%**

(a) Dry mass calculations based on log M = log *a* + *b* * log X) i.e. (log M = log *-2.5495* + *2.5127* * log L) (Berg 2000). (b) Dry mass calculations based on ln(W) = 2.394 + 0.373 ln(L) (Collins 1992). (c) Dry mass calculations based on $W = aL^b$ i.e. $W = 0.1 \times L^{1.57}$ for the suborder Nematocera (Sabo *et al*. 2002). (d) Dry mass calculations based on $\ln Y = a + bX + b^1X^2$, specifically for Coleoptera larvae: $\ln Y = -13.497 + 0.90848X + -2.0853 \times 10^{-2} X^2$ and Lepidoptera larvae: $\ln Y = -9.273 + .36998X + -3.9949 \times 10^{-3} X^2$ (Sage 1982). (e) Dry energy content values based on Westerterp *et al*. 1982. (f) Dry energy content based on Norberg (1978). (g) Ash content based on Wright *et al.* (1998).

Table 3.2 Estimates of the volume and energy content of prey items delivered to nestling Starlings at Wytham, Oxfordshire, UK. Estimates were made from video observations and data from the literature for: (i) the mean length of prey items; (ii) the dry mass of the mean length of prey items; (iii) the mean kilojoules (kJ) per item based on the mean length from samples; and (iv) the mean ash content of each prey item (see footnote). The proportion of each prey item in relation to their abundance in the diet (see Table 3.1) is shown in BOLD (e.g.3856 Tipulidae larvae were identified with a mean length of 27.53 mm thus the total length of Tipulidae larvae was 106147mm). This method was also used to calculate the total length of all prey items and the percentage of the total of each category. Calculations were based only on those categories for which there were data.

3.2.4 Factors determining the adult provisioning rate of Tipulidae larvae

Because energy needs increase with nestling growth (Tinbergen 1981), the latter stage of the nestling period is the most energy demanding. This demand reaches a plateau for Starlings at around day 10 and then decreases from day 15 onwards (Dunnet 1955, Westerterp 1973, Tinbergen 1981). Similarly, the effort required to feed larger broods means that parents are less likely to provision their young with prey that are difficult to access compared to those with smaller broods (Wright *et al*. 1998). Therefore we explore the relationship between both nestling age and brood size and the (A) quantity and (B) percentage of Tipulidae larvae provisioned to Starling nestlings. These relationships were tested as follows:

A. Total number of Tipulidae larvae units per nestling per day as the response variable with a poisson error structure and a log link function.

Total number of Tipulidae larvae units per nestling per day = number of nestlings + number of nestlings^2 + mean nestling age + Julian date + 1|nest + 1|observation

B. Percentage of Tipulidae larvae units in the diet per nestling per day as the response variable with a binomial error structure and a logit link function.

Percentage of Tipulidae larvae units per nestling = number of nestlings + mean nestling age + Julian date + 1|nest + 1|observation

All tests were performed using the program LMER in the lme4 package v.0.999375-42 (Bates *et al*. 2012) for R version 2.14.1 (R Development Core Team 2011). Models were generalized linear mixed-effects models (GLMMs) fit using the Laplace method for estimating parameters. Individual nextbox identity 'nest' was modelled as a random effect to acknowledge the hierarchical design of the data set and to control for possible temporal and spatial effects. In addition, we included an individual-level random effect to control for overdispersion by accounting for individual-level variability (Bates *et al*. 2012). The number of nestlings squared term was dropped from models if on its own it did not explain a significant amount of deviance. The number of nestlings and mean nestling age were negatively correlated (P = 0.01) meaning that older clutches were likely to be smaller as a result of nestling deaths. Julian date was included in the model to take account of the variation in nestling period start date between years. Mean nestling age was not correlated with Julian date (P =

0.93); however, the number of nestlings in the nest on the day of observation was negatively correlated (P = 0.03) meaning that older clutches were likely to be smaller as a result of nestling deaths. To check the robustness of models A and B and whether these variables were interchangeable GLMMs were also run with the number of nestlings and mean nestling age independently (referred to as ‘nestling number without age’ and ‘age without nestling number’ in Appendix 3.C and 3.D) and with the number of nestlings and Julian date independently (referred to as ‘nestling number without Julian date’ and ‘Julian date without nestling number’ in Appendix 3.C and 3.D). Given that we did not know the identity of individual birds our models assume that each ‘nestbox’ was independent. Starlings are known to be highly site faithful (Coleman 1974) and therefore we also assumed all birds nesting in the same box in different years were the same individuals.

3.3 Results

3.3.1 Diet of nestling Starlings

In total 7401 separate prey items were recorded: 3856 Tipulidae larvae (52%), 354 earthworms (5%), 805 winged insects (11%), 415 beetle larvae (6%), 407 caterpillars (5%) and 1562 unidentified items (21%) (see Table 3.1). Nestling Starling diet consisted predominantly of Tipulidae larvae irrespective of whether that was expressed as the abundance of dietary items (see Table 3.1) or on a per-nest basis (Appendix 3.B).

The results supported our earlier findings that Tipulidae larvae were the dominant prey item by length (58%), dry mass (77%) and the total energy provided (48%). Tipulidae larvae were also the source of the highest percentage of indigestible material, i.e. ash content (73%), due to them representing the largest percentage of the diet in terms of dry mass (77%). Compared to Tipulidae larvae (12% per gram), earthworms contain a higher percentage (19% per gram) and winged insects a similar amount (11 % per gram) of ash; however, both make up a smaller percentage of the overall dry mass of the diet (see Table 3.2).

Overall our findings suggest that whether abundance, percentage or energetic content is measured Tipulidae larvae dominate the diet of farmland Starlings on our sites during the study period. However, as we did not measure availability of prey this might have determined this pattern. We thus explored further patterns within our data.

3.3.2 Factors determining the adult provisioning rate of Tipulidae larvae

A. There was a significant curvilinear relationship between the number of Tipulidae larvae units per nestling per day and the number of nestlings in the nest on the day of observation (number of nestlings^2: P = 0.01) (Appendix 3.C). The number of Tipulidae larvae units per nestling dropped initially as number of nestlings per nest increased and then levelled off (Fig. 3.2). Older nestlings tended to receive fewer Tipulidae larvae (Fig. 3.3), but the relationship was not significant (P = 0.07) (Appendix 3.C). There was a significant negative relationship with Julian date (P = 0.04). The results were supported by the independent GLMMs (Appendix 3.C). Although the number of nestlings and nestling age were significantly negatively correlated they were not interchangeable within the full model, neither were the number of nestlings and Julian date.

B. There was no significant relationship between the percentage of Tipulidae larvae per nestling per day and the number of nestlings (P = 0.68) (Fig. 3.2) (Appendix 3.D). As mean nestling age increased the percentage of Tipulidae larvae units in the diet decreased (Fig. 3.3), but the relationship was not significant (P = 0.07) (Appendix 3.D). Although the number of nestlings and nestling age were significantly negatively correlated they were not interchangeable within the full model. However, Julian date and the number of nestlings were interchangeable. When Julian date was dropped from the model the negative relationship between mean nestling age and the percentage of Tipulidae larvae units became significant (P = 0.03) (Appendix 3.D).

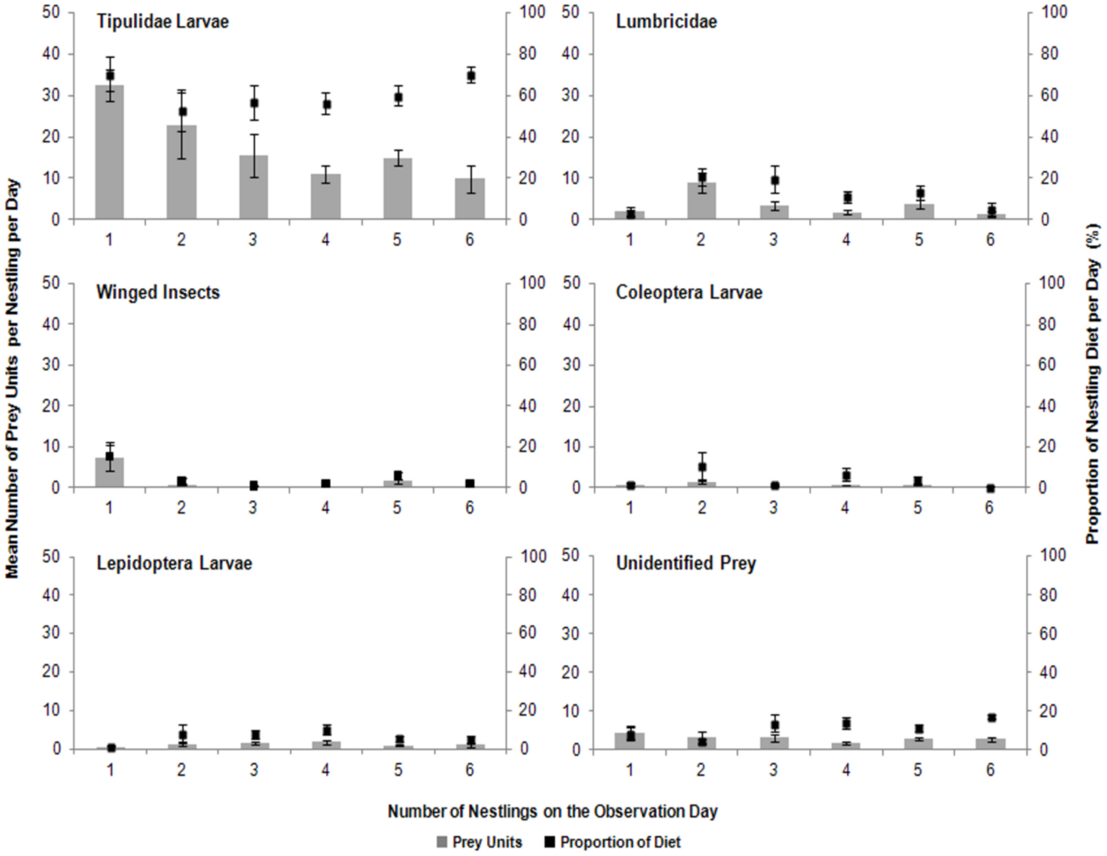

Figure 3.2 Mean number of prey units per individual (± se), measured against adult beak length in the daily diet of Starling nestlings at Wytham, Oxfordshire, UK in relation to the percentage of the overall diet and number of nestlings present in the nest on the day of observation. One prey unit is equivalent to one adult Starling beak length.

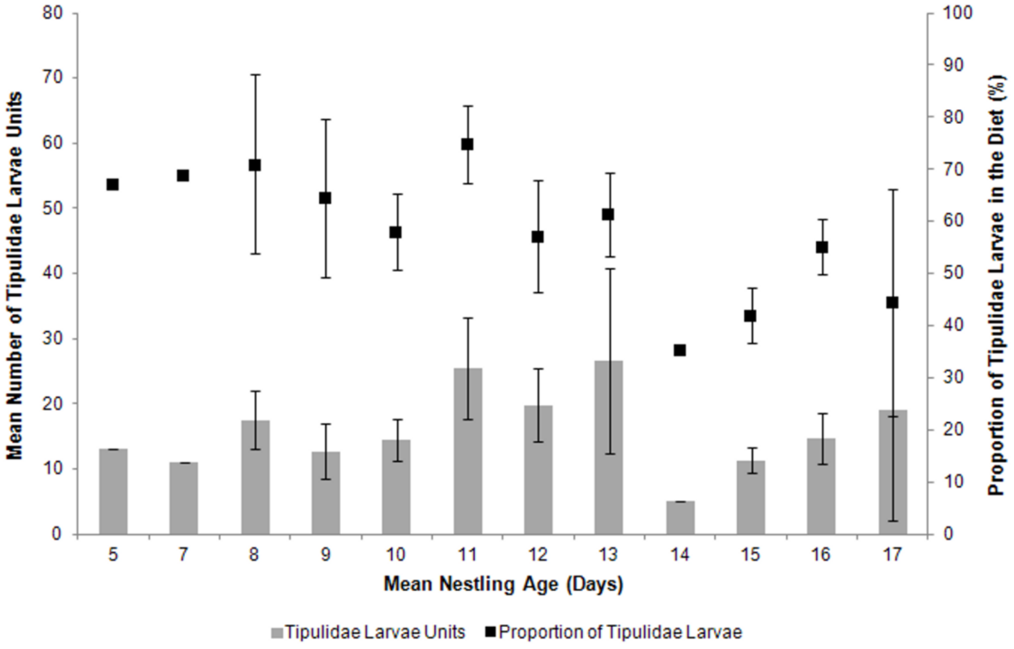

Figure 3.3 Mean percentage of Tipulidae larvae units per individual (± se) in the daily diet of Starling nestlings at Wytham, Oxfordshire, UK, in relation to total number of prey units (± se) and nestling age. One prey unit is equivalent to one adult Starling beak length. The percentage of Tipulidae larvae in the diet was not related to nestling age ($P = 0.07$).

3.4 Discussion

Tipulidae larvae consistently formed the majority (between 48-77%) of the nestling diet whether data were analysed as abundance, prey lengths, dry mass or energy (kJ) (Table 3.2). This concurred with a range of previous studies (e.g. Dunnet 1955, Tinbergen 1981, Westerterp 1982, Wright *et al*. 1998) and suggests that for our study populations below-ground prey, Tipulidae larvae in particular, form the majority of the diet of Starling nestlings. However, it should be noted that prey availability in our study areas was not measured and thus the patterns of provisioning we report may simply be a result of local prey abundance.

The total number of prey units per nestling was negatively correlated with brood size: more mouths means less food per nestling. The overall quantity of Tipulidae larvae per nestling declined with increasing brood size (Fig 3.2 – grey bars). Although nestling age had no effect on the number of Tipulidae larvae delivered to the nest, these results suggest that given the opportunity adults would increase the provisioning of Tipulidae larvae with nestling age, as found in other studies (Dunnet 1955, Westerterp 1973, Tinbergen 1981). However, it seems likely that they are constrained by brood size (Fig 3.4).

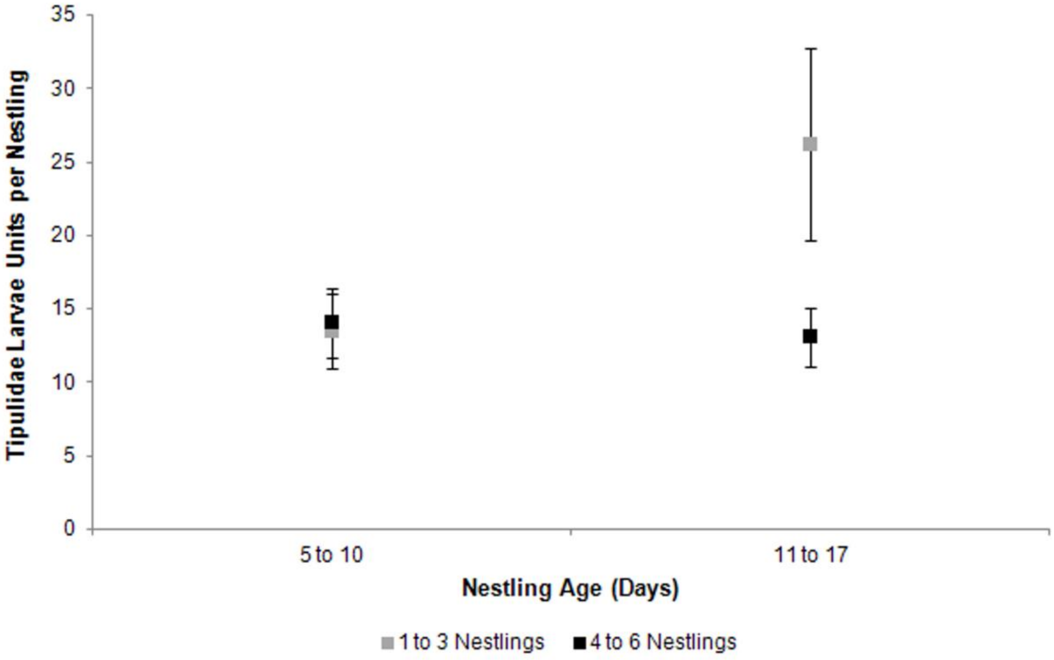

Figure 3.4 Mean number of Tipulidae larvae units per individual (± se) in the daily diet of Starling nestlings at Wytham, Oxfordshire, UK in relation to nestling age and brood size. One prey unit is equivalent to one adult Starling beak length. The number of nestlings and mean nestling age were negatively correlated (P = 0.01) meaning that older clutches were likely to be smaller as a result of nestling deaths. The data suggests that parents of older larger (4-6 nestlings) broods are unable to provision at the same rate per nestling as older smaller (1-3 nestlings) broods.

Despite being large prey items, earthworms (5%) and caterpillars (5%) represent a small percentage of the daily diet in terms of numbers. Earthworms are large and have a higher level of indigestible ash content than Tipulidae larvae, possibly due to the soil in their gut (Wright *et al.* 1998). An increase in the number of earthworms may result in a significant reduction in lipid content of the nestling diet and may explain why earthworms were not exploited more by parents with larger broods. Caterpillars are more digestible than Tipulidae larvae, due to their lower ash content (Wright *et al.*1998) and, given the choice, provisioning Starlings in the Netherlands selected caterpillars over Tipulidae larvae (Tinbergen 1981). Our study suggests an opposite pattern, although this may simply reflect the availability of caterpillars in the environment.

Our results are consistent with the idea that below-ground invertebrates form the key dietary items for Starling nestlings. However, it is unclear how environmental variation (e.g. in soil moisture, vegetation structure) alters provisioning rates and consequent reproductive performance in Starlings. This information is critical to determining management of habitats to enhance below-ground prey abundance and accessibility (e.g. Devereux *et al*. 2004; Whittingham & Devereux 2008).

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Appendix 3.A

The number of Starling nestboxes observed at each of four nest box colonies near Wytham, Oxfordshire, UK between 2005 and 2008. Not all nextboxes were occupied in any one year, out of a possible 53 monitored next boxes data were recorded in 42.

		Number of nest boxes occupied			
	Observation period	**Colony 1**	**Colony 2**	**Colony 3**	**Colony 4**
2005	**5th - 30th May**				5
2006	**9th - 20th May**	3		3	4
2007	**29th April - 7th May**	3	1	3	10
2008	**14th - 26th May**	1	1	3	5
Total number of available nestboxes		5	3	9	36

Appendix 3.B

Percentage of the total number of prey items in the Starling nestling diet per nest per day averaged for each year (mean value (± se) at Wytham, Oxfordshire, UK (n=number of nests).

	Tipulidae Larvae	**Lumbricidae**	**Winged insects**	**Coleoptera Larvae**	**Lepidoptera Larvae**	**Unidentified**
2005 (n=5)	45.98 ± 8.73	7.90 ± 2.79	1.59 ± 1.23	4.12 ± 1.73	4.65 ± 1.61	35.76 ± 5.99
2006 (n=10)	40.45 ± 4.04	6.50 ± 2.60	1.64 ± 0.60	8.33 ± 4.53	12.02 ± 2.41	31.06 ± 3.54
2007 (n=17)	59.31 ± 3.59	2.37 ± 0.48	18.80 ± 3.73	2.94 ± 0.98	4.70 ± 1.24	11.88 ± 1.33
2008 (n=10)	58.02 ± 6.47	8.73 ± 1.78	5.62 ± 1.23	9.70 ± 3.88	2.83 ± 0.93	15.00 ± 3.60
All years (n=42)	52.82 ± 2.87	5.86 ± 0.88	8.50 ± 1.58	6.47 ±1.66	5.82 ± 0.88	20.53 ± 1.99

Appendix 3.C

Results of a generalized linear mixed-effects model (GLMM) of the number of Tipulidae larvae units delivered by parents per nestling per day (*n* = 64) as a function of the number of nestlings present in the nest on the day of observation and mean nestling age, accounting for variations in Julian date between years. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	***se***	**df**	***z***	***P***
Full model [a]					
Intercept	6.25	1.07	1	5.84	< 0.001
Number of nestlings on the day of observation	- 1.43	0.47	1	- 3.07	0.002
Number of nestlings on the day of observation^2	0.16	0.06	1	2.57	0.01
Mean nestling age	- 0.07	0.04	1	- 1.79	0.07
Julian date	- 0.27	0.13	1	- 2.04	0.04
Nestling number without age [b]					
Intercept	5.01	0.85	1	5.90	< 0.001
Number of nestlings on the day of observation	- 1.32	0.47	1	- 2.79	0.005
Number of nestlings on the day of observation^2	0.16	0.07	1	2.43	0.01
Julian date	- 0.21	0.13	1	- 1.59	0.11
Age without nestling number [c]					
Intercept	2.77	0.49	1	5.62	< 0.001
Mean nestling age	- 0.027	0.04	1	- 0.70	0.48
Julian date	- 0.19	0.14	1	- 1.35	0.18
Nestling number without Julian date [d]					
Intercept	5.73	1.07	1	5.34	< 0.001
Number of nestlings on the day of observation	- 1.41	0.48	1	- 2.94	0.003
Number of nestlings on the day of observation^2	0.17	0.07	1	2.62	0.009
Mean nestling age	- 0.05	0.04	1	- 1.25	0.21
Julian date without nestling number [e]					
Intercept	2.77	0.49	1	5.62	< 0.001
Mean nestling age	- 0.03	0.04	1	- 0.70	0.48
Julian date	- 0.19	0.14	1	- 1.35	0.18

[a] AIC: 219, Random effects (variance): nest box = 0.07 , individual level = 0.54.
[b] AIC: 220, Random effects (variance): nest box = 0.10 , individual level = 0.54.
[c] AIC: 226, Random effects (variance): nest box = 0.17 , individual level = 0.59.
[d] AIC: 221, Random effects (variance): nest box= 0.08 , individual level = 0.57.
[e] AIC: 226, Random effects (variance): nest box= 0.17 , individual level = 0.59

Appendix 3.D

Results of a generalized linear mixed-effects model (GLMM) of the percentage of Tipulidae larvae units delivered by parents per nestling per day (*n* = 64) as a function of the number of nestlings present in the nest on the day of observation and mean nestling age, accounting for variations in Julian date between years. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	***se***	**df**	***z***	***P***
Full model [a]					
Intercept	1.55	1.02	1	1.53	0.13
Number of nestlings on the day of observation	- 0.06	0.15	1	- 0.41	0.68
Mean nestling age	- 0.08	0.05	1	- 1.81	0.07
Julian date	0.21	0.17	1	1.23	0.22
Nestling number without age [b]					
Intercept	0.03	0.58	1	0.06	0.95
Number of nestlings on the day of observation	0.06	0.13	1	0.46	0.64
Julian date	0.30	0.17	1	1.78	0.07
Age without nestling number [c]					
Intercept	1.20	0.53	1	2.25	0.02
Mean nestling age	- 0.08	0.04	1	- 1.82	0.07
Julian date	0.24	0.16	1	1.51	0.13
Nestling number without Julian date [d]					
Intercept	2.03	0.95	1	2.13	0.03
Number of nestlings on the day of observation	- 0.13	0.14	1	- 0.94	0.35
Mean nestling age	- 0.10	0.05	1	- 2.21	0.03
Julian date without nestling number [e]					
Intercept	1.20	0.53	1	2.25	0.02
Mean nestling age	- 0.08	0.04	1	-1.82	0.07
Julian date	0.24	0.16	1	1.51	0.13

[a] AIC: 183, Random effects (variance): nest box = 0.72 , individual level = 0.39.
[b] AIC: 184, Random effects (variance): nest box = 0.75 , individual level = 0.40.
[c] AIC: 181, Random effects (variance): nest box = 0.71 , individual level = 0.40.
[d] AIC: 182, Random effects (variance): nest box = 0.69 , individual level = 0.43.
[e] AIC: 181, Random effects (variance): nest box = 0.71 , individual level = 0.40.

Chapter 4: Soil Moisture alters Provisioning Rates of Nestling Starlings

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Short title: Soil moisture and Starling fledgling survival

Dr Claire Devereux and Dr Matthew Denny collected the data (foraging videos) between 2005 and 2008, prior to the start of this studentship. Caroline Rhymer extracted and analysed the data from the foraging videos and wrote the manuscript. Dr Mark J. Whittingham acted in a supervisory capacity.

4.0 Abstract

Capsule Decreased soil moisture can have a detrimental effect on reproductive success via changes in fledgling survival.

Aims **(i)** To describe Starling nestling diet on lowland farmland. **(ii)** To determine the effects of natural variation in soil moisture on diet composition **(iii)** To determine the effects of natural variation in soil moisture and Tipulidae larvae provisioning on fledging success

Methods Over 4 years, we observed parental food provisioning at 24 nests on lowland farmland in Oxfordshire, UK using nestbox video recorders. Mean daily volumetric soil moisture content surrounding the nest sites was recorded and related to Tipulidae larvae provisioning and fledgling survival.

Results Tipulidae larvae were the most frequent prey item recorded in provisioning loads (51%). Estimates of prey lengths, dry mass and total energy content also confirmed that Tipulidae larvae were the key prey source. Generalized linear mixed-effects models showed a curvilinear relationship between the number and percentage of Tipulidae larvae in the diet per nestling per day and volumetric soil moisture content. Both initially decreased as volumetric moisture content increased between 20% and 30% and then increased as the volumetric soil moisture content increased above 35%. Tipulidae larvae provisioning was not related to fledgling success. However, fledgling success responded in a similar manner as Tipulidae larvae provisioning to variations in volumetric soil moisture content.

Conclusion Our results support the idea that below-ground invertebrates form the key dietary items for Starling nestlings and that decreased soil moisture can have a detrimental effect on reproductive success via changes in fledgling survival.

4.1 Introduction

In lowland England, summer droughts are becoming more common and climate models predict further increases in their frequency due to a combination of decreased summer rainfall and rising temperatures, especially in the southeast of the country (Hulme *et al*. 2002). Agricultural and recent semi-natural grasslands appear to be particularly sensitive to drought (Morecroft *et al*. 2002). A number of species that probe the ground for invertebrate prey are associated with lowland grasslands during the breeding season (Starling *Sturnus vulgaris* L. - Feare 1984, Chough *Pyrrhocorax pyrrhocorax* L.- McCracken *et al.* 1992, Lapwing *Vanellus vanellus* L. and Redshank *Tringa totanus* L. - Ausden *et al*. 2003, Lapwing - Baines 1990, Golden Plover *Pluvialis apricaria* L. - Pearce-Higgins & Yalden 2003, Snipe *Gallinago gallinago* L.- Green 1986) and informed land management of their preferred habitats is crucial to successful targeting of these species. For conservationists aiming to manage grasslands to benefit populations of ground-probing bird species it is key to understand the significance of an increase in the frequency of drought conditions during the breeding season.

Here we focus on a target species, the Starling, that has undergone substantial declines in the UK (Robinson *et al*. 2002, 2005) and Europe (PECBMS 2010) since the 1980s. Currently, Starlings are Red-listed in the UK owing to their breeding population size experiencing a severe ‘longer- term’ decline since 1969 (i.e. since the first Birds of Conservation Concern review) and declining by more than 50% during the past 25 years (Gregory *et al*.2002, 2004; Eaton *et al*. 2009). It is thought that this decline is a result of decreasing survival rates, particularly of first-year birds (Freeman *et al.* 2002, 2007).

During the breeding season, soil dwelling Tipulidae spp. larvae (crane-fly larvae) have been found to be the dominant prey item in the diet of Starling nestlings (Dunnet 1955, Tinbergen 1981, Westerterp 1982, Wright *et al*. 1998, Rhymer *et al*. 2012 (Chapter 3)). Food is known to be a limiting factor to reproductive success (Martin 1987) and in a number of altricial species, including the Starling (Westerterp *et al*. 1982), experimental studies have shown a consistent increase in the size and survival of the young when brood sizes are artificially reduced or food supply is increased. On most soils, the lowering of soil moisture levels reduces soil penetrability making the ground too hard for surface probing (e.g. Green *et al*. 1990). Therefore, access to below-ground prey, such as Tipulidae larvae, may be restricted during periods of drought lowering the reproductive success of the species. In Europe, Tipulidae have been identified as an important dietary item for farmland birds (Holland *et al*. 2006), with up to 50% of lowland birds consuming Tipulidae larvae in the breeding season (Wilson *et al*. 1999). Thus, the mechanisms by which soil moisture affects reproductive success in the Starling may also apply to a range of species.

This study uses soil moisture as a proxy for access to below-ground prey and has two main aims. First, identify the relationship between Tipulidae larvae provisioning rates and soil moisture. Second, examine the relationship between Tipulidae larvae provisioning, soil moisture and fledging success.

4.2 Methods

4.2.1 Experimental set-up

Data were collected at the Sawmill colony next to Wytham Woods, Oxfordshire, UK (51°46'N, 01°19’W). From 36 nestboxes located around the colony, 21 Starling pairs in 24 nestboxes providing food for their young were observed over a 4-year period (2005-2008). Capturing and colour ringing breeding adults in 2005 resulted in high desertion rates. Therefore the identity of individual Starlings making each nesting attempt was unknown. Due to the potential for pseudoreplication (multiple records from individuals and/or pairs across years which we were unable to control for) we also examined patterns in each year individually (e.g. Table 4.1 split by year).

	Tipulidae larvae	**Lumbricidae**	**Winged insects**	**Coleoptera larvae**	**Lepidoptera larvae**	**Unidentified**
2005 (n=5)	677 (49%)	93 (7%)	13 (1%)	79 (6%)	49 (4%)	460 (33%)
2006 (n=4)	283 (43%)	5 (1%)	24 (4%)	9 (1%)	114 (17%)	221 (34%)
2007 (n=10)	1162 (61%)	45 (2%)	394 (21%)	47 (3%)	75 (4%)	172 (9%)
2008 (n=5)	238 (34%)	46 (7%)	38 (5%)	125 (18%)	51 (7%)	209 (29%)
All years (n=24)	2360 (51%)	189 (4%)	469 (10%)	260 (6%)	289 (6%)	1062 (23%)

Table 4.1 Abundance of prey items delivered to nestlings by 21 Starling pairs at the Sawmill colony, Wytham, Oxfordshire, UK over the duration of one day. Data were collected from nestbox video cameras (see methods for further details). If a beak-load of food contained two Tipulidae larvae and one earthworm (Lumbricidae) then a count of two would be entered into the Tipulidae larvae column and one into the Lumbricidae column in the Table. Tipulidae larvae were clearly the key dietary prey item in each year of the study. (n = number of nests).

Nestboxes were visited every 2-3 days from early April (pre-nest building) until mid-June and standard biometric and nest history data collected (CLD and M.J.H.D). Time-lapse video recorders were used to record the parental provisioning rates and the type and size of food items provided to nestlings in each nest. Each nest was videoed twice prior to fledging (mean nestling age on the first day of observation was 10.96 ± 0.47 and on the second observation day it was 14.50 ± 0.60). Cameras were fitted with motion-sensitive switches which recorded for a 10 second duration following any movement (continuous movement results in continuous recording). Cameras were attached to nestboxes after dusk once foraging had ceased. They recorded for a 24 hour period and were powered by12v battery. To aid with prey identification and estimation of prey size, a bird turner (clear tunnel) was permanently attached to the entrance of the nestboxes to ensure that birds always entered the nest facing in the direction of the camera.

The Sawmill colony (Colony 4, Appendix 3.A, Chapter 3) was chosen due to it having the closest proximity (approximately 650m) to the automatic weather station (AWS) located at John Krebs Field Station. Soil moisture was recorded (throughout our study) at the AWS using a ML2 ThetaProbe (AT Delta-T Devices Ltd, Cambridge, UK), which measures volumetric soil moisture content by responding to changes in the apparent dielectric constant (speed of electromagnetic waves) of moist soil, for a volume of 300mm^3 (60mm long x 26.5mm diameter), with ± 1% accuracy over the range of 0 to 60%. Volumetric soil moisture content is the ratio between the volume of water present and the total volume of the soil sample and is expressed as a percentage (% volume) (Delta-T Devices Ltd. 1999). The probe is positioned at a depth of 20cm and the mean values used represent a mean of the hourly recordings of 5 second samples taken over each 24hour period. Data were supplied by the UK Environmental Change Network, Centre for Ecology and Hydrology, Wallingford, UK.

4.2.2 Analysis

Data from the 24 nests at the Sawmill colony were used to examine (1) the diet of nestling Starlings and (2) the relationship between variations in volumetric soil moisture content, Tipulidae larvae provisioning and fledgling success. Although the diet of Starling nestlings has already been described in an earlier chapter (Chapter 3 - for all colonies combined) it is important to check that the patterns found overall were also found at the Sawmill colony. From the 24 nests, 473 hours of video recordings were collected and analysed from 36 video tape recordings (CMR). Random data were also cross-checked (MJW) (15 video recordings) and both prey identification and size estimates were found to be consistent. The total number of recording hours (shown in brackets) varied between years: 2005(118), 2006 (85), 2007 (148) and 2008 (122). On average, each nest was observed for 13.14 ± 0.64 hours during each 24 hour period. Each observation video was analysed frame by frame by a single observer (CMR) and a number of variables were recorded: video date and duration, the identity of prey items delivered (Chinery 2009), prey number (where possible to estimate) and the number of prey units in relation to adult beak length. The average adult beak length was taken to be 25mm (Feare 1984). A prey item that was the same length as the beak was therefore classed as measuring one unit.

We had three main aims. First, describe the diet of Starling nestlings at the Sawmill colony. Tipulidae larvae are the key part of the diet for all four colonies combined (see Chapter 3, Table 3.1) and therefore it was expected to be the same for the Sawmill colony. Second, determine the effects of natural variation in soil moisture on diet composition, in particular, the percentage and quantity of Tipulidae larvae in the diet. Third, determine the effects of natural variation in soil moisture and Tipulidae larvae provisioning on fledging success.

4.2.3 Diet of nestling Starlings at the Sawmill colony

Provisioning data recorded from the 36 nestbox foraging videos (from 24 nesting attempts) were analysed by a single observer (CMR). From these data the percentage of the total number of prey items made up by each prey type delivered per nest per day was calculated. The size and percentage of prey items was also calculated, in relation to the total number of prey units in the nestling diet per nest per day. Neither is as good a score of information as biomass, but they give an indication of the key dietary requirements of the young. In addition, we were not able to record the abundance of the key dietary items in the surrounding areas to determine whether dietary items were taken at random or not.

Although it was not possible to measure biomass or energetic value of the prey items directly we were able to approximate these values: (i) volume of prey was expressed as the number of units of each prey item as a percentage of adult beak length and (ii) mean dry mass, mean kilojoules per item and mean ash content were calculated for each prey species from data in the literature (see Table 3.2, Chapter 3).

4.2.4 Soil moisture and Tipulidae larvae provisioning at Sawmill colony

Tipulidae larvae have been shown to be the preferred prey item of provisioning adult Starlings at the study site. Because moist soils have a greater surface penetrability (Gerard 1967, Green *et al.* 2000) and support larger densities of soil invertebrates than dry soils (Milsom *et al.* 2000), it is probable that variations in soil moisture affect adult provisioning rates of Tipuldae larvae, as well as other below-ground prey. Therefore we explored the relationship between volumetric soil moisture content and the (A) quantity and (B) percentage of Tipulidae larvae provisioned to Starling nestlings. These relationships were tested using Generalized Linear Mixed Models (GLMMs) (where the random effect is indicated by 1|x where x is the random effect) as follows:

A. Total number of Tipulidae larvae units per nestling per day as the response variable with a poisson error structure and a log link function.

Total number of Tipulidae larvae units per nestling per day = mean volumetric soil moisture content on the day of observation + mean volumetric soil moisture content on the day of observation ^{2} + number of nestlings + number of nestlings^2 + Julian date + 1|nest + 1|observation

B. Percentage of Tipulidae larvae units in the diet per nestling per day as the response variable with a binomial error structure and a logit link function.

Percentage of Tipulidae larvae units per nestling = mean volumetric soil moisture content on the day of observation + mean volumetric soil moisture content on the day of observation ^{2} + mean nestling age + 1|nest + 1|observation

4.2.5 Soil moisture and Starling fledgling success at Sawmill colony

Since food is known to be a limiting factor to reproductive success (Martin 1987) we explore the relationship between soil moisture and Tipulidae larvae provisioning and fledgling success at the Sawmill colony. These relationships were tested as follows:

C. Number of nestlings that fledged as the response variable with a poisson error structure and a log link function.

Number of nestlings that fledged = number of nestlings that hatched + mean temperature over the nestling period + mean number of Tipulidae larvae units per nestling per day on the day of observation + mean volumetric soil moisture content over the nestling period+ mean volumetric soil moisture content over the nestling period ^{2} + 1|nest

All tests were performed using the program LMER in the lme4 package v.0.999375-42 (Bates *et al*. 2012) for R version 2.14.1 (R Development Core Team 2011). Generalized linear mixed-effects models were fitted using the Laplace method for estimating parameters. Individual nestbox identity ‘nest’ was modelled as a random effect to acknowledge the hierarchical design of the dataset and to control for possible temporal and spatial effects. In models A and B, we included an individual-level random effect to control for overdispersion, by accounting for individual variability (Bates *et al*. 2012). Squared terms were dropped from models if on their own they did not explain a significant amount of deviance. Given that we did not know the identity of individual birds our models assume that each ‘nest’ was independent. Starlings are known to be highly site faithful (Coleman 1974) and therefore we also assumed all birds nesting in the same box in different years were the same individuals.

For model A, number of nestlings, number of nestlings^2 and Julian date were included as they are known to influence the provisioning of Tipulidae larvae (see section 3.3.2, Chapter 3). Julian date and volumetric soil moisture content were negatively correlated ($P = 0.02$), meaning that soil moisture decreased as the nestling period progressed. To check the robustness of model A and whether these variables were interchangeable GLMMs were also run with volumetric soil moisture content and Julian date independently (referred to as ‘soil moisture without date’ and ‘date without soil moisture’ in Appendix4.B). In model C, the number of nestlings that hatched and the mean number of Tipulidae larvae units per nestling per day were positively correlated ($P = 0.01$), meaning that in terms of initial brood size individual nestlings in larger broods received more Tipulidae larvae units per day than those in smaller broods. To check the robustness of model C and whether these variables were interchangeable GLMMs were also run with the number of nestlings that fledged and Tipulidae larvae units per nestling per day independently (referred to as ‘hatch without Tipulidae larvae units’ and ‘Tipulidae larvae units without hatch’ in Appendix 4.D and 4.E). In models C, mean temperature over the nestling period was included as it is known that ambient temperature influences fledging success (e.g. Dawson *et al.* 2005).

4.3 Results

4.3.1 Diet of nestling Starlings at the Sawmill colony

In total 4629 separate prey items were recorded at the Sawmill colony: 2360 Tipulidae larvae (51%), 189 earthworms (4%), 469 winged insects (10%), 260 beetle larvae (6%), 289 caterpillars (6%) and 1062 unidentified items (23%) (Table 4.1). As previously observed at all nest colonies, nestling Starling diet consisted predominantly of Tipulidae larvae irrespective of whether that was expressed as the abundance of dietary items (Table 4.1) or on a per nest basis (Appendix 4.A). At the Sawmill colony, Tipulidae larvae were also the dominant prey item by mean dry mass (76%), length (57%) and energy content (46%) (see Table 3.2, Chapter 3 for calculations).

Overall our findings suggest that whether abundance, percentage or energetic content is measured Tipulidae larvae dominate the diet of farmland Starlings at the Sawmill colony during the study period. However, as we did not measure prey availability this alone might have determined this pattern. Nevertheless the predominance of the main dietary items were below ground and thus we felt it reasonable to explore how soil conditions influenced nestling provisioning.

4.3.2 Soil moisture and Tipulidae larvae provisioning at Sawmill colony

A. Volumetric soil water content (%) ranged from 21.43 to 40.71 (Table 4.2). After the number of nestlings and Julian date had been taken into account, there was a significant curvilinear relationship between the number of Tipulidae larvae units per nestling per day and the volumetric soil moisture content at the Sawmill colony on the day of observation (volumetric soil moisture content: P = 0.02, volumetric soil moisture content ^{2}: P = 0.03) (Appendix 4.B). The number of Tipulidae larvae units per nestling initially dropped as the soil increased in volumetric moisture content (between 20 and 35%) then increased as the volumetric soil moisture content increased to above 35% (Fig. 4.1). The results were supported by the independent GLMMs (Appendix 4.B). Although the volumetric soil moisture content and Julian date were significantly negatively correlated they were not interchangeable within the full model.

	Mean Volumetric Soil Moisture Content (%) over Nestling Period	Mean Volumetric Soil Moisture Content (%) at time of Observation 1	Mean Volumetric Soil Moisture Content (%) at time of Observation 2	Mean Daily Temperature (°c)	Mean Daily Rainfall (mm)	Mean Daily Surface Wetness (minutes per hr)
2005	32.81 ± 1.01	33.09 ± 1.44	31.35 ± 2.21	10.85 ± 0.17	0.05 ± 0.01	28.95 ± 1.13
2006	38.02 ± 0.06	38.27 ± 0.82	37.65 ± 0.13	13.21 ± 0.19	0.08 ± 0.02	32.67 ± 1.66
2007	23.90 ± 0.15	22.83 ± 0.28	22.08 ± 0.65	11.17 ± 0.26	0.07 ± 0.03	19.78 ± 1.86
2008	30.96 ± 0.09	30.64 ± 0.23	30.08 ± 0.85	10.80 ± 0.18	0.22 ± 0.06	29.53 ± 1.58
All years	30.19 ± 0.88	29.16 ± 1.26	30.32 ± 1.49	11.36 ± 0.10	0.10 ± 0.01	28.44 ± 0.75

Table 4.2 Mean volumetric soil moisture content (%) (± se) over the entire nestling period and on the day of observation at the Sawmill colony, Wytham, Oxfordshire, UK.

B. There was a significant curvilinear relationship between the percentage of Tipulidae larvae units per nestling per day and the volumetric soil moisture content at the Sawmill colony on the day of observation (volumetric soil moisture content: $P = 0.002$, volumetric soil moisture content ^{2}: $P = 0.003$) (Appendix 4.C). The percentage of Tipulidae larvae units per nestling initially dropped as the soil increased in volumetric moisture content (between 20% and 30%) then increased as the volumetric soil moisture content increased to above 35% (Fig 4.1).

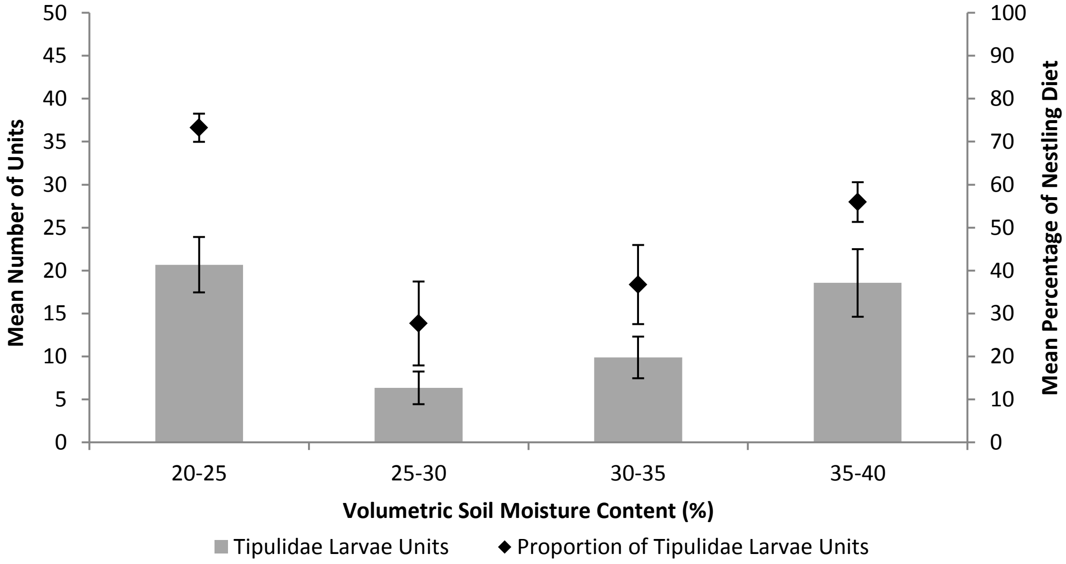

Figure 4.1 Mean number and percentage of Tipulidae larvae units per individual (± se), measured against adult beak length (i.e. 30 units on the y-axis is equivalent to 30 prey items equal to the bill length of the adult), in the daily diet of Starling nestlings at the Sawmill colony, Wytham, Oxfordshire, in relation to the volumetric soil moisture content on the day of observation.
The number (volumetric soil moisture content: $P = 0.02$, volumetric soil moisture content ^{2}: $P = 0.03$) and percentage (volumetric soil moisture content: $P = 0.002$, volumetric soil moisture content ^{2}: $P = 0.003$) of Tipulidae larvae were significantly related to volumetric soil moisture content, both declined initially as the volumetric soil moisture content of the soil increased between 20% and 30% then increased as the volumetric soil moisture content increased to above 35%.

	Number of Nestlings that Hatched	**Number of Nestlings that Fledged**	**Number of Nestlings that Died**	**Mean initial brood size per Nest**	**Mean Number that Fledged per Nest**	**Mean Percentage that Fledged per Nest**	**Mean Number that Died per Nest**
2005 (n=5)	24	17	7	4.75 ± 0.32	3.25 ± 0.37	72 ± 9.91	1.5 ± 0.60
2006 (n=4)	18	16	2	4.33 ± 0.21	4 ± 0.26	93 ± 6.67	0.33 ± 0.33
2007 (n=10)	48	37	11	4.75 ± 0.13	3.75 ± 0.37	80 ± 8.16	1. ± 0.41
2008 (n=5)	22	11	11	4.40 ± 0.16	2.2 ± 0.13	51 ± 4.27	2.2 ± 0.25
All years (n =24)	112	81	31	4.58 ± 0.10	3.25 ± 0.19	72 ± 4.47	1.33 ± 0.23

Table 4.3 The number of Starling nestlings that hatched, fledged and died per year and the mean initial brood size (± se), number that fledged (± se), percentage that fledged (± se) and number that died (± se) per nest per year at the Sawmill colony, Wytham, Oxfordshire between 2005 and 2008.

4.3.3 Soil moisture and Starling fledgling success at the Sawmill colony

Clutch initiations are highly synchronous within Starling populations in the early part of the breeding season (Feare 1984). This behaviour was evident at the Sawmill colony: 2005 (151 ± 2.95), 2006 (153 ± 0.89), 2007 (143 ± 0.47) and 2008 (161 ± 0.33) (numbers refer to the day of the year e.g. 26th May 2005 is day 146). In total 112 nestlings hatched at the Sawmill colony: 24 in 2005 (17 fledged, 7 died), 18 in 2006 (16 fledged, 2 died), 48 in 2007 (37 fledged, 11 died) and 22 in 2008 (11 fledged, 11 died) (Table 4.3).

C. After the number of nestlings that hatched and ambient temperature had been taken into account, there was no significant relationship between the number of nestlings that fledged and the mean number of Tipulidae larvae per nestling per day on the day/s that the nest was filmed (Tipulidae larvae units per nestling per day: P = 0.77) (Appendix 4.D, Fig. 4.2).

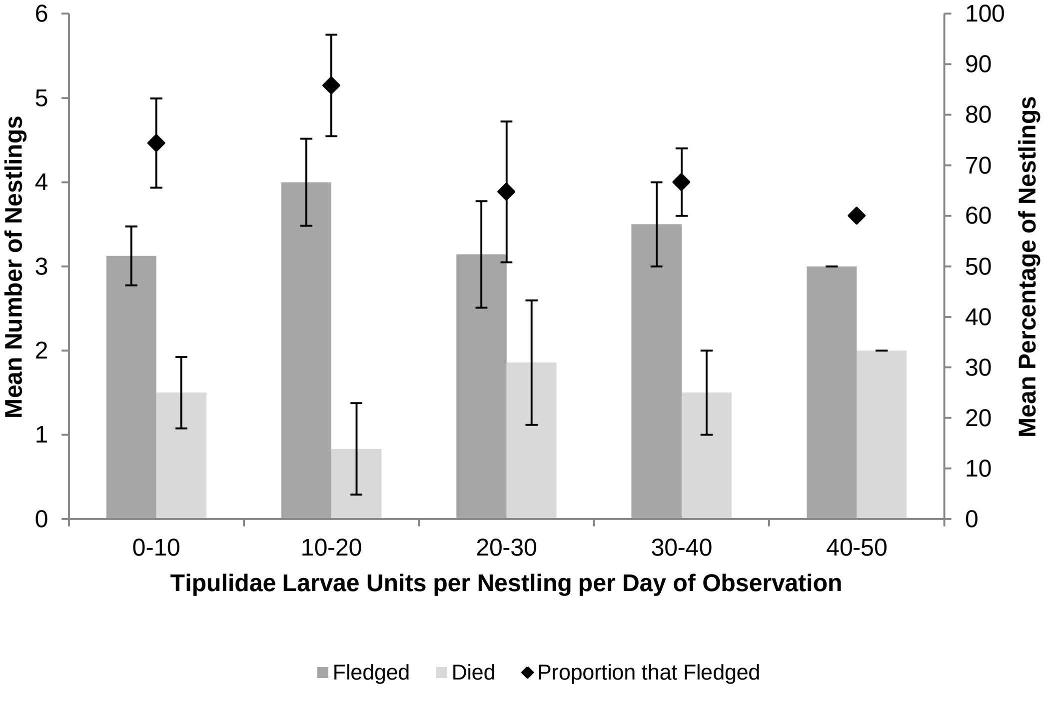

Figure 4.2 The mean number of Starling nestlings that fledged (± se) and died (± se) and the mean percentage of nestlings that fledged (± se) at the Sawmill colony, Wytham, Oxfordshire, between 2005 and 2008, in relation to the number of Tipulidae larvae units provided to Starling nestlings on either one or two days of observation by video camera. There was no significant relationship between the number of nestlings that fledged and the mean number of Tipulidae larvae per nestling per day on the day/s that the nest was filmed (Tipulidae larvae units per nestling per day: P = 0.77).

There was a significant curvilinear relationship between the number of nestlings that fledged and the mean volumetric soil moisture content on the day of observation (volumetric soil moisture content: P = 0.04) volumetric soil moisture content ^{2}: P = 0.04) (Appendix 4.D, Fig. 4.3).

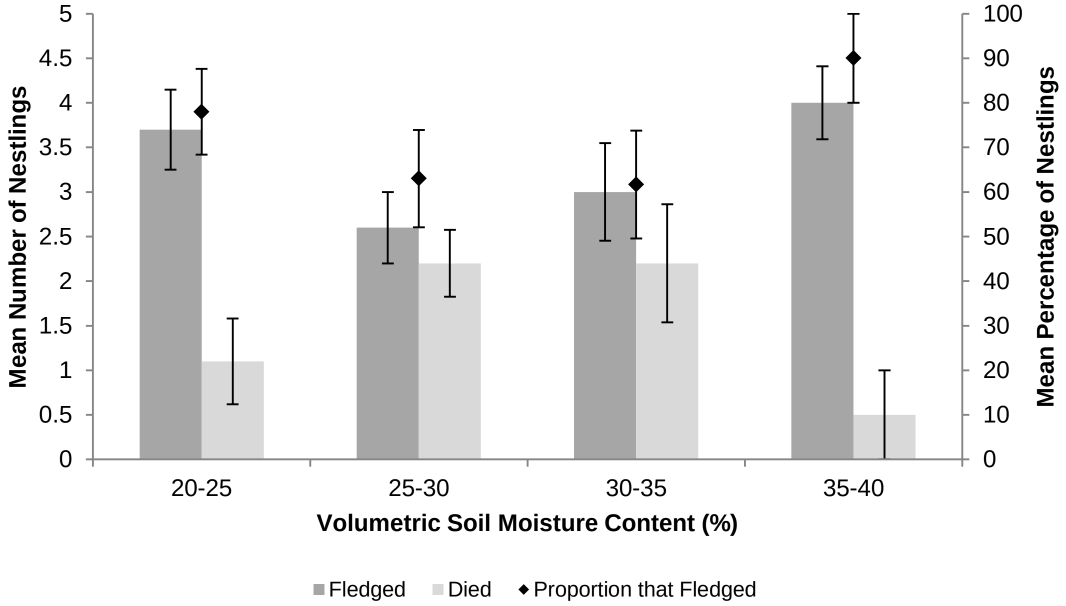

Figure 4.3 The mean number of Starling nestlings that fledged (± se) and died (± se) and the mean percentage of nestlings that fledged (± se) at the Sawmill colony, Wytham, Oxfordshire between 2005 and 2008, in relation to mean soil moisture during the nesting period. There was a significant curvilinear relationship between the number of nestlings that fledged and the mean volumetric soil moisture content on the day of observation (volumetric soil moisture content: P = 0.04, volumetric soil moisture content ^{2}: P = 0.04). Soil moisture was measured as volumetric soil moisture content at the nestbox colony. The nestling period covered 16 days in each year.

The number of nestlings that fledged initially dropped as the soil increased in volumetric moisture content (between 20% and 30%) and then increased as the volumetric soil moisture content increased to above 35%. The results were supported by the independent GLMMs (Appendix 4.D). Although the number of nestlings that hatched and the number of Tipulidae larvae units per nestling per day were significantly positively correlated they were not interchangeable within the full model. When model C was re-run, replacing the number of Tipulidae larvae per nestling per day with the percentage of Tipulidae larvae per nestling per day (as measured on the day, or sometimes two days, over which the nest was filmed), the relationship between Tipulidae larvae provisioning and the number of nestlings that fledge remained insignificant (P = 0.63) (Appendix 4.E) (Fig.4.4).

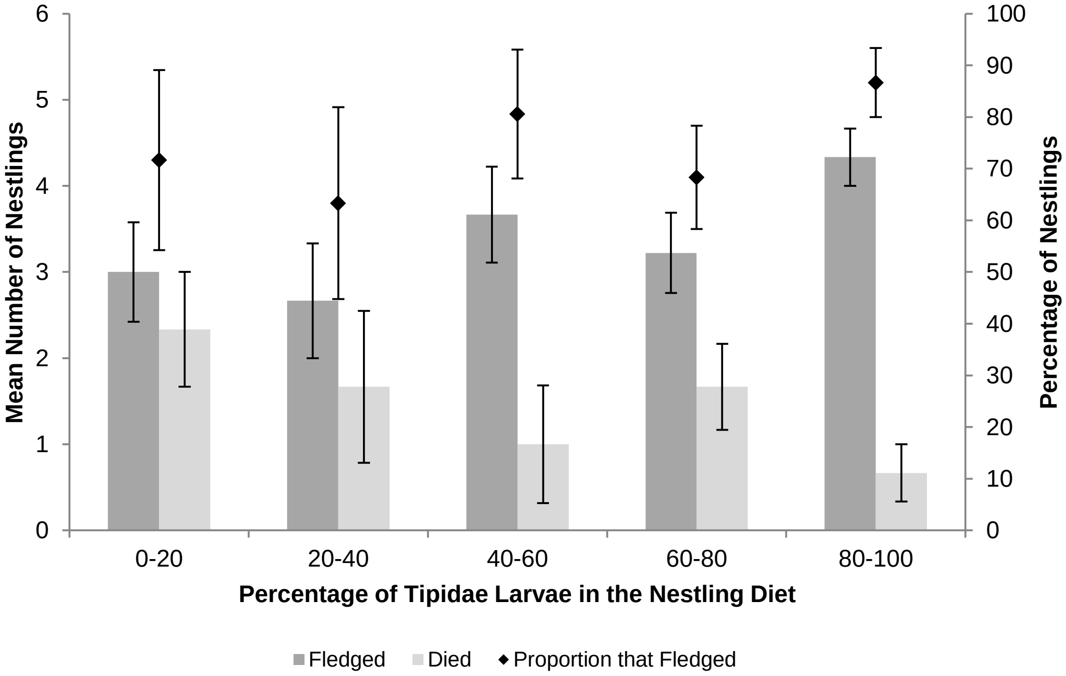

Figure 4.4 The mean number of Starling nestlings that fledged (± se) and died (± se) and the mean percentage of nestlings that fledged (± se) at the Sawmill colony, Wytham, Oxfordshire between 2005 and 2008, in relation to the percentage of Tipulidae larvae units per individual per day. The percentage of Tipulidae larvae in the diet per nestling per day as measured on the day/s on which the nest was filmed was not related to the number of nestlings that fledged.

4.4 Discussion

As was found in the larger population at John Krebs Field Station (Chapter 3), Tipulidae larvae formed the majority (between 46-76%) of the nestling diet at the Sawmill colony whether data were analysed as abundance, prey length, dry mass or energy (kJ). However, in contrast to all sites combined, nestlings received a similar proportion of winged insects, Coleoptera larvae and Lepidoptera larvae overall. This may reflect spatial variability in these prey items.

Between years, there was significant variation in mean daily volumetric soil moisture content over the nestling period (GLM: $F_{4, 3} = 1997.63$, $P < 0.001$) (Table 2). There was also significant variation in mean daily rainfall (GLM: $F_{4, 3}$

= 7.50, $P < 0.001$), temperature (GLM: $F_{4, 3} = 29.21$, $P < 0.001$) and surface wetness (the number of minutes per hour during which the soil surface is wet at ground level) (GLM: $F_{4, 3} = 9.25$, $P < 0.001$) over the nestling period between years (Table 4.2). When all years were considered, the number and percentage of Tipulidae larvae in the diet initially decreased with increasing soil moisture and then increased. This is counter to the *a priori* prediction that both would increase with increasing soil moisture. This may be partly explained by the fact that soil moisture varies both spatially and temporally and is only one of the soil variables related to penetration resistance (Vaz *et al*. 2001). The strength of the surface layer soil is due its bulk density (mineral content and degree of compaction) as well as its water status (Whalley *et al.* 2007). It may also be due to the depth of the soil moisture recordings. ThetaProbes are positioned at 20cm below the soil surface. Foraging Starlings will probe up to a maximum of approximately 25mm (the average adult beak length) into the top layer of soil. Low soil moisture readings at 20cm depth may not reflect what is occurring at the soil surface. For example, surface wetness will be affected by microclimatic atmospheric variations during the day, such as changes in relative humidity, net radiation, wind speed and temperature (Magarey *et al*. 2005), as well as intermittent rain showers. Even in years with comparatively low soil moisture content the soil surface at the study site was 'wet' for a period of time during the day (e.g. in 2007 the mean daily soil surface wetness during the nestling period was 19.78 ± 1.86 minutes per hour) (see Table 4.2). Short periods of surface wetness, although not reliable, would allow birds access to below-ground invertebrate prey during periods of drought.

Starlings feeding nestlings mostly limit their foraging to areas within 500 m of their nest (Feare 1984). The area of grassland and woodland within 500m radius of the Sawmill colony overlies top soils ranging from Elmton, a shallow fine loam over limestone to Denchworth, a slowly permeable clayey soil with fine loam (Kneale 1986, Farewell *et al*. 2011). Our results show that Tipulidae larvae numbers and percentages per nestling per day were initially high at low soil moisture levels (20-25%), decreased as soil moisture levels initially increased (25-30%) and then increased as volumetric soil moisture content reached 35-40 % (Fig 4.1). These results are unexpected as penetration resistance i.e. the force required by a bird to probe the ground for prey is expected to decrease with increased soil moisture. However, in clay loam the shear strength (soil adhesion/cohesion that binds together like structures in the soil) is weakest in very dry soils (< 12 %) and saturated soils (> 40%). Penetration resistance increases with moisture content, reaching a peak in the moisture content range 28-32%, and then decreases sharply to values similar to that of dry soil (Rajaram & Erbach 1998). During the Starling breeding season (April – June) Tipulidae larvae are at the third/fourth instar stage of development and are no longer prone to desiccation (Milne *et al*. 1965, Laughlin 1967, Blackshaw 2012). Their abundance and accessibility will not be affected by very dry soil, unlike other below-ground prey that are prone to desiccation (e.g. earthworms burrow deeper in dry soils and are thus likely to be out of reach for starlings). This is supported by our data which shows that at low soil moisture content (20-25%) earthworms decline in the diet while winged insects increase (Fig. 4.5). It should be noted, that the spatial patterns of Tipulidae larvae abundance may change as older larvae move to sites where the soil moisture is more favourable (wetter), particularly during extended periods of dry weather (Blackshaw 1999). Also, changes in the physical properties of clay loam soils will vary depending on the quantity of clay in the soil.

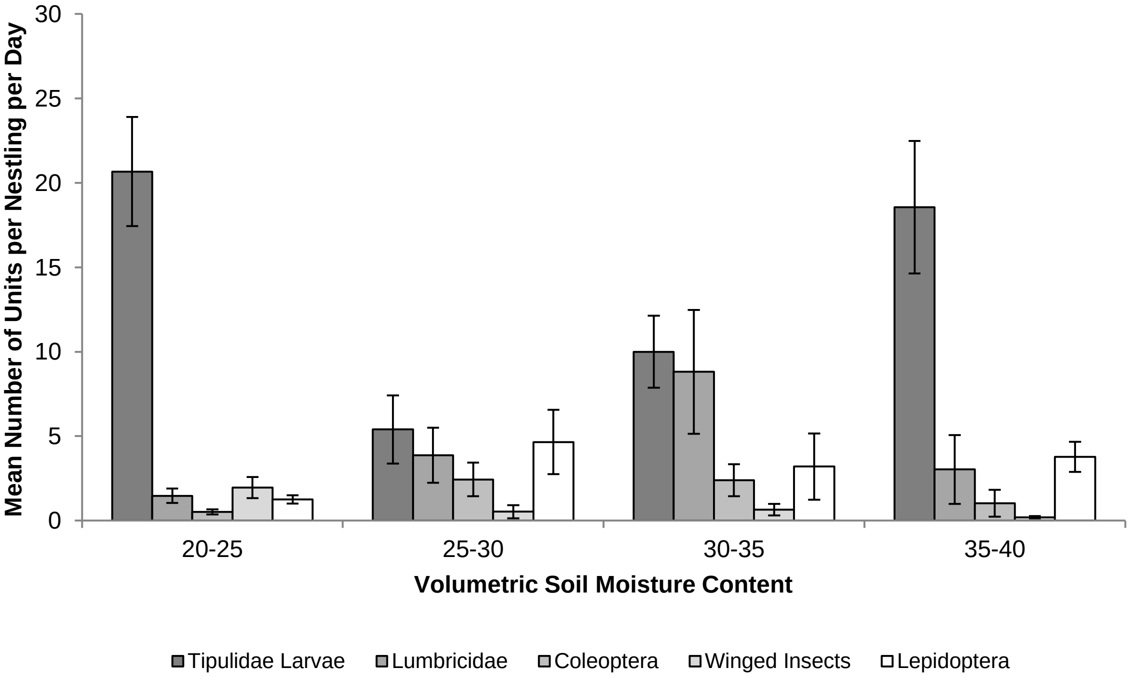

Figure 4.5 The mean number of units (± se) of different prey types delivered by adult Starlings per nestling per day at the Sawmill colony, Wytham, Oxfordshire between 2005 and 2008, in relation to volumetric soil moisture content.
One unit is equivalent to the average 25 mm adult Starling beak length.

There is no direct statistical evidence of the link between soil moisture and fledgling success. Due to the highly synchronous hatching of Starlings at the Sawmill colony there was little within-year soil moisture variation to explore differences in reproductive success within years and so there was only between year variation to explore this parameter. However, Tipulidae larvae provisioning and fledgling success both respond in a similar manner to variations in volumetric soil moisture content. As Tipulidae larvae form the majority of the Starling nestling diet in terms of prey units (57%) these results are consistent with the idea that below-ground invertebrates form the key dietary items for Starling nestlings and that decreased soil moisture can have a detrimental effect on reproductive success via changes in fledgling survival.

The findings suggest that on clay loam soils, intermediate soil moisture levels have the most impact on Tipulidae larvae provisioning. Penetration resistance is highest as soils shift from being very dry to wet or vice versa. Evidence suggests that as clay loam soils go through several seasonal cycles of wetting and drying the shear strength of the soil will increase further, although this is dependent on the extent of drying stress (Rajaram & Erbach 1998). Therefore, the penetration resistance of soils at intermediate levels of soil moisture will be higher in those that have been subjected to regular drought. Maintaining a high water table throughout the spring/summer through the use of features such as footdrains or rills may prevent this (see Chapter 6, section 6.4.1).

Although the overall pattern was of an increase in provisioning at higher soil moisture levels and a concomitant increase in breeding success this needs to be placed within the context that the soils in this chapter were far from saturated (e.g. compare with data in Chapter 1 based on Autumn/Winter foraging). The subtle complexities of how soil moisture interacts with the soil type found on this site highlight that the straightforward *a priori* expectation of increased soil moisture being positively linearly related to higher provisioning and breeding success did not hold here. However, penetration resistance will typically decrease with an increase in soil water content (Francis *et al*. 1987, Tekeste *et al*. 2008) and therefore our results may be more an exception than a general rule.

Future work needs to examine survival of young both before and after they leave the nest under differing soil moisture conditions with a sufficiently large number of samples to explore population level effects. Energy demands of the young are greatest after leaving the nest, young that have experienced food shortages or poor quality food during the nestling stage may have post-fledgling survival compromised. In addition, drought conditions during the post-fledging period may have a negative impact on recruitment in the following year. These issues will be examined in Chapter 5.

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Appendix 4.A

Percentage of the total number of prey items in the Starling nestling diet per nest per day averaged for each year (mean value (± se) at the Sawmill colony Wytham, Oxfordshire, UK (n=number of nests).

	Tipulidae Larvae	**Lumbricidae**	**Winged insects**	**Coleoptera Larvae**	**Lepidoptera Larvae**	**Unidentified**
2005 (n=5)	41.4 ± 10.9	19.97 ± 6.85	0.37 ± 0.25	3.80 ± 1.63	8.92 ± 3.91	25.63 ± 8.01
2006 (n=4)	53.53 ± 6.36	3.44 ± 1.80	0.95 ± 0.30	1.04 ± 0.72	20.43 ± 2.86	20.61 ± 5.11
2007 (n=10)	73.02 ± 3.14	5.49 ± 1.34	5.59 ± 1.46	2.46 ± 1.14	5.47 ± 0.98	7.97 ± 1.60
2008 (n=5)	39.31 ± 8.44	19.57 ± 3.29	4.22 ± 1.95	13.44 ± 5.64	8.53 ± 2.91	14.93 ± 4.65
All years (n=24)	53.37 ± 4.30	12.27 ± 2.18	3.28 ± 0.80	5.57 ± 1.80	9.58 ± 1.52	15.93 ± 2.57

Appendix 4.B

Results of a generalized linear mixed-effects model (GLMM) of the number of Tipulidae larvae units delivered by parents per Starling nestling per day (*n* = 36) as a function of the mean volumetric soil moisture content on the day of observation, accounting for variations in Julian date between years. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	***se***	**df**	***z***	***P***
Full model [a]					
Intercept	18.58	5.39	1	3.45	<0.001
Number of nestlings on the day of observation	- 3.37	1.18	1	- 2.86	0.004
Number of nestlings on the day of observation^2	0.44	0.15	1	2.89	0.004
Mean volumetric soil moisture	- 0.66	0.28	1	- 2.33	0.02
Mean volumetric soil moisture^2	0.01	0.01	1	2.23	0.03
Julian date	- 0.29	0.17	1	- 1.71	0.09
Soil moisture without date [b]					
Intercept	17.74	5.59	1	3.17	0.002
Number of nestlings on the day of observation	- 2.98	1.21	1	- 2.47	0.01
Number of nestlings on the day of observation^2	0.40	0.16	1	2.57	0.01
Mean volumetric soil moisture	- 0.70	0.28	1	- 2.34	0.02
Mean volumetric soil moisture^2	0.01	0.01	1	2.33	0.02
Date without soil moisture [c]					
Intercept	6.12	2.14	1	2.86	0.004
Number of nestlings on the day of observation	- 2.18	1.15	1	- 1.90	0.06
Number of nestlings on the day of observation^2	0.30	0.15	1	2.02	0.04
Julian date	- 0.21	0.16	1	- 1.31	0.19

[a] AIC: 120.2, Random effects (variance): nest box = 0.03, individual level = 0.04.
[b] AIC: 121, Random effects (variance): nest box =0.01, individual level = 0.04.
[c] AIC: 121.8, Random effects (variance): nest box = 0.14 , individual level = 0.37.

Appendix 4.C

Results of a generalized linear mixed-effects model (GLMM) of the percentage of Tipulidae larvae units delivered by parents per Starling nestling per day (*n* = 36) as a function of the mean volumetric soil moisture content on the day of observation, accounting for variations in Julian date between years. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	***se***	**df**	***z***	***P***
Full model [a]					
Intercept	17.77	5.45	1	3.26	0.001
Mean volumetric soil moisture	- 1.18	0.38	1	- 3.11	0.002
Mean volumetric soil moisture^2	0.02	0.01	1	2.99	0.003
Mean age	0.01	0.05	1	0.20	0.84

[a] AIC: 120.2, Random effects (variance): nest box = 0.51, individual level = 0.31.

Appendix 4.D

Results of a generalized linear mixed-effects model (GLMM) of the number of Starling nestlings that fledged (*n* =36) as a function of the mean number of Tipulidae larvae units per nestling per day and volumetric soil moisture content over the nestling period, accounting for mean ambient temperature and the number of nestlings that hatched. The GLMMs were fit using the Laplace method.

Fixed Effects	**Estimate**	***SE***	**df**	***z***	***P***
Full model [a]					
Intercept	9.44	4.17	1	2.27	0.02
Number of Tipulidae larvae units per nestling per day	- 0.003	0.01	1	- 0.30	0.77
Mean volumetric soil moisture over the nestling period	- 0.54	0.26	1	- 2.06	0.04
Mean volumetric soil moisture over the nestling period ^{2}	0.01	0.004	1	2.04	0.04
Mean ambient temperature over the nestling period	0.004	0.05	1	0.08	0.93
Number of nestlings that hatched	- 0.04	0.20	1	- 0.24	0.81
Hatch without Tipulidae larvae units [b]					
Intercept	9.44	4.11	1	2.30	0.02
Mean volumetric soil moisture over the nestling period	- 0.53	0.26	1	- 2.06	0.04
Mean volumetric soil moisture over the nestling period ^{2}	0.01	0.004	1	2.04	0.04
Mean ambient temperature over the nestling period	0.01	0.05	1	- 0.16	0.87
Number of nestlings that hatched	- 0.09	0.16	1	- 0.57	0.57
Tipulidae larvae units without hatch [c]					
Intercept	9.26	4.10	1	2.26	0.02
Number of Tipulidae larvae units per nestling per day	- 0.004	0.01	1	- 0.44	0.66
Mean volumetric soil moisture over the nestling period	- 0.54	0.26	1	- 2.06	0.04
Mean volumetric soil moisture over the nestling period ^{2}	0.01	0.004	1	2.05	0.04
Mean ambient temperature over the nestling period	0.004	0.05	1	0.09	0.93

[a] AIC: 26.53, Random effects (variance): nest box = 0.
[b] AIC: 24.73, Random effects (variance): nest box = 0.
[c] AIC: 24.58, Random effects (variance): nest box = 0.

Appendix 4.E

Results of a generalized linear mixed-effects model (GLMM) of the number of Starling nestlings that fledged (*n* =36) as a function of the percentage of Tipulidae larvae units per nestling per day and volumetric soil moisture content over the nestling period, accounting for mean ambient temperature and the number of nestlings that hatched. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	***se***	**df**	***z***	***P***
Full model [a]					
Intercept	1.04	1.25	1	0.83	0.41
Percentage of Tipulidae larvae units per nestling per day	0.01	0.01	1	- 0.49	0.63
Mean volumetric soil moisture over the nestling period	0.001	0.02	1	0.06	0.96
Mean ambient temperature over the nestling period	0.02	0.05	1	0.40	0.69
Number of nestlings that hatched	- 0.09	0.18	1	0.83	0.63
Hatch without Tipulidae larvae units [b]					
Intercept	8.75	4.11	1	2.30	0.02
Mean volumetric soil moisture over the nestling period	- 0.50	0.26	1	- 2.06	0.03
Mean volumetric soil moisture over the nestling period ^{2}	0.01	0.01	1	2.04	0.03
Mean ambient temperature over the nestling period	0.01	0.05	1	- 0.16	0.87
Number of nestlings that hatched	- 0.10	0.16	1	- 0.57	0.60
Tipulidae larvae units without hatch [c]					
Intercept	9.70	4.10	1	2.26	0.02
Number of Tipulidae larvae units per nestling per day	- 0.02	0.01	1	- 0.44	0.50
Mean volumetric soil moisture over the nestling period	- 0.49	0.26	1	- 2.06	0.03
Mean volumetric soil moisture over the nestling period ^{2}	0.01	0.004	1	2.05	0.03
Mean ambient temperature over the nestling period	0.03	0.05	1	0.09	0.89

[a] AIC: 27.48, Random effects (variance): nest box = 0

[b] AIC: 25.73, Random effects (variance): nest box = 0.

[c] AIC: 25.58, Random effects (variance): nest box = 0.

Chapter 5: Population-level effects of Climate Change at a National Scale: How do Soil Moisture Conditions alter British Starling Populations from 1981-2000?

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5.0 Abstract

Capsule In Britain, soils have become increasingly drier from 1980-1999 and these changes are negatively correlated with Starling populations.

Aims **(i)** To investigate changes in soil moisture deficit since the 1980s at a national scale. **(ii)** To examine the correlative effects of soil moisture deficit changes on Starling breeding populations.

Methods Starling breeding population changes and mean spring (April - June) and summer (July-September) soil moisture deficit values were recorded at 132 British Common Bird Census sites between 1981 and 2000.

Results Generalized linear mixed-effects models showed that spring and summer soil moisture deficit increased from 1980-1999. Drier soils were correlated negatively with Starling breeding populations even when significant negative temporal effects (likely linked to agricultural intensification) were also taken into account. Starling populations did best in years with wet springs (April-June) and dry summers (July-Sep).

Conclusion Our results support the idea that the drying of soils over a 20-year period correlates with poor Starling breeding performance.

5.1 Introduction

It is well established that farmland bird population declines are strongly linked to the land use and management changes associated with increased agricultural intensification (e.g. Chamberlain *et al.* 2000, Donald *et al*. 2001, and Gregory *et al.* 2004). The pressures of habitat destruction and management intensification are predicted to worsen over the course of the next century (Sala *et al.* 2000) in response to increasing demands for food by growing human populations (Green *et al*. 2005). In addition there are substantial effects predicted from climate change on species' distribution and abundance (Parmesan & Yohe 2003, Root *et al.* 2003, Thomas *et al.* 2004, Hickling *et al*. 2006).

A number of bird species associated with lowland farmland grassland feed predominantly on soil dwelling invertebrates and so will be sensitive to changes in soil conditions (e.g. waders such as Common Snipe *Gallinago gallinago L.* - Green 1986; Common Redshank *Tringa totanus L.* and Northern Lapwing *Vanellus vanellus L.* - Baines 1990, Ausden *et al*. 2003; European Golden Plover *Pluvialis apricaria L*. - Pearce-Higgins & Yalden 2003; corvids such as Chough *Pyrrhocorax pyrrhocorax L.* - McCracken *et al*. 1992 and passerines such as Song Thrush *Turdus philomelos* L. - Peach *et al*. 2004 a, b and European Starlings *Sturnus vulgaris* - Dunnet 1955, Tinbergen 1981, Rhymer *et al*. 2012 (see Chapter 3)).

Climate change is likely to have a significant impact on ground water levels and thus the availability of suitable feeding habitat for species that probe the ground for food (Hulme *et al*. 2002). Raised water levels keep the surface soil moist, increase soil surface penetrability (Gerard 1967, Green *et al*. 2000) and reduce vegetation growth when surface water is present (Ausden *et al*. 2001). In general, moist soils support larger densities of soil invertebrates than dry soils (Milsom *et al.* 2000). Moisture is one of the main factors determining earthworm abundance in the top 5–10 cm of soils (Gerard 1967, Green *et al*. 2000, Peach *et al*. 2004a) and influences pupation rates and larvae survival of terrestrial invertebrates (Meats 1974). The lowering of field water levels reduces soil penetrability making the ground too hard for surface probing. As the soil surface dries out, earthworms descend deeper into the soil and become less accessible to foraging birds. Laboratory and field studies have shown that *Tipulidae paludosa* larvae, an important prey item for the Starling nestlings (e.g.

Dunnet 1955, Tinbergen 1981, Rhymer *et al*. 2012), will move to preferred moisture levels (Blackshaw 1999). Egg and early instar larval survival are favoured by wet soil conditions associated with prolonged damp weather (Coulson 1962, Milne *et al*.1965, Meats 1974) or irrigation of pastures (Jackson & Campbell 1975) during late summer and early autumn. They are adversely affected by desiccation if the soil dries out quickly at a vulnerable stage in their life-cycle (McCracken *et al.* 1995, Bale *et al.* 2002). The lowering of field ground water levels will reduce both abundance and accessibility of food.

Increasing temperatures and accelerating evaporation through the spring and summer are known to lead to a progressive drying of the soil and the creation of a soil moisture deficit (SMD) (the amount of water in millimetres needed to bring the soil moisture content back to field capacity) (Hough & Jones 1997). Across all seasons, all regions of the UK have experienced an average increase of between 1.0 and 1.7 °C in annual average temperatures between 1961 and 2006 (http://ukclimateprojections.defra.gov.uk/21809). This combination of reduced precipitation and increased temperature (and the subsequent increased evapo-transpiration by plants: a 3°C increase in soil temperature can cause a 30% increase in evapo-transpiration and a 25% decrease in soil moisture (Harte *et al*. 1995)) will have had marked effects on soil moisture deficits.

In the future, rising mean annual air temperatures, increased evapo-transpiration and reduced summer precipitation, are predicted to combine to increase the frequency of intense short-term (3–6 month) summer desiccation in southern and eastern England over the next 100 years (Parry *et al*. 2004). Under the high emissions scenario, annual moisture content of soils is liable to decrease by 10-20% across the UK by the 2080s, with 20- 50% reductions in average summer soil moisture content occurring in South East England compared with a 0-20% in the North West (Bisgrove & Hadley 2002). Higher temperatures may also reduce the water holding capacity of soils; the lower the capacity, the greater the sensitivity to climate change (IPCC 2001).

Climate has become an increasingly important driver of bird populations since the mid-1980s (Devictor *et al*. 2008, Gregory *et al*. 2009) with food supply as a key determinant of local population density (e.g. Newton 1998). Thus, informed management of their preferred habitats is crucial to successful land management targeting these species. For conservationists aiming to manage habitats to benefit populations of a target species it is key to understand the effects of increasing spring and summer soil moisture deficit on breeding populations. Here we focus on a model species, the Starling, that has undergone substantial declines in the UK (Robinson *et al*. 2002, 2005) and Europe (PECBMS 2010) since the 1980s. Currently, Starlings are Red-listed in the UK owing to their breeding population size experiencing a severe ‘longer-term’ decline since 1969 (i.e. since the first Birds of Conservation Concern review) and declining by more than 50% during the past 25 years (Gregory *et al*. 2002, 2004, Eaton *et al*. 2009).

This study tests the hypothesis that Starling populations have responded to changes in soil moisture deficit conditions from 1981 to 2000 by examining yearly population estimates across 132 survey sites. Insights from this one species could potentially inform management for a range of species that forage by probing the ground for invertebrate prey. This will be explored in the discussion and subsequent review chapter (Chapter 6, Rhymer *et al*. 2010).

5.2 Methods

5.2.1 Data collection

Changes in the abundance of breeding Starlings were assessed through the analysis of UK annual census data from 1981 through to 2000. Data were collected by volunteers participating in the British Trust for Ornithology Common Birds Census (CBC) (Marchant *et al*. 1990). The CBC method requires seven to ten visits per site per breeding season to record the number and distribution of all the birds seen or heard (Marchant *et al*. 1990). It provides a precise assessment of the number of breeding bird territories occupied at individual sites (Marchant 1983, Marchant *et al*. 1990). The CBC has a number of limitations; census plots are biased in favour of the south and east of England where observer density is greatest, are few in number (approximately 200) due to time-consuming surveying and mapping, do not cover upland or urban areas well, are limited in sparsely populated regions, are variable in size and are not formally randomised (Marchant *et al*. 1990, Gregory *et al*. 2000). However, the CBC plots are considered representative of most of the lowland farmland within southern England, and more accurate than their successor, the Breeding Bird Survey, at monitoring site level population changes (Freeman *et al*. 2007). From

200 CBC plots, 149 plots were found to have Starling territories. Breeding numbers were estimated through a combination of nest counts and number of singing males recorded at each site. Only plots that had been surveyed for a minimum of 5 years (not always sequential) were include in the analysis (132) (Fig. 5.1).

Figure 5.1 Location of 132 Common Bird Census sites used in this study that contained Starling breeding pairs between 1981 and 2000
(note circles are overlaid).

Soil moisture deficit (SMD) data for the period 1980 to 1999 were obtained from the Meteorological Office Rainfall and Evaporation Calculation System (*MORECS*). SMD estimates, measured in millimetres (mm), for the UK are calculated from a modified form of the Penman–Monteith method (Monteith, 1973, Monteith & Unsworth 1990) using synoptic weather data (rainfall, sunshine, temperature, vapour pressure, wind speed), from a network of more than 200 stations across Britain, as well as soil type and land use information. The total moisture store of a soil is a pre-defined amount (the maximum available water capacity) which depends on the soil type and the rooting depth (the deeper the root system the greater the amount of water that can be extracted e.g. under deciduous trees much greater SMDs can be attained than under grassland). A SMD is defined when the actual water amount falls below the maximum due to evaporation exceeding rainfall. A zero soil moisture deficit is called field capacity, although this is known to be an approximation, especially for clay soils (Hough 2003).The soil available water capacity data in *MORECS* comes from the Land Information System developed by the Soil Survey Land Research Centre. For each *MORECS* square up to 1600 values are used to find the mean values for the square. *MORECS* provides a UK-wide assessment of *general* soil moisture status, divided into 40 km^2 areas based on general land cover and soil type (Hough & Jones 1997).

Soil type specific to the central grid reference provided for each CBC site, was obtained from Cranfield University's National Soil Research Institute Soilscapes (http://www.landis.org.uk/soilscapes/). A simplified version of the 1:250,000 scale Digital National Soil Map for England and Wales that includes 27 soil classes (Farewell *et al.* 2011).

5.2.2 Analysis

From 132 CBC sites, located within 67 *MORECS* squares, 1077 breeding territory estimates were made between 1981 and 2000. The total number of MORECS squares and CBC sites surveyed varied between years (Appendix 5.A). On average, 56.68 ± 1.56 (± se) CBC sites were surveyed within 37.37 ± 0.82 (± se) *MORECS* squares each year (each *MORECS* square contained 1.97 ± 0.18 (± se) CBC sites). Each CBC site was surveyed for 8 ± 0.35 (± se) years. For each CBC site a number of variables were recorded: number of breeding pairs, habitat type (farmland, woodland or other (lowland wetland or urban open spaces), soil type (for analysis purposes they were classified into the following categories: freely draining loamy soils, freely draining sandy soils, loamy and clayey soils, sandy and loamy soils or peat soils), mean altitude, mean area (hectares), Easting and Northing. Mean spring (April to June) and summer (July to September) SMD estimates were also recorded for each *MORECS* square per year. SMD estimates assume medium available water holding capacity soil (Loamy Sand, Sand, Loamy Fine Sand, Fine Sand, Sandy Loam, Fine Sandy Loam, Loam, Silty Loam, Clay Loam, Sandy Clay Loam, Silty Clay Loam, Sandy Clay, Silty Clay, Clay) with grass cover.

5.2.3 Variation in soil moisture deficit across MORECS sites

Central England Temperature has risen by about a degree Celsius since the 1970s while summer precipitation has decreased (Jenkins *et al*. 2009). It is therefore probable that spring and summer soil moisture deficits will have increased over the period 1980 to 1999. In addition, because soil moisture deficit varies both temporally and spatially (IPCC 2001) it would also be expected that mean spring and summer soil moisture deficit will vary according to location. These relationships were tested with GLMMs (with *MORECS* square as the random effect) as follows:

A. Mean April to June soil moisture deficit as the response variable with Gaussian errors and an identity link function.

Mean April to June soil moisture deficit = year + year ^{2} + 1|*MORECS* square

B. Mean July to September soil moisture deficit as the response variable with Gaussian errors and an identity link function.

Mean July to September soil moisture deficit = year + year ^{2} + 1|*MORECS* square

5.2.4 Variation in soil moisture and Starling breeding population changes

In the UK, the mean laying date of Starlings advanced between 1968 and 2008, from the 27th to the 22nd April (http://www.bto.org/birdtrends2010/wcrstarl.shtml#population). Fledging occurs at around 21 days and the parents feed the young for two weeks afterwards. A second clutch may be laid 40 to 50 days after the first clutch (Crick *et al*. 2002). Soil dwelling Tipulidae larvae are a key resource for adult Starlings provisioning their young on lowland farmland (e.g. Tinbergen 1981, Rhymer et al. 2012). Below ground invertebrate prey continue to be an important dietary source for juveniles throughout the summer, as well as arboreal invertebrates and fruit (Crick *et al*. 2002). During the early spring, Tipulidae larvae are located close to and sometimes on the soil surface. However, from mid-June onwards larvae stop feeding and move down to approximately 2-5 cm below the soil surface (Blackshaw 1999). Dry spring and summer soil conditions force larvae and other invertebrate prey (e.g. earthworms) to descend deeper into the soil, thus reducing prey abundance and accessibility during the breeding and post-fledging period forcing ground-probing bird species to switch to potentially less nutritional invertebrate prey (Gruar *et al*. 2003).

Starlings are known to be highly site faithful, returning to the same general area each year to breed (Feare 1984). While some females breed in the year after fledging, males do not start to breed until the next year (Coulson 1960, Feare 1984). It is therefore assumed that factors relating to post-fledging survival in one year may apply to changes in population size between that year and the following two years. The hypothesis that an increase in soil moisture deficit (drier soils) will reduce breeding population sizes by means of increased mortality through reduced parental and juvenile foraging opportunities was tested by modelling annual variation in Starling breeding population as a function of spring and summer soil moisture deficit one and two years previously. Soil moisture deficit was partitioned into spring (April to June) and summer (July to September) to acknowledge the difference between parental provisioning (spring) and post-fledging foraging (summer) as well as behavioural differences in Tipulidae larvae between these periods. The response variable was the number of Starling pairs breeding at 132 sites from a minimum of five years (between 1981 and 2000). These relationships were tested with various combinations (see below) of the following overall GLMMs as follows:

C. Total number of breeding pairs per site as the response variable with a Poisson error structure and a log link function.

Total number of breeding pairs per site = April to June SMD one year ago+ April to June SMD one year ago ^{2} + July to September SMD one year ago+ offset (log of the previous year's breeding pair numbers) + site area + year + habitat category + soil type +1|site

D. Total number of breeding pairs per site as the response variable with a Poisson error structure and a log link function.

Total number of breeding pairs per site = April to June SMD two years earlier + July to September SMD two years earlier + July to September SMD two years earlier ^{2} + + offset (log of the breeding pair numbers two years earlier) + site area + year + habitat category + soil type + 1|site.

All tests were performed using the program LMER in the lme4 package v.0.999375-42 (Bates *et al*. 2012) for R version 2.14.1 (R Development Core Team 2011). Models were generalized linear mixed-effects models (GLMMs) fit using the REML (models A and B) and Laplace (models C and D) methods for estimating parameters. Change in breeding bird numbers was modelled by incorporating the natural log of the previous years' count as an offset. The analysis therefore models the log-ratio of change from year to year (Pearce-Higgins *et al*. 2010) and also controls for density-dependence and survey error (Yalden & Pearce- Higgins 1997, Freckleton *et al*. 2006). Individual site identity 'site' was modelled as a random effect (written as 1|site above) to acknowledge the hierarchical design of the dataset and to control for possible temporal and spatial effects (Robinson *et al*. 2002). Site area was included in the models to take account of the variation in the area surveyed between sites. Population declines are known to have been greatest in woodland (Robinson *et al.* 2002, 2005) and therefore habitat category (woodland, farmland and other) was included to take account of this. Sites within the same *MORECS* square may have different soil types. Different soil types have different field capacities (Richards & Weaver 1944) and will have different soil moisture deficits from the average for the $40km^2$ area. In addition, the relationship between soil moisture and penetration resistance can differ between soil types. Therefore, soil type (five classes: loamy, sandy, loamy and clayey, sandy and loamy and peat (http://www.landis.org.uk/soilscapes/) is accounted for in the models.

Mean April to June SMD ($P < 0.001$) and July to September SMD ($P < 0.001$) were positively correlated meaning that July to September SMD is likely to be higher as a result of high April to June SMD. Mean April to June ($P < 0.001$) and July to September SMDs ($P < 0.001$) were also positively correlated with year meaning that both increased between 1980 and 1999. To check the robustness of model C and D and whether these variables were interchangeable GLMMs were also run with April to June SMD and July to September SMD independently (referred to as 'April to June SMD without July to September SMD' and 'July to September SMD without April to June SMD' in Appendix 5.D and 5.E) and with and without year (referred to as 'Full model with year' and 'Full model without year' in Appendix 5.D and 5.E). To investigate whether April to June SMD in model C or July to September SMD in model D explained variation in breeding pairs best, models C and D were also run omitting squared terms and year. The parameter estimates of these models were compared to determine which predictor variable explained the most variation. To justify the use of squared terms in a model, when the main effect was not significant, models were run first with both terms (main effect and main effect ^{2}) and then without both terms. The models were then compared using a maximum likelihood test to determine the best fit model.

5.3 Results

5.3.1 Variation in soil moisture deficit across MORECS sites

Over the nineteen year period, mean April to June SMD was 54.99 mm ± 0.82 (± se) and mean July to September SMD was 89.3 mm ± 1.06 (± se). As predicted, soils did indeed become drier through time: SMD increased across both the spring and summer from 1980-1999 across the 132 study sites (see A and B below). There was also significant difference in April to June SMD (GLM: $F_{4,3} = 4.80$, $P < 0.001$) and July to September SMD (GLM: $F_{5,4} = 15.82$, $P < 0.001$) between soil types (Table 5.1). July to September SMD (GLM: $F_{3,2} = 6.25$, $P = 0.002$) varied between habitats, however, April to June SMD did not (GLM: $F_{3,2} = 1.57$, $P = 0.21$) (Table 5.2).

	Number of CBC Sites	**Mean April to June Soil Moisture Deficit (mm)**	**Mean July to September Soil Moisture Deficit (mm)**	**Mean Number of Breeding Pairs per Hectare**
Loamy soils	28	53.4 ± 1.81	83.05 ± 2.54	0.08 ± 0.01
Sandy soils	5	51.2 ± 3.57	90.87 ± 4.61	0.03 ± 0.01
Loamy and clay soils	90	55.60 ± 0.99	91.50 ± 1.21	0.15 ± 0.01
Sandy and loamy soils	7	63.91 ± 3.61	104.77 ± 3.1	0.09 ± 0.01
Peat soils	2	36.28 ± 4.88	43.72 ± 8.3	0.10 ± 0.01

Table 5.1 Mean soil moisture deficit and number of Starling breeding pairs per hectare (± se) in relation to Common Bird Census site (n=132) soil type.

	Number of CBC Sites	**Mean April to June Soil Moisture Deficit (mm)**	**Mean July to September Soil Moisture Deficit (mm)**	**Mean Number of Breeding Pairs per Hectare**
Farmland	85	56.06 ± 1.03	88.01 ± 1.32	0.08 ± 0.01
Woodland	41	53.11 ± 1.44	89.54 ± 1.94	0.19 ± 0.02
Other	6	52.54 ± 3.82	106.24 ± 3.22	0.33 ± 0.06

Table 5.2 Mean soil moisture deficit and number of Starling breeding pairs per hectare (± se) in relation to Common Bird Census site (n=132) habitat.

A. There was a significant curvilinear relationship between April to June soil moisture deficit and year ($P < 0.001$) and year ^{2} ($P < 0.001$) (Appendix 5.B). The soil moisture deficit initially increased then levelled off (Fig. 5.2).

B. There was a significant curvilinear relationship between July to September soil moisture deficit and year ($P = 0.05$) and year 2 ($P = 0.05$) (Appendix 5.C). The soil moisture deficit initially increased then levelled off (Fig. 5.2).

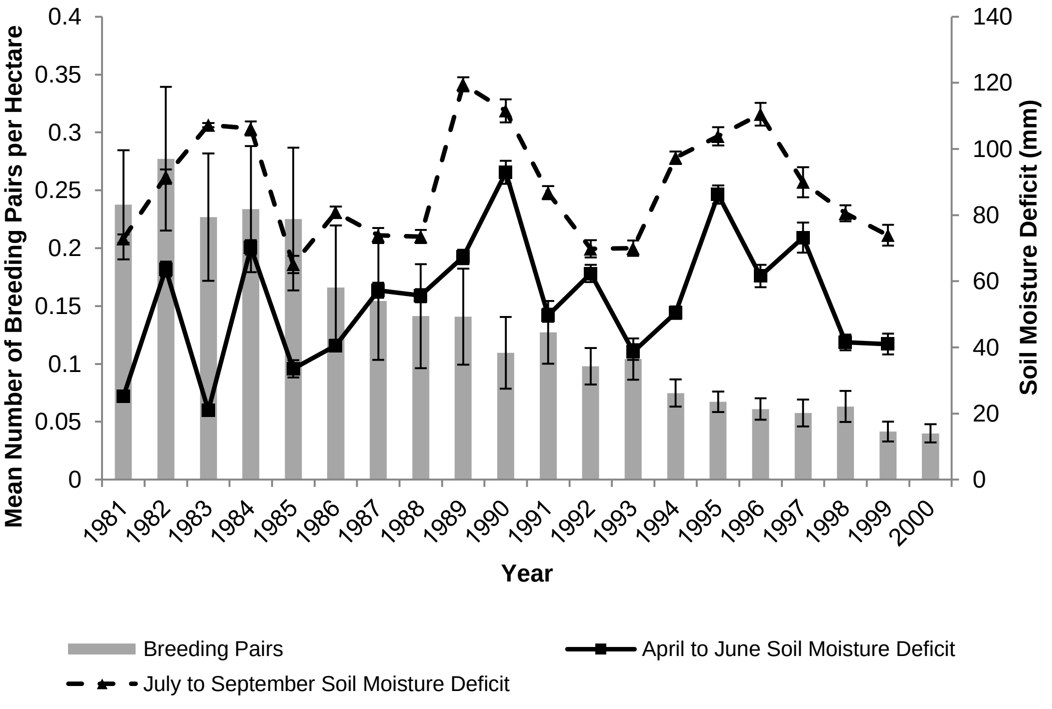

Figure 5.2 Mean number of Starling breeding pairs per hectare per year (± se) on 132 CBC sites in Britain in relation to mean April to June and July to September soil moisture deficit (± se). Between 1981 and 2000 the number of breeding pairs decreased ($P < 0.001$), whilst on the 67 40km ^{2} *MORECS* squares containing the CBC sites April to June (year: $P < 0.001$, year ^{2}: $P < 0.001$) and July to September (year: $P = 0.05$, year ^{2}: $P = 0.05$) soil moisture deficit increased.

5.3.2 Variation in soil moisture and Starling breeding population changes

Over the twenty year period, the mean number of breeding pairs per hectare across our study sites was 0.12 ± 0.01(± se). There was a significant difference in the number of breeding pairs per hectare between soil types (GLM: $F_{5, 4} = 5.17$, $P < 0.001$) (see Table 5.1) and habitats (GLM: $F_{3, 2} = 31.47$, $P < 0.001$) (see Table 5.2).

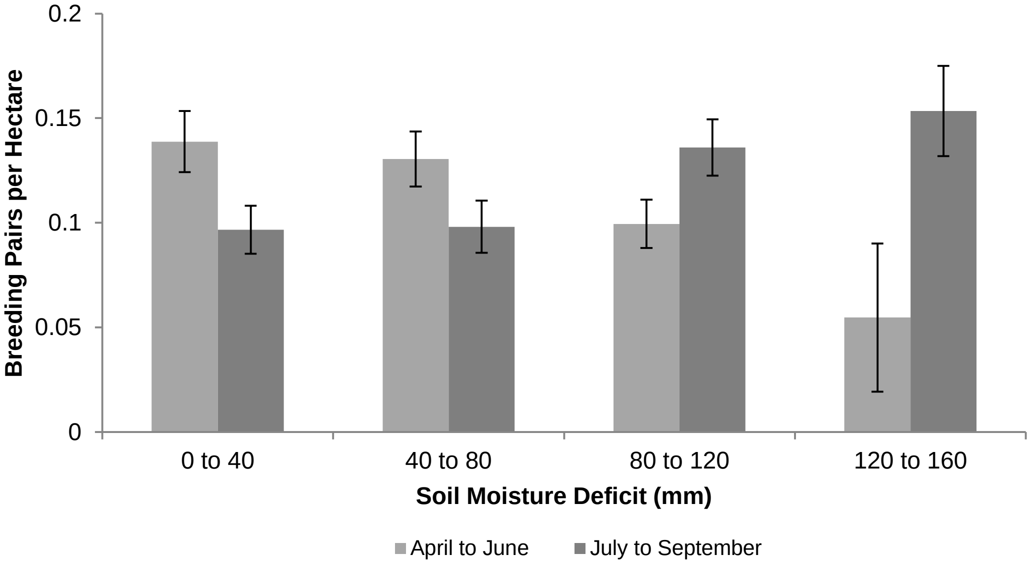

Figure 5.3 Mean number of Starling breeding pairs per hectare (± se) in relation to the mean soil moisture deficit of the Common Bird Census survey site (n=132) from April to June and July to September one year previously. The data suggests that the number of breeding pairs decreased as soil moisture deficit increased during April to June (April to June SMD: $P = 0.12$, April to June SMD$^{2:}$ $P < 0.001$, both main effect and squared term together: ANOVA: $X^{2}_{11,13} = 11.06$, $P = 0.004$), but increased with increased soil moisture deficit during July to September ($P = 0.09$).

C. There was a significant curvilinear relationship between April to June SMD the year before and breeding pair numbers per CBC site (April to June SMD: $P = 0.12$, April to June SMD$^{2:}$ $P < 0.001$) (Table 5.3) (Appendix 5.D) (both main effect and squared term together: (ANOVA: $X^{2}_{11, 13} = 11.06$, $P = 0.004$)). The number of breeding pairs per CBC site was initially stable and then declined as SMD increased (Fig. 5.3). The number of breeding pairs per CBC site tended to increase with increased July to September SMD, but the relationship was not significant ($P = 0.09$) (Fig. 5.3). The number of breeding pairs tended to decrease on sandy soils (Fig. 5.4), but the relationship was not significant ($P = 0.06$) (Table 5.3, Appendix 5.D). There was a significant negative relationship between the number of breeding pairs per CBC site and woodland ($P < 0.001$)

and year (P < 0.001) (Table 5.3, Appendix 5.D). The number of breeding pairs per CBC site declined between 1981 and 2000 (Fig. 5.2).

	With Year in the Model	**Without Year in the Model**
One Year		
April to June Soil Moisture Deficit	m + m^{2} **	m *(-) m^{2} *** AJ **.**(-) AJ^{2} ***
July to September Soil Moisture Deficit		m *(+)
Area		
Habitat		
Woodland	*** (-)	***(-)
Other		
Soil Type		
Sandy soils	**.** (-)	.(-)
Loamy and clayey soils		
Sandy and loamy soils		
Peat soils		
Year	m ***(-)	
Two Years		
April to June Soil Moisture Deficit		m * (-)
July to September Soil Moisture Deficit	m ***(+) m^{2} *	m *** (+) m^{2} * JS *(+)
Area		
Habitat		
Woodland	***(-)	*** (-)
Other		
Soil Type		
Sandy soils		
Loamy and clayey soils		
Sandy and loamy soils		
Peat soils		
Year	***(-)	

. < 0.1, * < 0.05, ** < 0.01, *** < 0.001
(-) = negative relationship, (+) = positive relationship
m = main effect m^{2} = squared term
Squared terms for April to June soil moisture deficit, July to September soil moisture deficit and year were fitted. Only the best fit models are reported.
April to June (P <0.001) and July to September (P <0.001) soil moisture deficits are inter-correlated. Models were therefore run with each variable dropped in turn.
AJ and AJ^{2} = April to June SMD without July to September SMD.
JS and JS^{2} = July to September SMD without April to June SMD.

Table 5.3 Results of Generalised Linear Mixed Effects Models investigating the effect of spring (April to June) and summer (July to September) soil moisture deficit on Starling breeding populations at Common Bird Census survey sites (n=132) at a national scale between 1981 and 2000 with a one and two year lag.

Although April to June SMD and July to September SMD were significantly positively correlated they were not interchangeable within the full model, neither was April to June SMD and year. However, July to September

SMD and year were interchangeable within the full model. When year was dropped from the model the positive relationship between July to September SMD and breeding pairs per CBC site became significant (P = 0.03) (Table 5.3, Appendix 5.D).

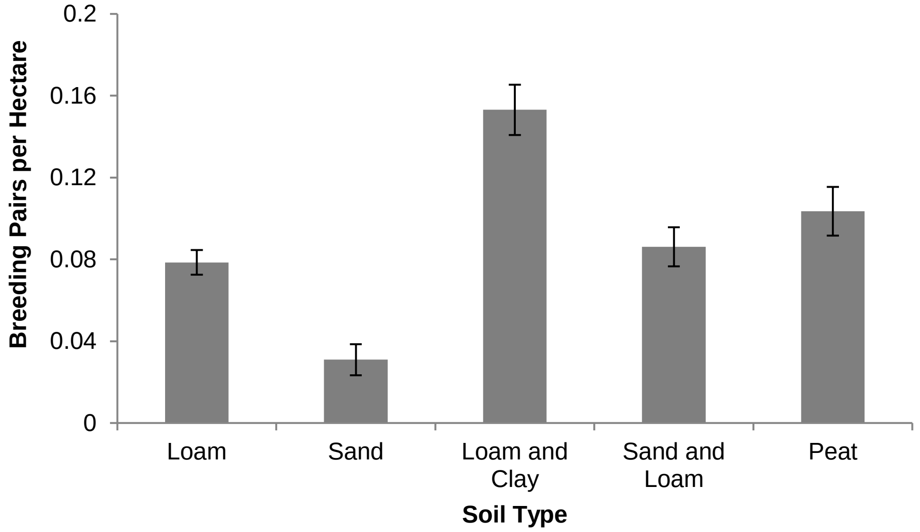

Figure 5.4 Mean number of Starling breeding pairs per hectare (± se) in relation to soil type on the Common Bird Census survey site (n=132). The number of breeding pairs tended to decrease on sandy soils, but the relationship was not significant (P = 0.06).

D. There was a significant relationship between July to September SMD two years earlier and breeding pair numbers per CBC site (July to September SMD: P < 0.001) (Table 5.3, Appendix 5.E). The number of breeding pairs per CBC site was initially stable and then increased as SMD increased (Fig. 5.5). The number of breeding pairs per CBC site tended to decrease with increased April to June SMD (Fig. 5.5), but the relationship was not significant (P = 0.27). There was a significant negative relationship between the number of breeding pairs per CBC site and woodland (P < 0.001) and year (P < 0.001) (Table 5.3, Appendix 5.E). The number of breeding pairs per CBC site declined between 1981 and 2000 (Fig. 5.2).

Although April to June SMD and July to September SMD were significantly positively correlated they were not interchangeable within the full model. When April to June SMD was dropped from the model July to September SMD squared term was no longer significant. The effect of July to

September SMD on its own was stronger than July to September SMD main effect and squared term combined. Therefore, only the results of the main effect were reported. July to September SMD and year were not interchangeable. However, April to June SMD and year were interchangeable within the full model. When year was dropped from the model the negative relationship between April to June SMD and breeding pairs per CBC site became significant (P = 0.01) (Table 5.3, Appendix 5.E).

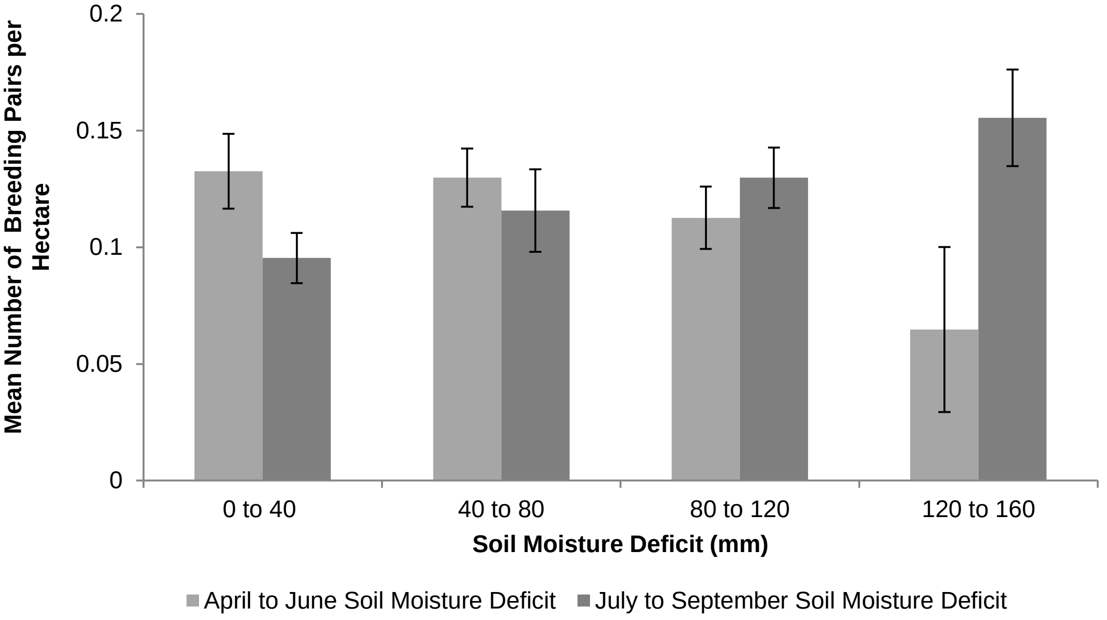

Figure 5.5 Mean number of Starling breeding pairs per hectare (± se) in relation to the mean soil moisture deficit of the Common Bird Census survey site (n=132) from April to June and July to September with a two year lag. The data suggests that the number of breeding pairs decreased as soil moisture deficit increased during April to June (P = 0.27), but increased with increased soil moisture deficit during July to September (July to September SMD: P < 0.001).

5.4 Discussion

The widespread declines of farmland birds have generally been linked to agricultural intensification and there is evidence of a temporal link between the two since the 1970s (Chamberlain *et. al.* 2000). Population effects could arise from reduced breeding productivity (Siriwardena *et al*. 2000), reduced survival (Siriwardena *et al*.1998), or a combination of the two. The mechanisms by which changes in management have affected ground-probing bird populations are diverse. In terms of reduced foraging opportunities during the breeding season there are known links to the loss of permanent pasture, the preferred foraging habitat of species such as the Starling, and the intensification of livestock management (Robinson *et al.* 2005). Specifically, the widespread spraying of grass fields to control Diptera spp. (Campbell & Cooke 1997; Garthwaite *et al.* 1997, Vickery *et al.* 2001), the decline in cattle and subsequent increase in sheep numbers that has resulted in different sward structures (Chamberlain *et al.* 2000, Fuller & Gough 1999, Devereux *et al*. 2004), the increased use of fertilizer that promotes taller, denser swards (Paoletti 1999) and the drainage of grassland (e.g. Smart *et al*. 2008). Starling population declines are thought to be as a result of decreases in survival rates, particularly of first-year birds over winter (Freeman *et al.* 2002, 2007). Here we show an additional independent correlative effect of soil moisture deficit (drier soils) during the spring (negative) and summer (positive) on Starling population changes at a national scale.

April to June soil moisture deficit was negatively correlated with Starling population change. These results concur with conclusions of previous chapters and are consistent with the idea that the drying of soils correlates with poor breeding performance (e.g. Song Thrush *Turdus philomelos L.* - Peach *et al.* 2004b, Chough *Pyrrhocorax pyrrhocorax L.* - Reid *et al*. 2008). Dry conditions result in fewer Tipulidae larvae prey and may result in more less nutritional items being provisioned to nestlings (see Chapter 4).

Contrary to *a priori* predictions, breeding numbers increased with July to September soil moisture deficit. An increased soil moisture deficit will occur as a result of decreased precipitation and increased temperature. Chick growth rate is known to be positively correlated with mean minimum temperature (Pearce-Higgins & Yalden 2002). In addition to the thermoregulatory costs of rain (e.g. Tinbergen & Dietz 1994), evidence suggest that birds reduce foraging during the rain and that feeding declines as rainfall becomes heavier (e.g. Kluijver 1950). Therefore, warm and dry conditions are preferable. During this time juveniles Starlings still feed predominantly on the ground but they will also gleen surface-dwelling invertebrates and fruit and may roam quite widely (Feare 1984). Overall it appears that a combination of wet (soil moisture deficit below 80 mm) spring and drier summers (soil moisture deficit over 80 mm) is best (Fig. 5.6).

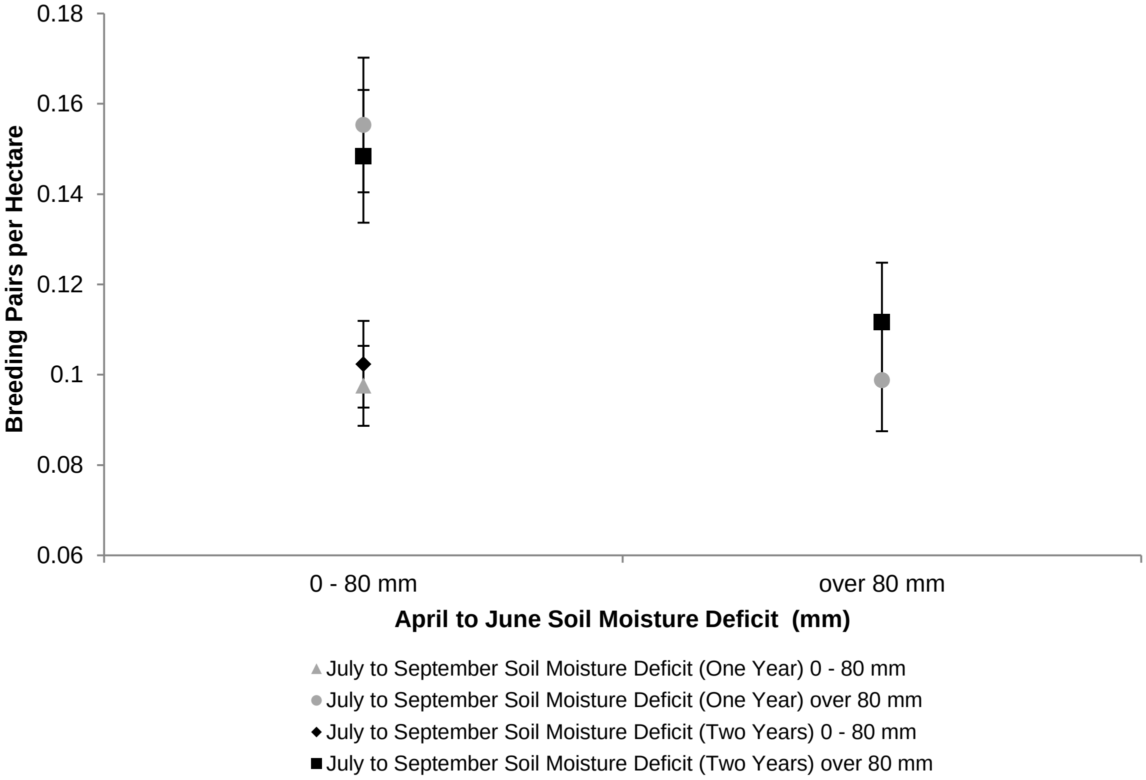

Figure 5.6 Mean number of Starling breeding pairs per hectare (± se) on Common Bird Census sites (n=132) in relation to April to June and July to September soil moisture deficit one year and two years earlier. Common Bird Census sites that experience wet conditions April to June followed by dry conditions July through to September have more breeding pairs per hectare.(Note – April to June soil moisture deficit refers to sites with 0-80mm and over 80mm to both one and two years earlier)

From these results it may be concluded that, although warm, dry summers appear to be beneficial to fledgling Starlings, future increases in spring SMD, as predicted by the IPCC (2001), will have a continued detrimental effect on Starling breeding populations, as well as those of other ground probing birds. Due to the spatial resolution of our *MORECS* data (40km^2), varying effects of soil type were not apparent. However, previous results have highlighted a complex relationship between soil type (hydraulic conductivity), soil moisture deficit and penetration resistance (see Chapter 4). For example, sandy soils can have greater penetration resistance when wet than dry and on clay loam the penetration resistance of soils at intermediate levels of soil moisture will be higher than those that have been subjected to water logging or drought (Rajaram & Erbach 1998). This relationship will vary with soil texture and relative compaction (Whalley *et al*. 2007).

A recent study by Eglington and Pearce-Higgins (2012) modelled the annual variation in population growth of 18 farmland bird species in the UK since the 1960s as a function of measures of land-use intensity and climate (inferred from weather trends). They concluded that despite more stable land-use intensity since the 1990s land use change has continued to be the dominant driver of farmland bird population changes. However, in the future, the effects of climate change may exceed that of agriculture intensification. This information is therefore critical to determining management of habitats to enhance below-ground prey abundance and accessibility (e.g. Devereux *et al*. 2004; Whittingham & Devereux 2008). If precipitation is low in the breeding season (spring), maintaining a high water table is likely to be crucial for ground probing birds, whilst avoiding waterlogging in the summer is also likely to benefit this group. A series of features such as footdrains or rills could be used to control water levels and these practical management options will be discussed in the next chapter.

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Appendix 5.A

The number of *MORECS* squares and Common Bird Census (CBC) sites included in the analysis by year.

Year	**Number of *MORECS* Squares**	**Number of CBC Sites on Farmland**	**Number of CBC Sites on Other**	**Number of CBC Sites on Woodland**
1980	40			
1981	37	28	6	19
1982	38	27	6	20
1983	37	30	6	20
1984	37	29	6	21
1985	33	30	6	18
1986	37	33	6	18
1987	35	28	2	17
1988	32	27	2	18
1989	37	41	0	13
1990	41	43	0	18
1991	41	44	2	16
1992	43	48	2	17
1993	43	42	2	17
1994	38	47	1	16
1995	38	44	1	17
1996	41	45	1	16
1997	33	40	1	21
1998	38	33	1	19
1999	38	32	2	17
2000	30	26	1	16
Total Number of Available Sites	67	85	6	41

Appendix 5.B

Results of a generalized linear mixed-effects model (GLMM) of the mean April to June soil moisture deficit at *MORECS* squares (n= 67) as a function of year. The GLMM was fit using the REML criterion method.

Fixed effects	**Estimate**	***SE***	**df**	**t**	**P**
Intercept	4.03	0.45		9.02	< 0.001
Year	194.79	21.13	1	9.22	< 0.001
Year ^{2}	-192.38	20.89	1	-9.21	< 0.001

AIC: 2691, Random effects (variance): square= 030.

Appendix 5.C

Results of a generalized linear mixed-effects model (GLMM) of the mean July to September soil moisture deficit at *MORECS* squares (n= 67) as a function of year. The GLMM was fit using the REML criterion method.

Fixed Effects	**Estimate**	**se**	**df**	**t**	**P**
Intercept	0.65	0.38		1.72	0.09
Year	33.80	17.56	1	1.93	0.05
Year ^{2}	-33.40	17.36	1	-1.92	0.05

AIC: 2338, Random effects (variance): square= 0.56.

Appendix 5.D

Results of a generalized linear mixed-effects model (GLMM) of the number of Starling breeding pairs at Common Bird Census sites (n= 132) as a function of April to June and July to September soil moisture deficit (SMD) one year earlier, site area, habitat type and soil type, accounting the previous year's count as an offset. The GLMM was fit using the Laplace method.

Fixed Effects	Estimate	SE	z	P
Full model with year [a]				
Intercept	-0.36	0.05	-7.25	< 0.001
April to June SMD	-0.03	0.02	-1.54	0.12
April to June SMD^2	0.04	0.01	3.50	< 0.001
July to September SMD	0.04	0.02	1.68	0.09
Site area	0.02	0.02	0.76	0.45
Year	-0.07	0.02	-4.13	< 0.001
Habitat category – other	-0.02	0.09	-0.26	0.80
Habitat category –woodland	-0.24	0.06	-4.04	< 0.001
Sandy soils	-0.35	0.18	-1.91	0.06
Loamy and clayey soils	0.07	0.05	1.24	0.21
Sandy and loamy soils	0.14	0.10	1.40	0.16
Peat soils	0.06	0.14	0.44	0.66
Full model without year [b]				
Intercept	-0.36	0.05	-7.31	< 0.001
April to June SMD	-0.05	0.02	-2.60	0.01
April to June SMD^2	0.04	0.01	3.47	< 0.001
July to September SMD	0.05	0.02	2.15	0.03
Site area	0.02	0.02	0.97	0.33
Habitat category – other	0.04	0.09	0.41	0.68
Habitat category –woodland	-0.20	0.06	-3.49	< 0.001
Sandy soils	-0.33	0.18	-1.80	0.07
Loamy and clayey soils	0.07	0.05	1.40	0.16
Sandy and loamy soils	0.14	0.10	1.37	0.17
Peat soils	0.10	0.13	0.75	0.46
April to June SMD without July to September SMD [c]				
Intercept	-0.36	0.05	-7.28	< 0.001
April to June SMD	-0.03	0.02	-1.68	0.09
April to June SMD^2	0.04	0.01	3.22	0.001
Site area	0.02	0.02	0.99	0.32
Habitat category – other	0.07	0.09	0.80	0.42
Habitat category –woodland	-0.19	0.06	-3.29	0.001
Sandy soils	-0.32	0.18	-1.74	0.08
Loamy and clayey soils	0.08	0.05	1.49	0.14
Sandy and loamy soils	0.15	0.10	1.54	0.12
Peat soils	0.06	0.14	0.45	0.66

July to September SMD without April to June SMD [d]				
Intercept	-0.31	0.05	-6.63	0.003
July to September SMD	0.02	0.02	1.12	0.26
Site area	0.02	0.02	0.85	0.40
Habitat category – other	0.06	0.09	0.67	0.51
Habitat category –woodland	-0.20	0.06	-3.47	0.001
Sandy soils	-0.33	0.18	-1.79	0.07
Loamy and clayey soils	0.07	0.05	1.33	0.19
Sandy and loamy soils	0.14	0.10	1.37	0.17
Peat soils	0.13	0.14	0.93	0.35

[a] AIC: 1441, Random effects (variance): site= 0.02.
[b] AIC: 1455, Random effects (variance): site= 0.01.
[c] AIC: 1455, Random effects (variance): site= 0.01.
[d] AIC: 1465, Random effects (variance): site= 0.01.

Appendix 5.E

Results of a generalized linear mixed-effects model (GLMM) of the number of Starling breeding pairs at Common Bird Census sites (n= 132) as a function of April to June and July to September soil moisture deficit (SMD) two years earlier, site area, habitat type and soil type, accounting for the previous year's count as an offset. The GLMM was fit using the Laplace method.

Fixed Effects	**Estimate**	**SE**	**z**	**P**
Full model with year [a]				
Intercept	-0.39	0.07	-5.92	< 0.001
April to June SMD	-0.02	0.02	-1.11	0.27
July to September SMD	0.11	0.03	3.92	< 0.001
July to September SMD ^{2}	0.04	0.02	2.31	0.02
Site area	0.00	0.03	0.06	0.95
Year	-0.13	0.02	-5.87	< 0.001
Habitat category – other	-0.13	0.12	-1.06	0.29
Habitat category –woodland	-0.43	0.08	-5.40	< 0.001
Sandy soils	-0.35	0.23	-1.52	0.13
Loamy and clayey soils	0.07	0.07	0.97	0.33
Sandy and loamy soils	0.13	0.14	0.94	0.35
Peat soils	0.13	0.19	0.68	0.50
Full model without year [b]				
Intercept	-0.39	0.06	-6.16	< 0.001
April to June SMD	-0.06	0.02	-2.74	0.01
July to September SMD	0.11	0.03	4.13	< 0.001
July to September SMD ^{2}	0.04	0.02	1.91	0.06
Site area	0.01	0.03	0.30	0.76
Habitat category – other	-0.02	0.12	-0.13	0.89
Habitat category –woodland	-0.37	0.08	-4.78	< 0.001
Sandy soils	-0.30	0.23	-1.32	0.19
Loamy and clayey soils	0.08	0.07	1.18	0.24
Sandy and loamy soils	0.13	0.13	0.98	0.33
Peat soils	0.19	0.18	1.09	0.28
April to June SMD without July to September SMD [c]				
Intercept	-0.36	0.06	-5.79	< 0.001
April to June SMD	-0.01	0.02	-0.61	0.54
Site area	0.01	0.03	0.23	0.82
Habitat category – other	0.07	0.12	0.61	0.54
Habitat category –woodland	-0.36	0.08	-4.46	< 0.001
Sandy soils	-0.28	0.23	-1.23	0.22
Loamy and clayey soils	0.09	0.07	1.27	0.20
Sandy and loamy soils	0.17	0.14	1.22	0.22
Peat soils	0.15	0.18	0.84	0.40

July to September SMD without April to June SMD [d]				
Intercept	-0.38	0.06	-5.98	< 0.001
July to September SMD	0.07	0.02	3.12	0.002
July to September SMD ^{2}	0.03	0.02	1.41	0.16
Site area	0.01	0.03	0.20	0.84
Habitat category – other	0.02	0.12	0.18	0.86
Habitat category –woodland	-0.36	0.08	-4.65	< 0.001
Sandy soils	-0.29	0.23	-1.26	0.21
Loamy and clayey soils	0.08	0.07	1.23	0.22
Sandy and loamy soils	0.13	0.13	0.96	0.33
Peat soils	0.21	0.18	1.15	0.25

[a] AIC: 1584, Random effects (variance): site= 0.04.
[b] AIC: 1616, Random effects (variance): site= 0.04.
[c] AIC: 1625, Random effects (variance): site= 0.04.
[d] AIC: 1621, Random effects (variance): site= 0.04.

Chapter 6: Can Ecosystem Services be integrated with Conservation? A Case Study of Breeding Waders on Grassland

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6.0 Abstract

Capsule There is a limited base of evidence on which to assess the potential linkage between ecosystem services and habitat management for grassland birds that obtain their food predominantly by probing the soil, particularly for non-wading bird species.

Aims (i) To describe the link between soil moisture, foraging by grassland waders and their macroinvertebrate prey, (ii) To examine evidence for population-level effects of soil moisture changes on waders and (ii) To review management options that could alter ecosystem services and habitat quality for farmland birds that derive the majority of prey from the soil.

Methods We review published studies to show that changes in soil moisture levels have significant impacts on a range of wading bird species that use UK lowland grassland, including wet grassland, and obtain their food predominantly by probing the soil. We examine both the hydrological and ecological literature and review how management options could alter (A) ecosystem services (via water quality and flooding) and (B) habitat quality for wading birds.

Results Combining biodiversity goals with broader ecosystem services has been widely advocated and we find that appropriate management at multiple scales (e.g. small-scale: ponds; large-scale: integrated washlands) could potentially provide both ecosystem services and habitat for wading grassland birds.

Conclusion We suggest that future work be directed at identifying (i) how crop yield, ecosystem services and biodiversity relate to each other, (ii) the extent of land needed to be managed in order to benefit these multiple purposes and bring about measurable gain (e.g. one or two ponds may make significant inroads in reducing run-off and pollution but make little difference to wading birds) and (iii) solutions to the challenges of setting up management options on large spatial scales (e.g. catchments).

6.1 Introduction

It is well established that farmland bird population declines are strongly linked to agricultural intensification (e.g. Donald *et al*. 2001) and that changes in climate are also predicted to affect these bird populations (Huntley *et al*. 2007). Climate change is likely to have a significant regional impact on groundwater levels and the availability of suitable feeding habitat, through a combination of changes in seasonal rainfall and rising sea levels (Hulme *et al*. 2002). In addition, agriculture, on a global scale, faces the challenge of providing food for approximately 50% more people by 2050 (Green *et al*. 2005). There is increasing interest in ecosystem services as a means of accounting for the full range of environmental, social and economic benefits provided by land management. A multi-functional farming landscape could potentially provide food, ecosystem services (e.g. flood control) and suitable habitats for biodiversity. Given that demands on land will increase, one key issue for the conservation of biodiversity is whether it can be linked directly to the provision of wider ecosystem services for which political pressure and budgets are often greater. This idea has been proposed in the literature many times (e.g. Morris *et al*. 2004, McInnes 2007). Here, we review the literature to provide examples to test this idea using birds feeding predominantly on soil invertebrates in lowland grass fields in the UK.

We reviewed the hydrological and ecological literature to describe (i) changes in soil moisture on lowland grassland, (ii) the link between soil moisture, foraging by farmland birds and their macro-invertebrate prey, (iii) evidence for population level effects of soil moisture changes on birds and (iv) how changes in climate, via rainfall patterns and rising sea levels, may alter grassland. We reviewed 251 papers resulting from a literature search in the ISI Web of Knowledge (up to 18 September 2009) using a combination of search terms including the keywords ‘UK, grassland, breeding/wintering birds, invertebrates, flooding, pollution, legislation and wetland’. The initial aim of the review was to consider all bird species living on farmland. However, most of the relevant literature identified focused on waders. Therefore, the study focuses on this group, with reference to studies of other bird species in the discussion. Finally, we summarise how proposed management options may affect both hydrology and farmland birds that derive the majority of their invertebrate prey from the soil. We consider how these management options could be applied in two different situations: (1) protected areas in which the main focus is nature conservation and (2) the wider countryside in which the focus of land-use is varied but typically focuses on agricultural yield.

6.2 Mechanisms leading to the decline in area and suitability of lowland grassland habitat

6.2.1 Direct effects of land drainage

The main aim of lowering the water table of wet grasslands was to facilitate reduced water-logging in the upper layers of soil to increase the length of the grazing season (Bradbury & Kirby 2006). By the end of the 19th century most of lowland England's wetlands (Werritty 2006) and 5 million hectares of lowland floodplains (Smout 2000) had been drained and converted into productive agricultural land. Many of these drainage systems fell into disrepair during a period of agricultural recession, following a collapse in farm prices after World War I (Dobbs & Pretty 2004). To prevent further recession (Dobbs & Pretty 2004) and promote national self-sufficiency in food production (O'Connell *et al*. 2004), the UK government encouraged intensification and modernisation of British agriculture from 1930 onwards. Existing drainage systems were restored and, to increase agricultural output, the drainage of additional wetlands was encouraged through government subsidies (Acreman *et al*. 2007). In the 1970s, the practice reached a peak of around 100 000 ha/year and was particularly common in the clay-dominated arable areas of eastern England (Green 1979). In addition, complex ditch networks, which naturally divided wetlands into small fields (Thompson 2004) and maintained high water tables, were removed to create larger fields. Few of the remaining ditches retain moisture throughout the year due to under-field drainage.

On grassland, loss of botanical heterogeneity and invertebrate species-richness is often associated with improved drainage and the subsequent increased use of fertiliser, reseeding with ryegrass mixes, increased stocking densities and earlier grazing seasons (Morris 2000, Wilson *et al*. 2005). Short periods of high-intensity stocking on clay grazing marshes and the use of heavy machinery result in the formation of a hard surface mat of vegetation and compaction of the soil, leading to high surface penetration resistance

(Armstrong 2000, Hamza & Anderson 2005). Increased fertiliser application is likely to (1) have a negative impact on the existing soil moisture deficit because increased availability of nitrogen for plant uptake increases plant growth and evapotranspiration (Garwood 1988) and (2) reduce plant diversity and consequently the range of invertebrate prey present in the sward (McCracken & Tallowin 2004). These reduce both abundance and accessibility of food for wading birds. In addition, nests and chicks are vulnerable to trampling by livestock (e.g. Green 1988) and the timing of stock turn-out and mowing is known to inhibit re-nesting and therefore limit breeding success (Beintema & Muskens 1987).

Widespread land drainage over the last 200 years has resulted in a reduction in the quantity of grassland through conversion of wetland habitats to arable farmland. Subsequent intensive management of the remaining grassland resource means that it is of limited quality for wading birds through reductions in suitable nesting habitat, direct effects of trampling on nests/chicks, soil degradation and compaction and reduced abundance, availability and access to invertebrate prey.

6.3 Current policy

Grassland systems outside areas managed specifically for other purposes (e.g. nature reserves focused on biodiversity needs) primarily produce agricultural goods (mainly grass for fodder). These agricultural grass fields could potentially yield a range of indirect benefits, including flood protection, biodiversity and high water quality. Funds previously committed to support farm output are increasingly diverted to encourage land managers to deliver these environmental benefits (Defra 2002). A number of specific measures promoted by these policies are likely to become increasingly important in the conservation and protection of water resources. However, the voluntary nature of the schemes may result in poor uptake (Davey *et al*. 2010). Also, if payments are not considered sufficient, farmers will be reluctant to install measures that they may perceive to be detrimental to their livelihoods. Currently, there is little research on the trade-offs between agricultural yield, ecosystem services and biodiversity (e.g. Vickery *et al*.1994, Morris *et al*. 2008) upon which to base policy decisions and guide levels of compensation schemes.

Increasingly, government and conservation agencies now recognise the benefits of a systematic approach to conservation, with clear objectives and measurable targets, and the need to integrate grassland management with wider issues relating to water management (e.g. flood mitigation) (Benstead *et al*. 1997). For example, the governmental strategy for flood risk management in England, '*Making Space for Water'*, emphasises the need for integrated land and water management through ecological enhancement and non-structural solutions (e.g. wetlands), to 'reduce the threat to people and their property and deliver environmental, social and economic benefit consistent with sustainable development principles' (Defra 2005a). The ecosystem approach was first adopted by the Convention for Biological Diversity (CBD), in 1992. It provides a framework for the integrated management of land, water and living resources to achieve a number of CBD objectives, including the conservation of biodiversity and the sustainable use of its components. Since then it has been adopted across the European Union (EU) as an approach through which to deliver several environmental directives, strategies and agreements (Apitz *et al.* 2006, McInnes 2007) and to achieve sustainable development, through the maintenance of fully functioning ecosystems (Laffoley *et al*. 2004). The ecosystem services approach is now more widely recognised and reflects the emphasis placed on the benefits that society can derive from ecosystems: provisioning, regulating, supporting and cultural (Millennium Ecosystem Assessment (MEA) 2005). Within the EU, the Water Framework Directive (WFD) promotes the integration of land-use and water policy and the positive use of floodplains through the development of River Basin Management Programmes, by member states. To meet the ecological water standards set by the WFD, member states are required to address issues relating to sustainable water resource management in individual river basin management systems. In England, projects such as the Fens Floodplain Project, part of the EU's Wise Use of Floodplains Project, assess how floodplain wetlands contribute to water resource management and identify ways to help implement the WFD throughout the EU. Catchment Flood Management Plans have also been developed by the Environment Agency to monitor the effects of factors such as changes in land management, loss of habitat and climate change on floods at the river catchment scale, with an aim to identifying effective methods of long-term integrated flood risk management (Environment Agency 2004). Because of the need to comply with multiple objectives that may be the remit of different government and non-governmental organisations and departments, partnership working and cross-stakeholder support is central to the successful application of the ecosystem services approach (ELP 2008). To understand how best to manage grasslands to achieve different goals, such as nature conservation, maximising agricultural yield (to maintain food security) and minimising flood risk, research needs to address how the different competing needs relate to each other.

6.4 Soil moisture, wading birds and their prey

6.4.1 Soil penetrability, wader foraging and habitat selection

A range of wading species that feed predominantly on soil invertebrates are associated with lowland grasslands during the breeding season (Common Snipe *Gallinago gallinago* L. Green 1986; Common Redshank *Tringa totanus* L. and Northern Lapwing *Vanellus vanellus* L. Baines 1990, Ausden *et al*. 2003 and European Golden Plover *Pluvialis apricaria* L. Pearce-Higgins & Yalden 2003). These species feed on macro-invertebrates such as earthworms and tipulid larvae. Grassland also provides foraging opportunities for a number of species during the winter, including Golden Plover and Lapwing (Fuller &Youngman 1979, Tucker 1992). Permanent pasture (grass more than 5 years old) is of particular importance because of significantly higher earthworm biomass compared to other field types (e.g. bare till, winter cereal) (Tucker 1992).

Soil surface strength is correlated with soil moisture content. For most soils, this is associated with the water table depth from the surface (Armstrong 2000). Raised water levels keep the surface soil moist, increase soil surface penetrability (Gerard 1967, Green *et al*. 2000) and reduce vegetation growth when surface water is present (Ausden *et al*. 2001). The lowering of field water levels reduces soil penetrability, making the ground too hard for surface probing. It should be noted, however, that the relationship between soil moisture and penetration resistance can differ between soil types. For example, sandy soils can have greater penetration resistance when wet than dry. Soil types can be differentiated by their hydraulic conductivity (Armstrong 1993). For instance, clay soils have low hydraulic conductivity; water will not move easily through these soils and they tend to retain surface water for long periods. Peat soils tend to have highly variable hydraulic conductivity, influenced by soil particle size, shape and structure and degree of decomposition (Wong *et al*.2009). There is a range of other factors, such as aspect, slope and vegetation cover, that will further alter soil moisture. However, changes in the water table are likely to result in variations in soil moisture and have been shown to have marked effects on waders. Green (1988) used a penetrometer to measure the maximum force (kgF) required to push a steel probe 10cm into the soil, mimicking the behaviour of the beak of a Snipe and providing a measure of penetration resistance (Green 1986, 1988, Green *et al*.1990). Soil surface penetrability is an indirect measure of soil moisture that provides an indication of the difficulty a bird might be expected to have when probing the soil to forage (Armstrong 2000).

Wet features, such as ponds, ditches, footdrains and rills (Table 6. 1) may retain water throughout the breeding season, maintaining a higher water table in the surrounding soil than in other parts of the field. The area affected is dependent on soil type. Milsom *et al*. (2000) established that the distribution of breeding Redshank and Lapwing on coastal grazing marshes is strongly positively influenced by the availability of rills that retained water in early June. Footdrains have been successful in maintaining localised shallow surface water in spring and the density of associated ‘footdrain floods’ positively influences field selection in Lapwings (Eglington *et al*. 2008). As birds concentrate on water margins to feed, the perimeter of these wet features is more important than their area. Redshank breeding densities are positively correlated with wet feature length, the combined total of rills, footdrains and pools (Fig. 6.1) (Smart *et al*. 2006). The success of any scheme of wet feature creation is dependent on the ability to maintain wetness throughout the breeding season. In the case of breeding Snipe, drying out can lead to limited opportunities for replacement nesting after early breeding failures, as breeding ceases when the penetration resistance exceeds 5.8 kgF (Green 1988). However, when good feeding conditions persist (e.g. penetration resistance is < 5.8kgF) Snipe will continue to initiate nests well into July, potentially doubling the number of chicks hatched (Green 1988). It is important to note two caveats: (1) above-ground prey (on which many wading species also feed) could also be an important influence on distribution and (2) soil moisture can affect prey both within and above the soil surface.

	Definition
Pond	A body of water, both natural and man-made, between 1-2 m² and 2 ha in area, which may be permanent or seasonal (Davies *et al*. 2008a, Williams *et al*. 2008).
Paired ponds	Paired ponds, varying in size from 1.5m² to approximately 50m², located alongside field ditches. The upper pond is fed by water diverted from the ditch and the second pond is fed, via a vegetated buffer strip, from the first pond, before overflowing back to the ditch system (Bailey *et al*. 2007).
Ditch	Man-made channel created primarily for agricultural purposes and which usually follow linear field boundaries (Davies *et al*. 2008a).
Bunded ditch	An existing ditch which has been dammed (bunded), to retain water (Bailey *et al*. 2007).
Footdrain	A shallow channel historically used for drainage on grazing marshes (Eglington *et al*. 2008).
Footdrain flood	An area of surface flooding resulting from water spilling over from footdrains (Eglington *et al*. 2008).
Rill	Relict salt-marsh creek and drainage channels (Milsom *et al*. 2000).
Small Constructed Wetland	A wetland constructed in a terraced design to reduce downhill flow velocity by means of a series of weirs (Raisin *et al*. 1997).
Wetland	'Areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres' (Ramsar Convention 1971).
Washland	'An area of the floodplain that is allowed to flood or is deliberately flooded by a river or stream for flood management purposes, with potential to form a wetland habitat' (Morris *et al*. 2004).

Table 6.1 Definitions of wet feature types

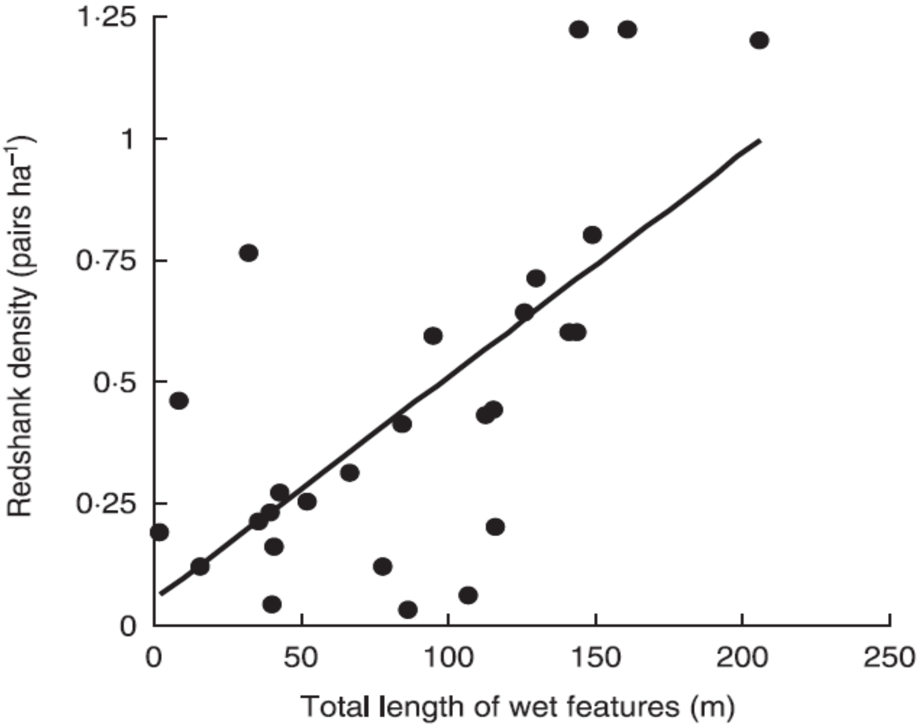

Figure 6.1 The relationship between Redshank breeding density and the total length of wet features (footdrains, rills, pools and ditches) in fields occupied by breeding Redshank on grazing marshes ($y= 0.005x + 0.052$, $R^2 = 0.47$, $n=27$, $P < 0.001$) (Smart *et al*. 2006 – reproduced with permission from *J. Appl. Ecol*).

6.4.2 Soil invertebrates

Moist soils support larger densities of soil invertebrates than dry soils (Milsom *et al.* 2000). Moisture is one of the main factors determining earthworm abundance in the top 5–10 cm of soils (Gerard 1967, Green *et al*. 2000, Peach *et al*. 2004a) and influences pupation rates and larvae survival of terrestrial (Meats 1974) and obligate aquatic invertebrates. As the soil surface dries out, earthworms descend deeper into the soil and become unavailable to foraging birds, forcing them to switch to potentially less nutritional invertebrate prey (Gruar *et al*. 2003). Important prey, such as crane flies (e.g. *Tipula paludosa* L.), can be adversely affected by desiccation if the soil dries out quickly at a vulnerable stage in their life-cycle (McCracken *et al.* 1995). The maintenance of high water tables until mid-summer is therefore important for ensuring that earthworms remain within reach of probing birds and that soil invertebrate larvae remain viable as prey.

On sites subjected to flooding, the water-holding capacity and organic matter content of soil will have an influence over invertebrate survival because prolonged water-logging can have an adverse affect on soil-dwelling invertebrates and larvae (McCracken *et al.* 1995, Plum 2005). Tipulid larvae may die as a result of surface flooding (Meats 1970) and decaying vegetation on previously fertilised grassland can cause anoxic conditions harmful to the soil fauna (Ausden *et al*. 2001). Managed surface flooding is used to increase the area of shallow flooded grassland and soft, wet soil conditions available for breeding waders. However, prolonged surface flooding in winter and/or spring reduces the abundance of soil macro-invertebrates and can result in compaction and consolidation of the upper soil, making it difficult for birds to probe (Ausden *et al*. 2001).

When flooding is (re)introduced in grassland, initially it can attract large numbers of wading birds as prey migrate to the soil surface, but numbers decline with time as terrestrial soil invertebrates species struggle to survive in soil with prolonged flooding. Ausden *et al*. (2001) found soil macro-invertebrate densities in unflooded pasture land were 10 times higher than in flooded wet pasture land. If flooding is at a large spatial scale, re-colonisation by macro-invertebrates from unflooded refuges is unlikely to occur (Plum & Filser 2005) due to the negative effect of regular flooding on spring populations of soil macrofauna. To maintain viable populations of annelids, the time interval between two flood events should not exceed the development time from cocoon to adult of the earthworm species present (approximately 6 months) and during the spring, when earthworms serve as food for ground-probing birds, a new inundation in this recovery period should be avoided or kept short (Plum & Filser 2005). A trade-off therefore exists between maintaining optimum soil penetration resistance for probing birds and the adverse effects of too much flooding (Smart *et al*. 2008). Unflooded grassland provides a high biomass of soil macro-invertebrates beneath vegetation, whereas winter flooded grassland provides damp surface soil with short, open conditions for feeding.

Prime conditions for both invertebrate survival and reproduction and for foraging waders require a trade-off between soil conditions. Dry summer soil conditions result in the death of invertebrate larvae and force earthworms to descend deeper into the soil, thus reducing prey availability. Conversely, prolonged flooding results in invertebrate prey that are accessible but at low abundance because excessive water-logging reduces populations. The exact requirements of different wading bird species at different times of year are likely to differ in the precise optima of this relationship but the general themes described above are likely to hold.

6.5 Changes in soil moisture and wader populations

Wet grassland breeding wader distribution is strongly related to site wetness (e.g. Green & Robins 1993, Vickery *et al*. 1997, Paillissona *et al*. 2002). In the Somerset levels, the range contraction of breeding Snipe and Redshank accompanied the acceleration of drainage improvement that began in the late 1960s (Williams & Bowers 1987). Recent work has shown that Snipe breeding populations are more likely to have persisted in fields where the soil conditions are wet and soft (Fig. 6. 2, Smart *et al*. 2008). Despite the introduction of management aimed at improving conditions, breeding Snipe populations have continued to decline (Ausden *et al*. 2001, Ausden & Hirons 2002, Wilson *et al.* 2004) with declines more marked on mineral soils and in the south and east of England (Smart *et al*. 2008).

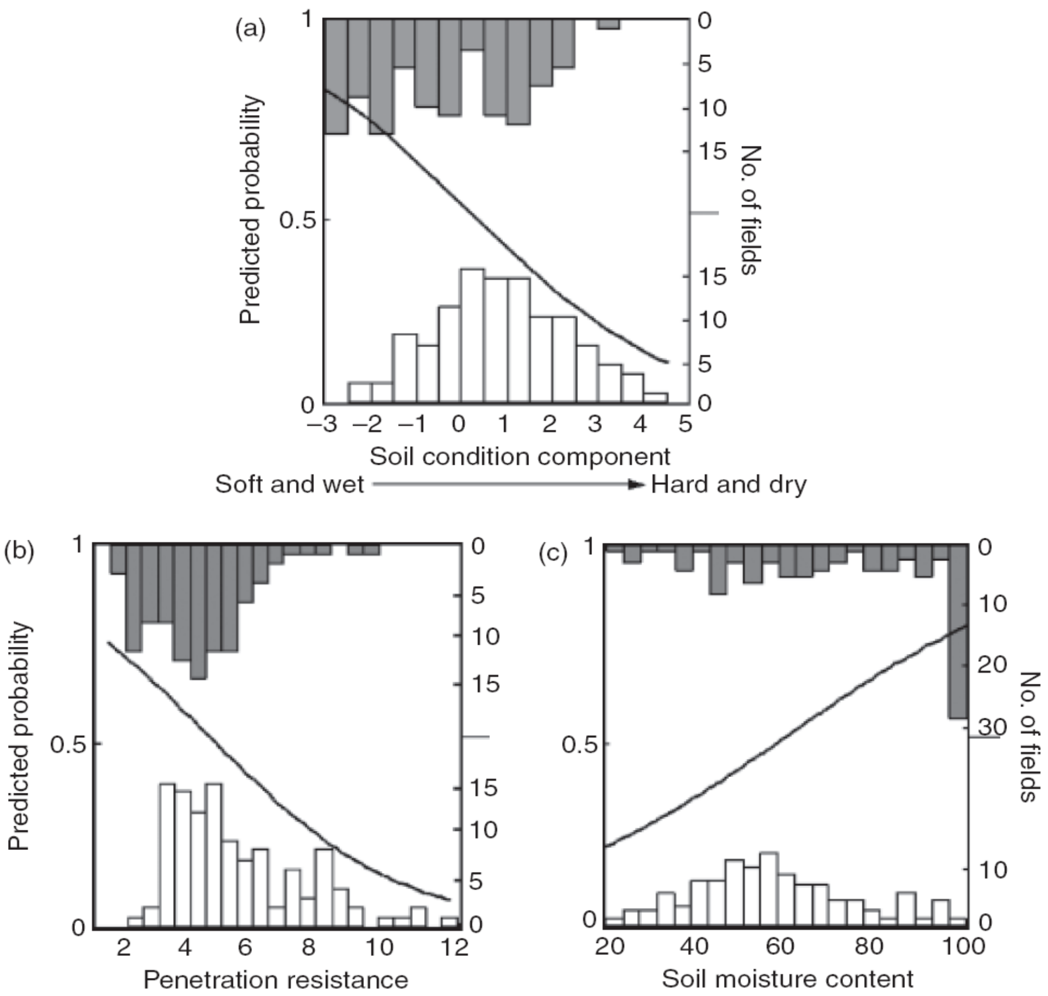

Figure 6.2. The probability of breeding Snipe *Gallinago gallinago* populations in fields persisting (numbers maintained, gained or increased) or becoming extinct between episode 1 (1990/1991/1992) and episode 2 (2006) in relation to (a) the soil condition component which is the gradient from soft and wet to hard and dry soil conditions, (b) penetration resistance (mean visits 2 and 3, kgF) and (c) soil moisture content (mean visits 2 and 3, % water). Bars show the frequency distribution for fields where Snipe persisted (grey bars) and fields where Snipe became extinct (white bars). The line shows the fitted logistic regression curve (Smart *et al*. 2008 – reproduced, with permission, from *Anim. Conserv.*).

Wader population trends are affected by a range of factors e.g. conversion of grassland to arable (Robinson & Sutherland 2002). However, in England, declines of wader species have been so extreme that 64% of wet grassland wader populations are currently concentrated onto eight key wet grassland sites. These declines may have been driven by changes in wetness rather than land-use change because, since 1982, there has been little further loss of grassland habitat (Wilson *et al*. 2005).

6.6 Climate change and grassland

Future UK climate change scenarios predict that, by the 2080s, annual average temperatures are likely to rise by more than 2ºC. In the southwest, summer precipitation may decrease by up to 40%, under the medium emissions scenario (Jenkins *et al*. 2009) and large parts of England may experience more than a 40% reduction in summer soil moisture (Hulme *et al*. 2002). It is likely that the UK will experience ‘higher water demand, more widespread water stress with increased risk of drought, more water quality problems, as well as more extreme downpours with a higher risk of flooding’ (Defra 2008). Flood protection and biodiversity will be lost as wetland habitats are destroyed or dry out (Defra 2008). Increased transpiration and evaporation and reduced rainfall in some regions will put further pressure on remaining wetland habitats, resulting in lower soil water table levels in late summer/autumn (pers. comm. Mike Acreman 2007, in Hume 2008). Increased frequency of winter/spring flooding or summer droughts could also have a detrimental affect on the suitability of remaining grazing marsh habitats (Ausden *et al*. 2001, Milsom *et al*. 2002).

In addition to the changes in climate, over 50% of grade one agricultural land, predominantly in the southeast of England, will be at risk of flooding due to rising sea levels (NFU 2005). Flooding, particularly by saline water, and water-logging have major implications for land use, farming practices, productivity and farm incomes to the point where farming futures will be threatened (Morris *et al.* 2003). Although most grasslands are in the west, rising sea levels will have a significant impact on coastal grasslands and grazing marshes (e.g. the UK extensive grazing marshes in Kent and Sussex).

6.7 Options for grassland management

We consider here potential land-management options for grassland and how they may, or have been shown to, affect wading bird species. We assess how these relate both to land managed specifically for conservation and land-management options which are more likely to be useful when applied to the wider countryside.

6.7.1 Protected areas

Raising water levels is known to affect waders positively. However, there are negative consequences for crop yields and so this type of option is more likely to be used in protected areas than in the wider countryside. There are several ways to raise water levels such as ditches and rills.

Ditches, modified to stay wet longer through the use of water-retaining structures such as penning boards, sluice gates or bunds, could display many of the same attributes as ponds (Bradbury & Kirby 2006). The *Wetting Up Farmland for Birds and other Biodiversity* project is currently examining the use of bunded (dammed) ditches (Table 6.1) to provide wet features for farmland birds (Bailey *et al*. 2007). Bunded ditches retain water and create wet areas alongside fields, creating greater availability of damp soil and more areas of permanent water, thus making water more available at critical times during the year. Ditches may be beneficial to farming systems by providing water for irrigation and stock.

Arterial drainage infrastructure influences the ability to manage water tables in field centres (Armstrong & Rose 1999). Eglington *et al*. (2008) described how by using a system of pumps and sluices, water levels could be raised in ditches and fed out into the centre of the grazing marshes using footdrains. Water levels can be raised to over-top footdrains, creating a mosaic of unflooded grassland interspersed with wet features and areas of shallow surface water, favoured by waders during the breeding season. An important feature of footdrains is that they provide a high level of control over surface water and cause little disruption to activities such as livestock management and sward production (Eglington *et al*. 2008), offering a management option that could be used on lowland wet grassland sites in the wider countryside. Footdrains could also act as water storage during drought periods and drainage channels during flooding events (Eglington *et al*. 2008).

6.8 Wider countryside

There are a range of options at different scales which could be used in the wider countryside. Flood risk management often relies on multiple management options, co-ordinated within a large catchment. The placement of these management options offers the potential for gains for biodiversity, such as waders. We begin by looking at the small-scale options and then move on to the co-ordinated catchment scale options.

6.8.1 Small-scale solutions

Ponds serve two purposes: pollution control and reduction of flood risk. Their effectiveness in controlling pollution is subject to location. For example, upstream wetlands (Table 6.1) trap few nutrients, whereas downstream wetlands, in key watershed positions, can remove up to 80% of inflowing nitrates (Crumpton *et al.*1993, cited by Zedler 2003). Yet, during large storm events, a number of small wetlands strategically placed in the upper reaches of catchments will have a greater cumulative nutrient interception rate and be more cost effective than larger downstream structures (Raisin *et al*. 1997). A combination of approaches may therefore be necessary.

The use of farm ponds is being increasingly encouraged to mitigate diffuse, land-based sources of pollution due to their ability to retain nutrients. Vegetation inside ditches has been shown to enhance mitigation of the impacts of herbicides and some insecticides (Moore *et al*. 2001). Sustainable Drainage Systems (SuDS), designed to manage run-off associated with urbanised areas (e.g. roads), regulate flow rate and water quality in stages. Techniques include the use of vegetated filter strips and swales (channels), retention ponds and wetlands, and have been shown to be effective in the filtration and sedimentation of pollutants (Lawrence *et al*. 1996). SuDS also make a significant contribution to macro-invertebrate biodiversity (Scher & Thiéry 2005, LeViol *et al*. 2009) and have the potential to provide habitat corridors and refuges. In agricultural landscapes, Small Constructed Wetlands (SCWs) (Table 6.1), pond-like structures designed to promote the filtration and sedimentation of run-off in a similar way to SuDS, have been found to be very effective at reducing nitrogen export in sub-surface drainage from cattle-grazed pasture (Tanner *et al*. 2005) and if the subsurface water originates from hill slopes, the nitrate content can be reduced by up to 97% (Haycock & Burt 1993). When a number of ponds are placed in sequence, those receiving water that has been previously filtered may be of higher ecological value than those higher in the catchment (Stoate 2003). Nutrient interception and habitat quality may decrease as sediment accumulates and excess vegetation develops.

Performance will also vary seasonally (Thorén *et al.* 2004) and with changing hydraulic and pollutant loadings (Fink & Mitsch 2004).

Surface waters, such as streams, remain in 'good ecological status' (only slightly deviating from conditions expected in the absence or near absence of anthropogenic impacts) until agriculture exceeds 30-50% of the catchment area (Allan 2004). In Britain, permanent and temporary grasslands occupy approximately 7 million hectares, over 65% of the agricultural land (MAFF *et al*. 1997). Vast areas would need to be de-intensified to reach the maximum threshold of 30-50% agricultural use of a catchment area. This is impractical where agricultural production is the primary goal. Davies *et al*. (2008a) contrasted catchment characteristics among different water body types and concluded that de-intensification of agriculture at the scale of pond 'microcatchments' is more feasible and effective than it is on the catchment scale of larger aquatic systems, such as rivers or lakes. To attain 'good ecological status', an average pond requires only 4 hectares (ha) to be de-intensified, compared to 10, 086 ha for a river (Davies *et al*. 2008a).

In a modelling exercise, Heathwaite *et al*. (2005) found that small ponds that store water temporarily at the bottom of a field were effective in reducing overland flow following storm events. SuDs have demonstrated this ability (Mance *et al*. 2002, White & Howe 2002, Scholz 2003) and in Belgium, retention ponds were found to be very effective, reducing the peak discharge and total runoff volume by 40% (Evrard *et al*. 2007). It is likely that SCWs will function in a similar way. Small wetlands located high up in the catchment are also effective (Potter 1994). However, the value of small, widely distributed wetlands for flood control is dependent on the amount of storage relative to the volume of floodwater, as well as their capacity for evapotranspiration and infiltration (Potter 1994).

Strategic placement of pond type structures therefore offers reduced flood risk, but what gains can they give for waders? On lowland grassland, high densities of breeding waders are associated with wet features and ponds with large perimeters and shallow sloping edges that provide significant areas of bare, damp soil suitable for foraging and habitat for obligate aquatic invertebrates. It is possible, therefore, to create ponds in all parts of Britain, including intensively managed agricultural landscapes. Williams *et al*. (2008) suggest that it may be possible to influence national breeding populations of wading birds through the development of a number of small-scale pond creation schemes within grassland systems. In addition, preliminary results have shown that established paired ponds (Table 6.1) are likely to be an important habitat for a wide range of non-wading bird species, as they retain water for longer than conventional unbunded ditches (Bailey *et al*. 2007). The schemes would consist of a waterbody mosaic in floodplain grassland including ponds that differ in size, substrate, water source and hydrological regime. Pond creation is most likely to be of benefit in open areas, such as field centres, where some wetland habitat already exists, for example, alongside rivers, in existing areas of damp grassland, or beside reservoirs and gravel pits. In these areas, some feeding habitat may already be available, even when habitats are unsuitable for breeding.

6.8.2 Large-scale solutions - Wetlands

Floods can be controlled or prevented through the ‘complementary roles’ played by wetlands of varying sizes and at different locations (Zedler 2003). For example, large wetlands located low down in the watershed can be managed to reduce peak flood levels (Potter 1994). In addition to flood mitigation, wetlands also regulate river flows and promote groundwater recharge, although the capacity to perform these functions varies across wetland types (MEA 2005).

The surface area, depth and shoreline complexity of new wetlands can also be constructed to aid both nutrient retention and biodiversity (waders and their prey). Shallow, large wetlands with high shoreline complexity are likely to attract waders and have high macro-invertebrate biodiversity (Thiere *et al*. 2009) and nitrogen retention (Hansson *et al*. 2005). Conversely, small deep wetlands are less valuable for biodiversity but will have more efficient phosphorous retention (Hansson *et al.* 2005). Therefore, dual-purpose wetlands with high nutrient retention may not have a high potential for increasing biodiversity and vice versa (Zedler 2003, Hansson *et al*. 2005).

A recent study concludes that, on average, ecosystems take approximately 50 years to recover from agriculture (Jones & Schmitz 2009), and that the stochasticity of natural systems means that they may never return to levels found in pre-perturbation conditions. New wetlands are unlikely to perform the same functions or support the same biodiversity as historic wetland habitat (MEA 2005) as it is difficult to recreate conditions in areas where cultivation has altered topography, soil quality and biodiversity (Zedler 2003). To be successful, restored habitat must be sustainable, have comparable composition, productivity and nutrient retention to the ‘target habitat’ (Acreman *et al.* 2007), and be near to remnants of original habitats (Cedfeldt *et al*. 2000).

6.8.2 Large-scale solutions - Washlands

Washlands (Table 6.1) are typically found in areas of floodplain surrounded by river banks that provide a low level of flood protection (Morris *et al*. 2004). In a flood event higher than the banks the washland fills with water and acts as a flood storage area, significantly reducing flood peaks downstream (Acreman *et al*. 2003).

By storing floodwaters in their soils or on the surface, washlands have the potential to provide wetland habitat, determined by the dominant land use on the washland and the catchment as a whole (Morris *et al*. 2002, 2004). This will be greatest in grassland or woodland areas that typically experience more frequent flooding and wetter ground conditions compared to arable land that requires infrequent flooding and drained soils (Morris *et al*. 2004). Wetness regime, substrate type, vegetation structure, grassland management and disturbance can influence washland habitat biodiversity (Joyce & Wade 1998) and variations in these factors can result in a mosaic of habitats (Morris *et al*. 2004).

Morris *et al*. (2004) describe three categories of washland: flood management washlands, integrated washlands and conservation washlands. These categories represent a range of flood management and biodiversity options. Where flood management is the primary objective of washland creation, biodiversity objectives will be met as long as they do not significantly compromise flood management purposes and vice versa. Integrated washlands give equal consideration to both. For breeding waders, flood duration and flood seasonality determine the suitability of a washland creation scheme and uncontrolled flooding can have a detrimental effect on breeding populations. For example, the Ouse Washes, designed originally for flood management, are now being managed as an integrated washland scheme (Morris *et al*. 2004). On integrated washlands emphasis is placed on the retention of surface water and soil wetness beyond the flood event period to create suitable habitat for breeding waders. However, since the 1980s, an increased frequency of flooding at the site has compromised biodiversity benefits. In particular, a dramatic decline in breeding Snipe and Black-tailed Godwits *Limosa limosa* L. has been attributed to an increase in the frequency of spring and summer flooding, effectively rendering the site unavailable during some breeding seasons (Ausden & Hirons 2002, Ratcliffe *et al*. 2005).

Conservation washlands may offer the best option for breeding waders. On conservation washlands, the creation of wetland habitats is the key objective and the frequencies, depths and timings of flood events are managed so as to maintain habitat quality (Morris *et al*. 2004). Prohibitive flood management regimes give rise to wetlands that function as reserves rather than truly multifunctional landscapes. As a result, individual wetlands may offer limited contribution to flood management. However, the cumulative effect of a number of wetlands over a whole catchment may be significant.

6.9 Discussion and Conclusions

Future grassland management can potentially, at a range of spatial scales, provide some solutions for both ecosystem services (water quality and flood alleviation) and grassland bird conservation. Factors influencing the use of wet features as foraging and nesting habitat by ground-probing birds are summarised in Table 6.2. At present, the Environmental Stewardship scheme (Natural England 2010) provides opportunities for the restoration, creation and maintenance of wet grassland for breeding waders. Wet feature creation is not currently included as an option. However, ponds offer good potential for both ecosystem services (through pollution control and reduced flood risk) and, if designed with gentle sloping sides and placed in suitable areas, benefits to breeding waders. Higher Level Stewardship includes the option ‘to provide additional flood water storage and flood defence through the restoration and recreation of wetland habitat for other objectives’ (Natural England 2008). It also offers some possibility for the inclusion of catchment de-intensification as a method of improving the ecological condition of water bodies (Davies *et al*. 2008b). However, agri-environment schemes are taken up on a voluntary basis. Where areas identified for de-intensification or flood mitigation cross farm boundaries, cooperation between land owners and a coordinated approach would be necessary for success. A landscape-scale approach is essential to avoid creating isolated fragments of high-quality habitats (Benton *et al*. 2003, Whittingham 2007) and, particularly as climates change, landscapes will be required to be increasingly permeable to allow species to shift and adapt their ranges. A landscape-scale approach to placement of ponds is also crucial to maximise benefit of flood risk and pollution control. It seems feasible that future new management options for farmland could include targeted schemes for both 'water' issues and biodiversity. These schemes may focus on different scales to the current Agri-Environment Schemes (AESs). For example, schemes at a local scale may be useful in protected areas (e.g. footdrains) and perhaps there is the opportunity to develop these within future high-intensity AESs. However, if future AESs are to be linked to wider ecosystem service goals and biodiversity in the wider countryside (i.e. outside protected areas) then they will need to address the issue of co-ordinated implementation at the appropriate scale. For example, the placement of ponds within a catchment needs careful planning to maximise both reduction in pollution, flood control and benefit for waders and this is not likely to happen if determined solely by land-owner uptake. Thought is needed as to how these types of schemes could operate and the input of social scientists may be needed to help with this issue.

	Factors influencing habitat use
Ponds	Retention of water and moist soil for probing during the spring and summer[1]. Proximity to other wet habitats providing foraging and nesting habitat opportunities. E, V, P, W, L.
Ditches	Maintenance of water levels at mean field height throughout spring and summer to provide moist soil for foraging. Hydraulic conductivity of the soil[2]. E, V, P, W, L.
Footdrains	Water levels in ditches feeding into footdrains. E, V, P, W, L.
Wetlands	Depth, size and shoreline complexity[3]. Previous land use; e.g. to recreate productive habitat it is beneficial to choose restoration sites next to remnants of original habitats[4].
Floodplain Washlands	Abundance of soil invertebrate prey in relation to frequency, seasonality and prolonged surface flooding[5,6]. Spatial scale of flooding and availability of refuge for soil invertebrate prey[5, 6.] Previous field use; e.g. the flooding of previously fertilised grassland can result in anoxic conditions for soil invertebrates[5.] V, P, W.
Integrated Washlands	The level of flood control during the nesting season; e.g. increased flooding frequency at the Ouse washes has shortened the nesting season for Snipe[7]. Abundance of soil invertebrate prey, as mentioned above[5, 6]. V, P.
Conservation Washlands	Wetness regime and vegetation structure suitable for foraging and nesting. Grassland management and freedom of disturbance[8]. V, P.

E, sloping edges for foraging; V, vegetation swards for nesting; P, pollutant loading; W, frequency and seasonality of high water flow during the nesting season; L, perimeter length.

References: [1]Bradbury *et al*. 2004; [2] Gavin 2003; [3]Hansson *et al*. 2005; [4]Cedfeldt *et al*. 2000; [5]Ausden *et al.* 2001; [6]Plum 2005; [7]Ausden & Hirons 2002; [8] Joyce & Wade 1998.

Table 6.2. Factors influencing the use of wet features as foraging and nesting habitat by ground-probing birds.

We have focused this review on waders due to the relative lack of studies on other bird species identified by our literature survey. However, there was some evidence for the effects of soil moisture on other species. Between the mid-1970s and the early 1990s the UK Song Thrush *Turdus philomelos L.* experienced a significant population decline, with approximately 70% of pairs lost on farmland alone (Baillie *et al*. 2001). Now only a fraction of the population lives on grassland. The timing and spatial distribution of the population decline is consistent with the pattern of land drainage in Britain, with the worst affected areas being the arable-dominated counties of eastern England (Peach *et al*. 2004b). Soil moisture is likely to be an important factor, but much of the effect may be in non-grassland areas. Although this does not necessarily imply causation of population decline it is consistent with this explanation. Compared to arable farmland, mixed farmland has areas of permanent pasture that retain damper soil conditions later in the breeding season, which in turn increases the length of time that earthworms, an important component of breeding season diet, are available (Gruar *et al*. 2003). During dry periods, provisioning adults forage further from their nest (Peach *et al*. 2004a) and the summer weights of chicks and adults are negatively related to the dryness of surface soils (Gruar *et al*. 2003). The duration of summer droughts is also negatively correlated with annual variation in adult survival rates, a key demographic rate (Robinson *et al*. 2004). Hot, dry weather is likely to affect Song Thrushes through the drying out of ditches and under hedges, thus reducing both above- and below-ground access and abundance of prey. Significant temporal and small-scale spatial variation in Chough *Pyrrhocorax pyrrhocorax* L. pre-breeding survival can also be linked to the effects of drier weather conditions on invertebrate prey abundance and accessibility (Reid *et al*. 2008). A range of other species, including the Mistle Thrush *Turdus viscivorus* L., also probe the ground for food, and soil moisture may act in similar ways for these species, although it is unlikely that the types of large-scale wet feature creation discussed here would be a viable option for wide-ranging and open grassland species.

Land use in the ‘wider countryside’ needs to integrate crop yield, ecosystem services and biodiversity if it is to be truly multi-functional (Firbank 2005). To date the extent of research in this area is limited (e.g. Vickery *et al*. 1994). However, the combined pressure of global food production and climate change make it questionable if AESs in their present form can be sustained at high levels (Ausden & Fuller 2009). The schemes of the future may benefit from an integrated ecosystem services approach. By linking biodiversity objectives with other ecological objectives set out by policies, such as the Water Framework Directive, conservation targets can continue to be met. At present, there is a lack of direct evidence of the quantative impacts of management solutions on biodiversity and ecosystem services. However, there is the potential to help mitigate damaging effects of climate change and pollution and provide high-quality habitat for birds in both protected areas and the wider countryside via options such as appropriately designed and located ponds and for the latter (to a lesser extent) the use of integrated washlands. Not all water management options will benefit waders and the aims for any area need to be prioritised and co-ordinated at local, regional and national levels to maximise benefit for the different dimensions of land use.

One note of caution for future schemes linking biodiversity and ecosystem services is that ultimately the latter can be viewed in terms of ‘benefits’, such as clean drinking water, which are assessed in economic terms (Fisher *et al*. 2008). This carries with it some issues that impact on biodiversity. For example, the natural capital of the ‘biodiversity’ component may be identical but other factors may intervene. If a dam is built up-stream in a water catchment, the measures (such as biodiversity) to alleviate flood control downstream are then of less economic value. The spatial location of the resource is important; for example, a wetland next to a source of pollution that can act as a filter is of greater value than one that is not (Vira & Adams 2009). Whilst the ecosystem services agenda is likely to impact on current AES policy the devil may be in the detail in terms of the benefit for biodiversity.

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Chapter 7: Discussion

The link between farmland bird population declines and agricultural intensification has been clearly demonstrated (e.g. Donald *et al*. 2001). In the future, climate change is likely to become an increasingly important driver of bird populations. A number of studies have investigated the large scale impacts of climate change on species' distribution and abundance (e.g. Thomas *et al*. 2004). However, few have examined, in detail, specific ecological impacts of climate change on bird demographics that would allow predictions of the effects of climate on bird populations (e.g. Great Tit *Parus major* Cresswell & McCleery 2003, Golden Plover Pearce-Higgins *et al*. 2010). The overall aim of this thesis was to provide evidence of the link between variations in soil moisture, due to climate change, and population changes in ground-probing birds, using the Starling as a study species.

Specific aims of the thesis were:

1. To conduct detailed experiments to examine the effects of varying soil moisture and Starling foraging success (Chapter 2).
2. To quantify the relationship between soil moisture and reproductive performance in the Starling (Chapter 3-4).
3. To quantify the pattern between soil moisture and reproductive success at a national scale for the Starling (Chapter 5)
4. To review management options that would alter soil moisture content to benefit both ground-probing birds and ecosystem services (e.g. flood mitigation (Chapter 6).

In Chapter 2, results of foraging experiments revealed a trade-off between soil moisture, prey abundance and accessibility for ground-probing birds. Soils with intermediate moisture provided the best foraging opportunities with both saturated and dry soils being suboptimal. Spring and summer would be the ideal time for such a study; it is easier to experimentally increase the small moisture levels on dry soils than decrease soil moisture levels on saturated soils. However, the study was conducted during the autumn and winter so as to not interfere with birds during the breeding season. Nevertheless, results of the field experiments showed that soil moisture mediated intake rates of below-ground prey in wild-caught Starlings.

Previous studies of Starling nestling provisioning have shown that Tipulidae larvae were the dominant prey item in the diet (Dunnet 1955, Tinbergen 1981, Westerterp 1982, Wright *et al*. 1998). The findings in Chapter 3 concur with previous studies and confirm that despite widespread spraying of grass fields to control Diptera spp. larvae over the past 30 years (Campbell & Cooke 1997, Garthwaite *et al.* 1997) Tipulidae larvae remain the key dietary item of nestling Starlings on farmland. This is in line with earlier studies which showed that Tipulidae have been identified as an important dietary item for farmland birds (Holland *et al*. 2006), with up to 50% of lowland birds consuming Tipulidae larvae during the breeding season (Wilson *et al*. 1999).

Chapter 4 established that the delivery of below-ground prey, specifically Tipulidae larvae, was associated with changes in soil moisture and linked to Starling reproductive success via changes in fledgling survival. At the study site, counter to *a priori* predictions, both Tipulidae larvae provisioning and fledgling success was highest on wet and dry soils, whereas in contrast intermediate soil moisture content was suboptimal. The study was conducted in the spring and soils were relatively dry compared to the conditions in Chapter 2. In addition, the observed soil type on the study site (clay loam) has been shown to have an unusual relationship between soil moisture and penetration (highest surface strength at intermediate levels of soil moisture), which matches the observations of starling foraging. Overall the results highlight the subtle complexities of how soil moisture interacts with the soil type. Chapter 5 explored population level effects of differing soil moisture conditions on the survival of young both before and after they leave the nest. Analysis of fledgling success at a range of sites (n=132) provided evidence that an increase in the mean spring (April-June) soil moisture deficit over a twenty year period was a significant driver of Starling population dynamics in Britain. Starling populations did best in years with wet springs (April - June) and dry summers (July -Sep). This relationship was robust to the inclusion of temporal changes in Starling populations which are likely to be linked to agricultural intensification. Substantial changes in agricultural land-use occurred at the same time as the data used in Chapter 5; between the late 1960s and the late 1980s management and productivity of improved grassland was transformed by an increase in use of fertilisers (86% of all grassland is now fertilized with inorganic N) and insecticides (Chamberlain *et al*. 1999, Chamberlain *et al*. 2000), changes in stocking densities and changes in crop type, from hay to silage (Fuller & Gough 1999, Fuller 1987,Stoate 1996)).

UK climate change projections suggest that annual moisture content of soils is liable to decrease by 10-20% across the UK by the 2080s, with 20- 50% reductions in average summer soil moisture content occurring in South East England compared with 0-20% in the North West, under the high emissions scenario (Bisgrove & Hadley 2002). These predictions are relative to a standard baseline climate period (1961-1990). In this study, spring soil moisture deficit (mean value from April-June) the previous year was found to have a curvilinear relationship with breeding pair numbers at CBC sites between 1981 and 2000. The number of breeding pairs per CBC site was initially stable, but then declined as soil moisture deficit increased above 80 mm (Chapter 5, Fig 5.3). Assuming that agricultural practices remain the same, predictions of how future spring soil moisture deficits may further affect UK Starling breeding populations, at these study sites, were made using a soil moisture deficit ‘baseline climate period’ of 1980 to 1990 (soil moisture deficit data for the study sites was only available from 1980 to 1999). Spring (April to June) soil moisture deficit values for increases of 10, 20, 30, 40 and 50% were calculated for the 67 *MORECS* squares, relative to the baseline climate period. Following the same model structure as described in Chapter 5 (section 5.2.4. C), five models were run using the 10, 20, 30, 40 and 50% increase soil moisture deficit values as the ‘April to June SMD one year ago’ and an arbitrary baseline population value of 1 for 1990. The back transformed (exponential) fixed effects parameter estimates from each of the models were then used to predict Starling population changes over the period 1990 to 2080:

Total number of breeding pairs per site as the response variable with a Poisson error structure and a log link function.

Total number of breeding pairs per site = April to June SMD one year ago + offset (log of the previous year’s breeding pair numbers) + site area + habitat category + soil type +1|site

Under the high emissions scenario, populations of breeding Starlings would decline by 4.3% with a 10% increase in soil moisture deficit, 8.4% with a

20% increase, 12.3% with a 30% increase, 16% with a 40% increase and 19.7% with a 50% increase by 2080 at the study sites (Fig. 7.1). Changes would vary by region and the relationship is likely to be more complex. For example, periods of stability at low population levels will be followed by periods of decline as a result of the cumulative effect of a number of years of high spring soil moisture deficits. Between 1981 and 1999 there was a 64% increase in mean April to June soil moisture deficit from 25.18 ± 1.23 (± se) to 40.59 ± 3.09 (± se), across all 67 *MORECS* sites used in the analysis in Chapter 5. Put another way there was an increase of 61% when comparing the mean soil moisture deficit for the period 1980 to 1990 (53.50 ± 1.16 (± se)) with the mean for the period 1990 to 1999 (86.54 ± 1.53 (± se)). Starling breeding populations at these sites declined by 82% over the same period, from 0.22 ± 0.04 (± se) in 1981 breeding pairs per hectare to 0.04 ± 0.01(± se) in 1999.

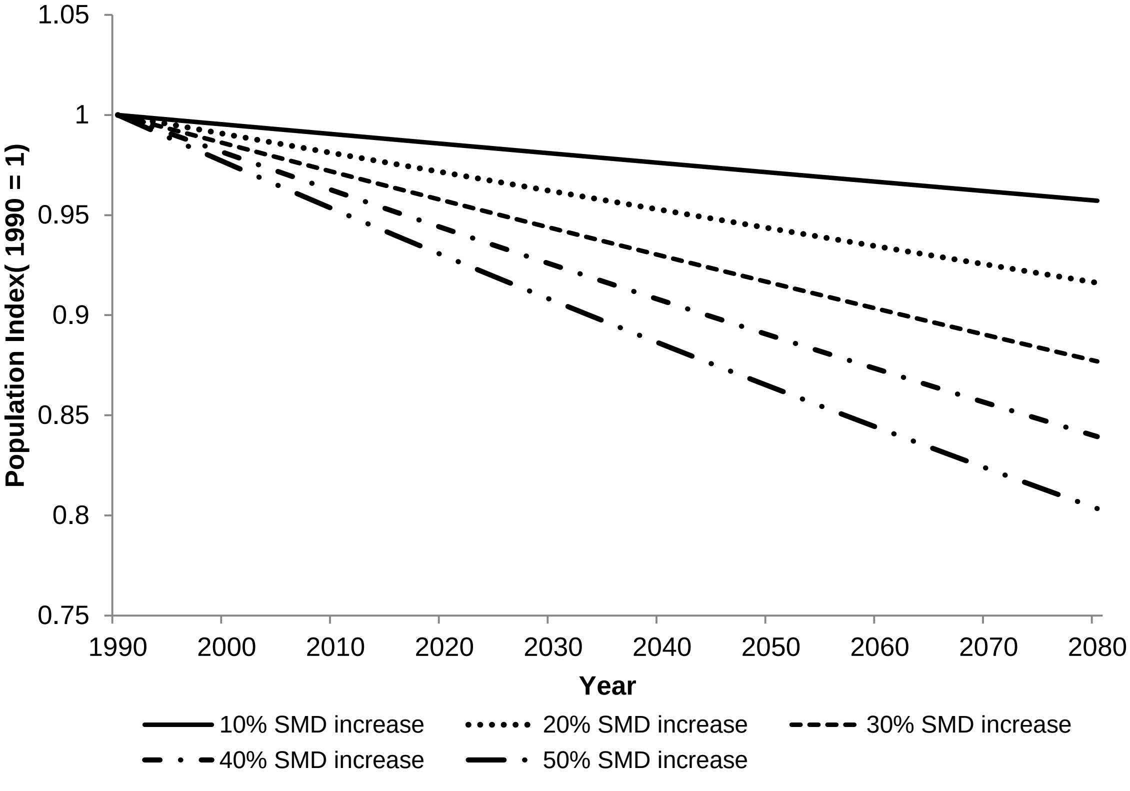

Figure 7.1 Predicted Starling breeding population declines in relation to predicted spring (April to June) soil moisture deficit (SMD), ranging from 10 to 50% (Bisgrove & Hadley 2002), at Common Bird Census sites (n=132). Breeding population decline values are relative to an arbitrary value of 1 in 1990. Percentage increases in SMD are relative to the mean spring SMD of the period 1980 to 1990 (Bisgrove & Hadley 2002). Breeding populations will decline between 8 and 20% by 2080 dependent on the level of soil moisture

deficit. (y = exp (-0.00811 * x) + -0.31569)). April to June soil moisture deficit was negatively correlated with the number of breeding pairs per site, but the relationship was not significant (although the main effect and squared term was significant).

Although there is a significant effect of soil moisture in the models it is not clear what percentage of the decline in Starling populations can be attributed to increased soil moisture deficit because of the concomitant changes in other predictors. In particular, agricultural intensification (e.g. in the past 50 years over 97% of lowland grassland has been improved (Fuller 1987, Vickery *et al*. 1999)) increased substantially over this period (Chamberlain *et al*. 2000). It should be noted that soil moisture deficits had already began to increase by the 1980s and therefore predictions for these sites, based on a baseline climate period of 1980 to 1990 will likely be higher than those based on the period 1961-1990. However, even a 10% increase will result in a 4.3% decline in breeding populations independent of the effects of year (likely to be linked with agriculture). Chapter 5 identifies the link between soil moisture content, mediated by climate change, and possible future population declines in the Starling. It is likely that decreased soil moisture will have a detrimental effect on the reproductive success of other ground-probing species, via fledgling survival.

I have shown that soil moisture levels (which are a product of soil type, precipitation, wind, aspect, slope and vegetation cover) alter foraging conditions, reproductive success and population dynamics for a ground-probing bird species. How can soil moisture be manipulated by management to improve conditions for ground-probing birds? In Chapter 6, I conclude by discussing different management options to alter soil moisture levels on grassland to benefit both ground-probing birds and the impacts on a range of other ecosystem services (e.g. reducing flood risk). Combining biodiversity goals with broader ecosystem services has been widely advocated and following a review of the ecological and hydrological literature I establish that there is a limited base of evidence on which to assess the potential linkage between ecosystem services and habitat management for grassland birds that obtain their food predominantly by probing the soil, particularly for non-wading birds species. However, appropriate management at multiple scales (e.g. small-scale: ponds; large-scale: integrated washlands) could potentially provide both ecosystem services and habitat for wading grassland birds. On smaller scales management of soils to alter their field capacity (e.g. by changing soil structure) can potentially yield significant improvements. For example, an on-going DEFRA project (BD5001) has shown on three different soil types that alleviating soil compaction via mechanical loosening (at 30cm depth) can improve water retention by up to 400% even two years after treatment with little effect on bird foraging or soil macro-fauna.

Future research work on managing soil moisture may be profitably targeted at the following four areas.

1. MACROINVERTEBRATE ABUNDANCE: What are optimal soil moisture conditions for dietary important macro-invertebrate species, such as Tipulid larvae and earthworms? Does this vary with soil type? How do these species respond to sub-optimal conditions, in relation to accessibility for ground-probing birds?
2. SCALE: Can small-scale management techniques (such as mechanical alleviation or grass margins) be effectively scaled up (e.g. to farm or catchment scale) and would such measures affect crop yield and ecosystem services?
3. QUANTITY: the extent of land needed to be managed in order to benefit multiple purposes and bring about measurable gain (e.g. one or two ponds may make significant inroads in reducing run-off and pollution but make little difference to wading birds).
4. UPTAKE: what are the challenges faced when introducing these management options to land managers (e.g. see McKenzie *et al*. in press for a similar study focussed on biodiversity alone within agri-environment schemes).

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