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The breeding ecology of the Spotted Flycatcher *Muscicapa striata* in lowland England

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Danaë K Stevens

A thesis submitted to the University of Reading for the degree of
Doctor of Philosophy

Centre for Agri-Environmental Research

School of Agriculture, Policy and Development

March 2008

DEDICATION

Dr Brendan Sheehan

1910 – 1994

This thesis is dedicated with love to the memory of my grandfather, who first instilled in me a love of natural history and a desire to ask questions and find answers. His support, encouragement and the memories I have of those have given me the courage to pursue my goals and realise my potential.

"Learn from yesterday, live for today, hope for tomorrow. The important thing is not to stop questioning…. He who can no longer pause to wonder and stand rapt in awe is as good as dead; his eyes are closed"

Albert Einstein

AUTHOR'S DECLARATION

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Danaë Stevens

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March 2008

ABSTRACT

The breeding ecology of the Spotted Flycatcher *Muscicapa striata* in lowland England

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A thesis submitted for the degree of Doctor of Philosophy, Spring 2008

There is compelling evidence that wide-ranging and diverse changes in the English landscape have contributed to the widespread decline of many bird communities, most notably those of farmland and woodland. In common with many other declining species, the Spotted Flycatcher *Muscicapa striata* has shown a long-term population decline since the 1960s, but being a long-distance migrant, it was believed that problems encountered on the wintering grounds, or on migration were the most likely factors contributing to the population decline. Recently, regional differences in population trends have been established, suggesting that factors on the breeding grounds require consideration. This study examined the breeding ecology of Spotted Flycatchers in farmland, woodland and garden habitats in two regions of lowland England with contrasting population trends.

Nest survival was higher in gardens than in woodland or farmland, although no regional differences were detected. The proximate cause of nest failure was predation by avian predators, primarily the Eurasian Jay *Garrulus glandarius*. Simulation models that allowed for the probability of re-nesting generated habitat- and region-specific productivity estimates. Productivity was high in gardens in both regions, but low in farmland and woodland. Additionally, regional differences in productivity were detected for woodland and farmland. Modelled population trends for both study areas were consistent with observed regional trends, thus providing evidence that demographic parameters operating at a regional level during the breeding season may be contributing to the observed UK population decline of this species. Thus, we present reasonable support that the recent population decline is consistent with being caused primarily (but not necessarily exclusively) by factors affecting productivity, through the proximate mechanism of predation by avian predators. This, plus the observed differences in UK regional breeding population trends, provides further evidence that population limitation mechanisms have acted in the breeding season for this species.

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Chapter 1

General introduction

1.1 Aims and overall approach of the thesis

Between the years 1980-2005, the population of Spotted Flycatchers *Muscicapa striata* in the UK fell by 79%. The species is now on the Red List of birds of Conservation Concern, and is listed as a Biodiversity Action Plan (BAP) Priority Species.

Although it is recognised that factors outside the UK (on migration routes or on wintering grounds) may be impacting upon Spotted Flycatcher populations, the aim of this thesis is to examine the ecology of the Spotted Flycatcher in the UK, thus focusing on factors which may be affecting Spotted Flycatchers on their breeding grounds. Recent changes in breeding habitats (brought about by changes in management at different scales) may affect Spotted Flycatchers in the UK by impacting upon the abundance (or accessibility) of invertebrate prey. This will have consequences in terms of productivity and survival, and hence population trends. This thesis covers various aspects of population biology, conservation biology and ecology, carrying out studies to determine demographic and ecological causes of population change. In a detailed field study from two regions of contrasting breeding population trend, the thesis examines the habitat around Spotted Flycatcher breeding territories and nest-sites to test the hypothesis that variation in habitat structure affects the breeding ecology of this species in the UK. Detailed monitoring of nesting attempts will establish how nest success (and productivity) may be related to habitat and the availability/accessibility of invertebrate food. Finally, the thesis compares data collected during the course of the study to large-scale data sets to understand potential demographic causes of population declines.

1.2 General introduction

1.2.1 The changing landscape in England

Agriculture dominates the English landscape, occupying approximately 70% of the land area, as opposed to forestry and woodland, which combined make up 8% of the land area, with towns and cities taking up 12% (Defra 2000). In the last 50 years, the farmed landscape in England has been through a period of unprecedented change, leading ultimately to the extreme intensification of agricultural management practices and increased mechanisation, coupled with a geographical polarisation of arable and pastoral farming, encouraged through increased specialisation. Prior to this period, the farmed landscape of England was dominated by extensively managed mixed farming, characterised by small fields with abundant hedgerows and trees. Grassland was managed either as low-intensity rough-grazing, wet meadow or species-rich hay sward, whereas arable land was managed using crop rotations to maintain fertility, often with organic manure added as the only available fertiliser. Intensification of these agricultural practices has resulted in a farmed landscape largely dedicated to increased productivity, enhanced by enlarged field sizes, specialist machinery and an increased array of super-efficient agrochemicals. Alongside this efficiency drive, farming has become increasingly polarised, such that Eastern England is now arable dominated, with the pastoral landscape being largely confined to the Western England (Fig. 1).

Although less well documented than factors associated with agricultural intensification, there has nevertheless been a number of factors that may have brought about significant changes to woodland habitat in the UK. Firstly, and possibly in association with the period of agricultural intensification, it is likely that there may have been changes that affect the quality of habitat either at the edges of, or in the landscape immediately adjacent to woods (Fuller *et al.* 2005). Secondly, a reduction in the level of management of woodland in England, particularly in the lowlands would have a myriad of effects, predominantly impacting upon the structure of woodland habitat (Fuller *et al.* 2005).

By causing changes to ecosystem processes, habitat and consequently the availability and abundance of food, urbanisation has direct effects on bird populations (Marzluff 1997). Vegetation in urban habitats is typically more fragmented, less heterogeneous in nature and is generally less diverse in native species, these being replaced by exotics (Beissinger & Osborne 1982, Blair 1996).

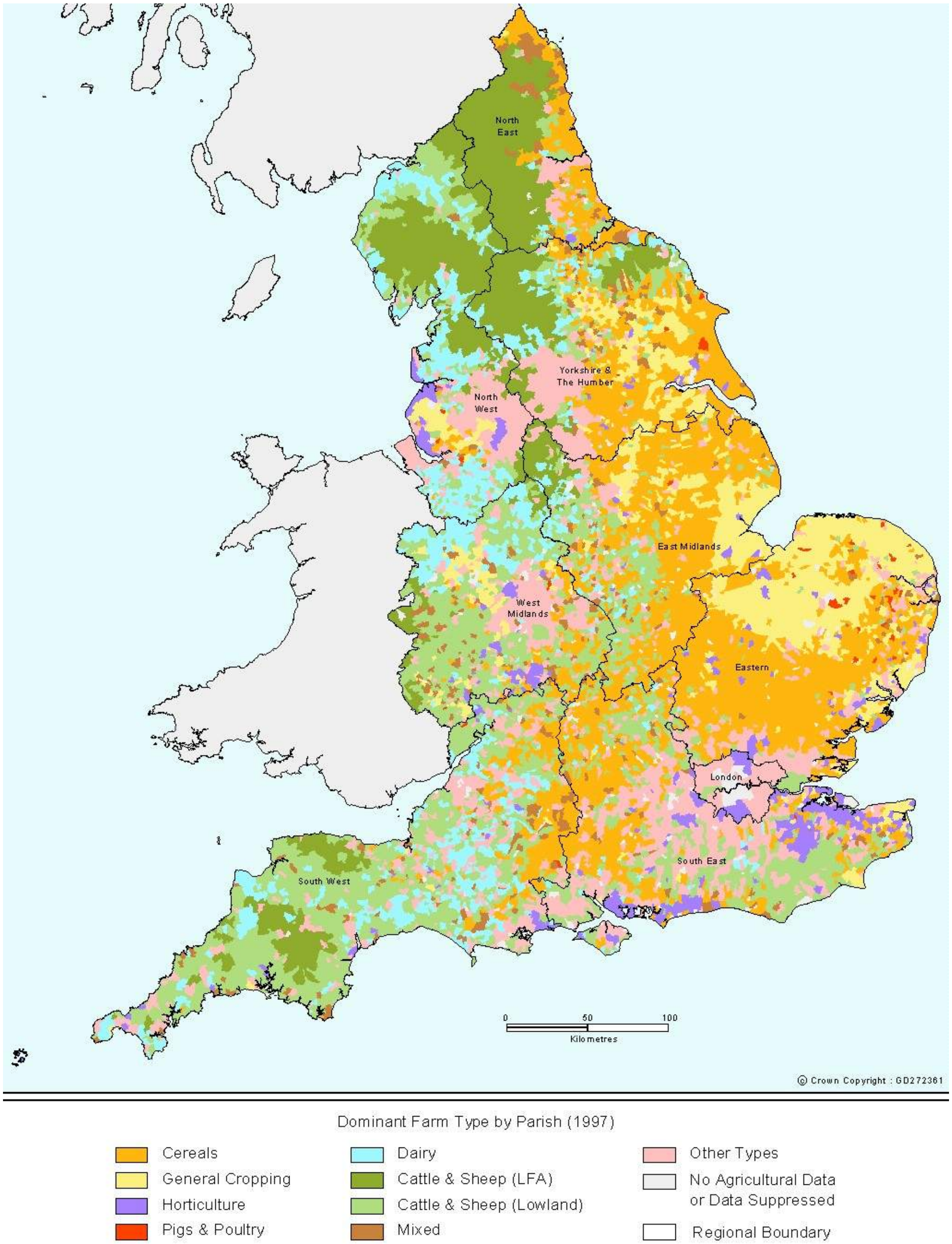

Figure 1. Map showing dominant farm type by parish, and highlighting the increasing polarisation of agricultural practices (Reproduced from: Defra 2000)

1.2.2 Recent population trends of English bird communities

Many formerly abundant species of birds have shown dramatic population declines in recent years, and in the UK these trends have been particularly apparent for habitat specialists and long-distance migrants. Recent population declines and range contractions of many farmland birds in the UK are now well documented (Fuller *et al.* 1995, Siriwardena *et al.* 1998a, Aebischer *et al.* 2000, Gregory *et al.* 2004), and are associated with the intensification of agricultural production (Siriwardena *et al.* 1998a, Chamberlain *et al.* 2000b, Fuller 2000). Although not immediately appreciated, similar declines for woodland bird species have also now been established (Vanhinsbergh *et al.* 2003, Fuller *et al.* 2005), being linked to a suite of factors associated with changes in land management and land-use, in the quality of woodland habitat and in pressures from other organisms (Vanhinsbergh *et al.* 2003). More recently, declines in the population trends of many long-distance Afro-Palearctic migrants, and especially those wintering in dry, open habitats have also been documented (Sanderson *et al.* 2006). Although such declines may be regulated by processes that impact on survival in the non-breeding season (Baillie & Peach 1992), a complete understanding of the causative factors also requires knowledge of events operating during the breeding season.

1.2.3 Overview of density-dependent population regulation in birds

Mechanisms concerned with population regulation in birds are poorly understood, though many are density-dependent processes, whereby the overall population increases when density is low and decreases when density is high. Such processes are often regulated by extrinsic factors such as the availability of food resources, predation risk and disease (Newton 1998), and consequently the density at which an animal exists is often used as a measure of the quality of the habitat in which it is living, because increased resources need to be available in order to sustain a greater number of individuals in a population (van Horne 1983). However, although it may generally be true that bird populations are generally found at a higher density in higher quality habitats (Galbraith 1988, Newton 1998), for species that are highly territorial, the converse may be true, or alternatively density and habitat quality may be completely unrelated (van Horne 1983). During the breeding season, habitat features that influence breeding success and survival will regulate the number of birds using that habitat, and breeding success is often positively correlated with habitat quality (Krebs 1971, Galbraith 1988, Petit & Petit 1996, Smith & Bruun 2002). Similarly, the relative importance of a habitat to a species is frequently inferred by measuring the density of individuals occurring within it, and comparing this with other habitats (Vickery *et al.* 1992). However, in situations of high population density, or in territorial species, a proportion of individuals will occupy sub-optimal or marginal habitats (Kluyver & Tinbergen 1953, Vickery 2001), as the available territories in the preferred or higher quality habitat become occupied. Kluyver and Tinbergen (1953) called this the 'Buffer Effect', and it has subsequently been demonstrated in many species (Kluyver & Tinbergen 1953, Brown 1969, Petit & Petit 1996, Gill *et al.* 2001, van den Berg *et al.* 2001, Gunnarsson *et al.* 2005). This follows the pattern of an ideal preemptive distribution (Pulliam & Danielson 1991), and gives rise to source-sink population dynamics governed by density-dependent processes. Although a landscape heterogeneous in both source and sink habitats, may maintain a population in both habitats for a long period of time (Pulliam 1988), large-scale changes in the availability, or relative balance of source and sink habitats may bring about population regulation. For some species, occupying these sub-optimal habitats incurs a fitness cost in terms of reduced fecundity or survival (Gill *et al.* 2001, Gunnarsson *et al.* 2005), thus having an indirect impact on intrinsic demographic processes.

Population stability can be maintained regardless of density provided that the intrinsic demographic processes that bring about a decrease in numbers (mortality and emigration) are balanced by those that bring about an increase (birth and immigration, Newton 1998). Differences in annual productivity play a large role in determining changes in population size in short-lived species (Sæther & Bakke 2000). Similarly predation is the primary source of nest mortality in many species of birds (Lack 1954, Ricklefs 1969, Martin 1992, Martin 1993), and in some circumstances may limit population growth below levels that local resources, such as the abundance and availability of either food or nest sites, would otherwise allow (Lack 1954, Newton 1993). As such, demographic processes, particularly those that impact upon fecundity and survival, have been frequently studied in order to provide clues to elucidate the causes behind population change. (Peach *et al.* 1994, Peach *et al.* 1995, Peach *et al.* 1999).

1.2.4 Optimal foraging theory

How birds are able to utilise a habitat and the resources within it depends on the foraging strategy of the species. Optimal foraging theory, first developed by MacArthur and Pianka (1966), but also independently and concurrently by Emlen (1966), stated that predators would forage to maximise the "net amount of energy gained from a capture of prey as compared to the energy expended in searching for the prey". In practice, optimal foraging is a hierarchical, decision-making process, with several constraints that may apply in different circumstances. Perhaps the most notable is the marginal value theory (Charnov 1976), which, with respect to patchy food resources, suggests that animals make decisions about their use of a patch based on the value of that patch in terms of food availability. This led to the development of 'giving up density' (GUD) and 'giving up time' (GUT) models (Brown 1988, Brown *et al.* 1997). The GUD is reached when the energetic value of food available in a patch is no longer offset by the energetic costs of foraging, with the GUT being the time it takes to reach this critical point. If a forager is to make such a decision however, then there must be some knowledge of the potential profitability of other 'patches' within an area, leading perhaps to energetic, territorial or vigilance trade-offs, which may further adjust the optimality of foraging. If foragers are faced with constraints to the size of the patch they may utilize, for instance when birds must return to a nest with food ('central-place foraging'), the trade-off may require that they forage selectively for prey items with a higher energetic value the further they are from the nest. Multiple prey loaders may compensate for this energetic requirement by collecting several smaller prey items, whereas single-prey loaders must select prey that is either larger, or of better quality (Orians & Pearson 1979, Schoener 1979, Stephens & Krebs 1986).

1.3 The Spotted Flycatcher

1.3.1 General characteristics

The Spotted Flycatcher is a member of the family Muscicapidae, or Old World flycatchers. It is one of 23 flycatchers in the genus *Muscicapa*. The nominate race was first described by Pallas in 1764, initially as *Motacilla striata.* The species has subsequently been known by several names before settling on that commonly used today, including *Muscicapa grisola* and *Butalis grisola* (Brodkorb 1935). Spotted Flycatchers are Afro-Palearctic migrants, with a wide-ranging breeding distribution which extends across the Palearctic ecozone, encompassing an estimated area of 10 000 000 km^{2,} and it is therefore both the commonest and most widespread flycatcher in the Palearctic. Across this range there are seven recognized subspecies (Table 1), five of which are found in the western Palearctic. Despite the extensive breeding range, all subspecies winter in sub-Saharan Africa, most south of the equator (Cramp & Perrins 1993). Based upon recoveries of birds ringed across Europe, a migratory divide is thought to operate between populations either side of a line of longitude approximately 12°E (Cramp & Perrins 1993, Baker & Baker 2002). Thus, it appears that the majority of birds breeding to the west of this line (therefore including the UK population) spend the non-breeding period in sub-Saharan West Africa.

Table 1. Worldwide distribution of subspecies of *Muscicapa striata*

Subspecies	First described		Range
striata	1764	Pallas	Europe (except Balearics) & western Siberia
neumanni	1904	Poche	Eastern Siberia, Asia Minor
tyrrhenica	1910	Schlegal	France, Italy, Corsica & Sardinia
balearica	1913	Von Jordans	Balearic Islands
sarudnyi	1928	Snigirewski	Transcaspia to China
inexpectata	1932	Dementiev	Crimea
mongola	1955	Porlenko	Russia & Mongolia

Although by size they are the largest representative of their family in the western Palearctic, they are nevertheless relatively small birds, with a body length a little over 14 cm and a wing span of approximately 23 – 25.5 cm (Cramp & Perrins 1993, Robinson 2005). Wing length of nominate race birds ranges from 82 – 94 mm (Svensson 1992, Robinson 2005 and DS, unpublished data). The sexes are alike, both on plumage characteristics and size. In 1909, they were described by the Rev C.A. Johns as having "neither song to recommend them nor brilliancy of colouring" (Johns 1909). The plumage is a uniform grey-brown colour on the upperparts, with the exception of the forehead and forecrown, which appear slightly paler and are streaked with a darker brown. The under parts are off-white, with the throat, neck and breast being lightly streaked with a darker grey-brown. The legs and feet are brown-black, as is the bill, although the base of the lower mandible is a slightly paler pinkish-brown. Juvenile birds can be readily distinguished from adult bird until completion of the post-juvenile moult, being spotted with pale buff-white markings on the upperparts, with the under parts also appearing spotted or scaled, rather than streaked as in the adult.

1.3.2 Habitat

On their breeding grounds Spotted Flycatchers are a 'habitat-edge' species, characteristic of the transition between wooded and open habitats, typically found in parkland, gardens, orchards, woodland edge, open woodland and associated with lines or copses of mature trees on farmland or farmyards, particularly those with livestock (Cramp & Perrins 1993). Good quality habitat is characteristically heterogeneous in nature, containing a mixture of raised perches from which birds may forage, and open spaces for catching the flying insects, on which the birds forage. Which habitat really is the primary breeding habitat for this species is a matter of debate, though recent research suggests that it should be best classed as a woodland species (Fuller *et al.* 2001). On the continent at least, density of breeding birds appears to be higher in open woodland than in other habitats. An average of 100 pairs/km^2 were recorded over a 13-year period in parkland in West Germany (Kämpfer & Lederer 1990), in Switzerland 40 pairs/km^2 were found in deciduous woods (Schifferli *et al.* 1980) whilst in Finland, 50 pairs/km^2 were recorded in grazed woodland (Palmgren

1930). In contrast, breeding densities recorded in farmland habitats are very much lower; in a study of birds breeding on mixed farmland in Suffolk, only 2.2 pairs/ km^2 were recorded (Benson & Williamson 1972).

Given the structural requirements of foraging habitat during the breeding season, habitat preferences on the non-breeding grounds are surprisingly similar to those in the UK. They are found in a wide range of habitats including cultivated and disturbed areas, planted areas in villages and towns, habitat edges, open woodland, thorn scrub and grassland savannah (Urban *et al.* 1997). Although they avoid dense forested areas, they are nevertheless able to make use of open areas within these such as logging trails and tree fall gaps.

1.3.3 Diet

Spotted Flycatchers are classic optimal foragers, feeding almost exclusively on insects, with feeding behaviour consisting primarily of 'sallying' after aerial or arboreal insects from a convenient perch (Davies 1977). A wide range of prey items are taken in this manner, but particularly Diptera, Hymenoptera and Lepidoptera (Cramp & Perrins 1993). Feeding sites and methods of taking prey however seem to relate to both the abundance and type of prey available and are adjusted to maximize energy intake and hence increase foraging efficiency (Davies 1977, Stephens & Krebs 1986). Although aerial feeding is by far the most important method, in periods of poor weather when the activity of aerial invertebrates is reduced, flycatchers will also take food from the ground (Ruttledge 1953, Kovshar 1966, Alatalo & Alatalo 1979), or by gleaning from the undersides of leaves (Edington & Edington 1972, Davies 1977). Although this increases the range of prey available, the majority of prey taken in these circumstances is of a smaller size, such as Aphididae, and flycatchers have to work harder to maintain the same rate of energy intake (Davies 1977).

Although flycatchers feed almost exclusively on flying insects, in order to maximise foraging efficiency, they prefer to take larger bodied insects when provisioning young. In an intensive study of the species, Davies (1977) found that a reliable abundance of large insects was vital for the adults to feed their nestlings adequately. Unlike many other insectivores, adult flycatchers do not seem to carry a large beak full of small prey, but increase foraging efficiency by taking mainly large prey items back to the nest (Davies 1976). Accordingly, Davies (1977) reported that adults had a wider range of acceptable prey when feeding themselves than when collecting food for nestlings, and the capture interval when self-feeding was shorter (12.6 seconds) than when catching food for young (18.9 seconds). Even among large insects, there was choice for certain taxa, notably the less mobile Diptera (such as Scatophagidae).

Although sometimes regarded as an obligate insectivore, Spotted Flycatchers have also been recorded taking berries, particularly, but not exclusively, during the autumn. These are taken on the wing by hovering and plucking the berries directly from the bush (Hollick 1961, Scott 1962, Urban *et al.* 1997).

1.3.4 Breeding ecology

Spotted Flycatchers are one of the latest migrants to return to the UK, and although there are some early arrivals each year, birds do not begin to arrive in good numbers until the first or second week of May, or even later. Although males may arrive on the breeding grounds slightly ahead of females (Ryves & Ryves 1950), pair bonds form very soon after birds appear on territories. Nest site selection may take several days, with the male leading the female around a series of potential nest sites, performing a 'nest-showing' display at each, before the female selects the preferred site (Cramp & Perrins 1993). A wide variety of sites and locations are used for nesting, including holes or platforms in walls and trees, within creepers, open nests on boughs, in disused nests of other species and as well as in more natural locations, can be in open-fronted buildings or nest boxes. Nest height is similarly variable and ranges from 0.5 – 20 m (Summers-Smith 1952, Cramp & Perrins 1993, Kirby *et al.* 2005). Nests are constructed in 3 – 7 days (von Haartman 1969, Epprecht 1985), the cup being formed out of fine twigs, rootlets, grass, moss and lichens and lined with hair, fine fibres and occasionally small feathers (Cramp & Perrins 1993). Clutch size in the UK ranges from 2 – 6 eggs (mean 4.25, Cramp & Perrins 1993), although there is a seasonal decline, with clutches being smaller later in the season (Summers-Smith 1952). Eggs are laid at daily intervals, with incubation commencing once the clutch is complete (von Haartman 1969). If nests are lost at the egg stage, replacement clutches are laid. Whilst most Spotted Flycatchers are single brooded in Britain, second broods are not infrequent (Witherby *et al.* 1958). An enquiry launched by the Devon Bird Watching and Preservation Society (DBWPS) in 1950 recorded instances of double brooding almost annually (Ellicott 1958), and also recorded that clutch sizes were smaller in subsequent nesting attempts. The incubation period, defined as the interval between the laying of the last egg and the hatching of the first young, lasts between 10 – 17 days (mean 13.2 days), with no variation related to date or clutch size (Summers-Smith 1952). Eggs usually hatch within a 24-hour period (Ryves & Ryves 1950, Epprecht 1985), with the young being subsequently cared for by both parents (Cramp & Perrins 1993).

In common with most altricial young, Spotted Flycatchers are naked and blind at hatching. Consequently, in order to maintain thermoregulation, they require frequent bouts of brooding, which are carried out only by the female (Cramp & Perrins 1993), with the male doing the greater part of provisioning. However, as the nestlings grow they become increasingly homeothermic by means of improved heat retention, resulting from an increase in mass-to-surface ratio, the developing feathers and a number of other physiological mechanisms. In response, the female is able to reduce the amount of time spent brooding and increase her level of participation in provisioning (O'Connor 1984). Food supplied to the nestlings provides the energy required for the maintenance of basal metabolism, digestion, physical activity and thermoregulation, as well as for the biosynthesis of the new tissue required during growth. As such, nestlings generally require a greater intake of energy, and consequentially food, than adults, and the amount of food ingested by nestlings is correlated with their growth rate. Nestlings remain in the nest for a period of 10 – 17 days (mean 13 days), with no variation related to date or brood size (Summers-Smith 1952). Once fledged, young birds remain dependent on their parents for food for two to three weeks, whilst learning the skills they require to forage independently (Davies 1976).

1.3.5 Dispersal

Since, for British birds at least, the return migration does not start until the middle of August, most young flycatchers spend some period in the UK before migrating southwards. There is some evidence that young birds and family parties may aggregate in wooded areas in loose 'flocks' of 20 or more birds during this pre-migratory period (Clarke 2005, L.H. Campbell pers.comm.), often feeding high up in the canopy.

1.3.6 Population trends

1.3.6.1 The European population

The Spotted Flycatcher is widespread and ubiquitous in Europe, found at the highest densities in northern and central Europe. Nevertheless, by the mid-1990's, consistent population declines had been reported in several European countries aside from the UK (Tomiałojć 1994). Curiously, the spread of these countries (Czech Republic, Finland, Germany, Ireland, Lithuania, The Netherlands, Spain and Ukraine) has no obvious geographical pattern and is therefore indicative of the probability that there may be several causative reasons. However, assessment of population trends for the species are often made more complicated by distinct fluctuations in breeding numbers in some parts of the species range (Peklo 1987, Cramp & Perrins 1993). Indeed a more recent assessment of population trends (BirdLife International 2004), highlighted population declines only in Belgium, France, Greece, Ireland, Moldova, Norway and the UK, whilst reporting stability, or even increase across the rest of Europe. Despite this, and due to the more widespread historical declines, the European population has yet to return to a level similar to that recorded before the mid-1960's, and from a conservation listing point of view, its status is regarded as Depleted (BirdLife International 2004).

1.3.6.2 The UK population

In the 19th, and for much of the 20th century, the species was distributed throughout England, and although numbers showed small annual fluctuations, Spotted Flycatchers were thought to be one of the commonest summer migrants (Holloway 1996). In 1909, the Rev C.A. Johns said of them "there are few birds with whose haunts and habits we are more familiar than those of the common flycatcher", and that one may observe them "at any time during the months of June, July and August, in most country and suburban gardens" (Johns 1909). Indeed, even right up to 1968, when fieldwork for the first *Atlas of Breeding Birds* began, few long-term changes in either numbers or distribution had been recorded (Sharrock 1976). However, by the time the *Atlas* was published in 1976, data from the BTO/JNCC Common Bird Census (CBC) had revealed a 50% decline in the population from a peak in 1965. During fieldwork for the first *Atlas*, Spotted Flycatchers were recorded in 86% of 10km squares, with breeding being confirmed in 90% of cases. Densities on census plots were similarly high, ranging from approximately one pair/km^2, through to 10 or more pairs/km^2 in plots containing more favoured breeding habitats. When the first *Atlas* was published, the breeding population of Spotted Flycatchers in Britain was estimated at between 100,000 – 200,000 pairs (Sharrock 1976), although this may have been an underestimate as a revised figure of 300,000 pairs was later published by Hudson & Marchant using 1982 CBC mean densities (Hudson & Marchant 1984). Whichever figure is correct, it is probably fair to say that the population at that time was somewhere around 200,000 pairs, and that in 1950, the population of these enigmatic yet familiar birds would have been somewhere near its peak.

By the end of the first *Atlas* period, results from the CBC, a scheme monitoring populations of common breeding birds in, primarily, woodland and farmland habitats, were already beginning to show a worrying downward trend (Marchant *et al.* 1990). Subsequently, declines have been rapid and consistent, and the once familiar Spotted Flycatcher is now perhaps better known as one of the UK's most rapidly declining birds: in the twenty-five year period 1979-2004, the breeding population fell by an estimated 82% (Baillie *et al.* 2007). The current UK population estimate is now only 63,700 pairs (BirdLife International 2004, Baker *et al.* 2006). As a result of these declines, the species was placed on the 'Red' list of birds of conservation concern in the UK (Gibbons *et al.* 1996) and was included on the list of 26 priority bird species in the UK Biodiversity Action Plan, with a species action plan being published in 1998 (Anon. 1998b).

Although population declines were previously thought to be similar between different regions and habitats within the UK (Freeman & Crick 2003), recent analyses have highlighted potential regional differences in population trends. For instance, analyses of BTO/JNCC/RSPB Breeding Bird Survey census data for the period 1994 – 2000 suggests a considerable population decline (albeit non-significant) in the Regional Development Agency Regions of East England (-34%) and South East England (-20%), compared to an increase in South West England (+19%; Noble *et al.* 2001, Noble & Raven 2002). Similarly, analyses of data collected as part of the joint RSPB/BTO Repeat Woodland Bird Survey (RWBS), also detected regional differences in population trends, with declines recorded in all regions except the south west, where data indicated a large increase (Amar *et al.* 2006). The combined evidence from these two studies, although not significant, is suggestive that there may be factors operating in the UK, possibly at a regional scale that are contributing to the national population decline.

1.4 Suggested causes of decline

Potential causes of decline during the breeding season include reduced abundance and availability of invertebrate food, loss of foraging habitat, increased predation risk and reduced nest survival, which in some open nesting passerines is known to be affected by surrounding habitat (Martin & Roper 1988, Kelly 1993, Tarvin & Smith 1995).

1.4.1 Demographic causes

Analyses of Spotted Flycatcher data collected by the British Trust for Ornithology (BTO) as part of the Nest Record Scheme reveals an increase in the failure rate of chick-stage nests and data collected through the Constant Effort Scheme reveals a decrease in the ratio of juvenile Spotted Flycatchers to adults, indicating that productivity may have changed (Baillie *et al.* 2007). Demographic modelling of combined BTO data has suggested that declines are most likely to have been driven by a reduction in the survival rate of birds in the first year of life, although it seems unclear whether this is driven by changes in survival in the immediate post-fledging period, or changes in first-winter survival (Freeman & Crick 2003).

Although there seems to be no evidence that laying date has changed (Baillie *et al.* 2007), it is possible that there may be subtle differences in the number of nesting attempts each individual makes in a breeding season, resulting from slight differences in habitat quality, as yet not explored. In migratory species, such as the Spotted Flycatcher, the length of the breeding season is often constrained by the date that adults return from the wintering quarters, and birds that breed early are more likely to attempt second broods (Ogden & Stutchbury 1996). In general, there is little evidence to suggest any changes in the phenology of migration of Spotted Flycatchers (Loxton 2002). In common with many long-distance migrants, the timing of departure of Spotted Flycatchers from their southern African wintering ground is determined by day length (Kok *et al.* 1991). Although previous studies have suggested that first arrival dates of birds in the UK have changed little (Huin & Sparks 2000), more recent work reveals that there may have been some small changes in these since the early 1970's, which would result in birds being in the UK for longer than previously (Cotton 2003). However, it has also been demonstrated that arrival dates in the UK are influenced by weather conditions in southern Europe in the month preceding arrival in the UK (Huin & Sparks 2000), thus accounting for small amounts of annual variation in arrival dates.

1.4.2 Ecological causes

1.4.2.1 Changes in habitat

Although traditionally regarded as a woodland species, being included in the composite index of woodland bird populations that form part of the UK Government's wild bird indicator (Anon. 1998a, 1999, Gregory *et al.* 2003), Spotted Flycatchers are in fact more generalist in their choice of breeding habitat. Consequently, they are potentially exposed to the effects of change in each of the broad habitat types that they occupy, whether farmland, woodland or suburban.

Intensification of farming practices, particularly in the east of England, has resulted in the loss of habitat that may have been formerly suitable for breeding flycatchers. Specifically, the loss of active livestock farms, and associated farm buildings, together with a reduction in the number of hedgerows, boundary trees and farm copses, will have reduced both nesting and foraging opportunities for flycatchers. When coupled with a more general degradation of farmland habitat in terms of a reduction in the abundance of invertebrate food (Woiwood & Thomas 1993, Benton *et al.* 2002, Conrad *et al.* 2006), farmland would now appear to be a poorer quality breeding habitat for Spotted Flycatchers than it was formerly.

Simplification of the structure of habitat in the immediate vicinity of woodland, for instance the removal of hedgerows or tree lines which serve to link woodland to the surrounding farmland, reduces the foraging and nesting opportunities of birds to the woodland interior, removing the opportunity for birds to extend their foraging range to include nearby field margins. Alternatively, spray drift and incursion of agro-chemicals may have indirect effects by reducing the invertebrate diversity of woodland edges, making these areas less profitable for foraging birds. Structural changes within woodland brought about by reduced management, and in particular increased shading and the loss of open glades, would potentially reduce the abundance and/or activity of the aerial invertebrates on which Spotted Flycatchers primarily forage.

Although Spotted Flycatchers may be able to withstand some aspects of change associated with urban habitats, being relatively tolerant of man and able to utilise many man made features as perches and nest sites, these would still need to be allied with a reliable food supply. Unless urban habitats contain sufficient quantities of the food plants and nectar-rich sources used by aerial invertebrates, urbanisation is likely to lead to a decrease in available prey for Spotted Flycatchers. Additionally, urbanisation leads to changes in the relative abundance and importance of different predator species, with introduced mammals such as the Domestic Cat *Felis catus* increasingly featuring. Other predators, such as accipiters and squirrels may concentrate their activities in areas around feeding stations, where prey are abundant. Since the birds found in gardens are influenced by the habitat surrounding it rather than the habitat within the garden *per se.* (Chamberlain *et al.* 2004), increasing urban sprawl and degradation of the habitat around towns would likely influence bird populations in a negative manner.

Although it has been hypothesised that changes in habitat may affect Spotted Flycatchers directly by reduced availability of nest sites, this is probably the least likely of the breeding season hypotheses. Since Spotted Flycatchers are readily able to utilize a range of nesting locations within different habitats, with nests located both in trees and on, or in buildings, it would be surprising if the availability of nest sites were a limiting factor.

1.4.2.2 Food availability

In 1954, David Lack hypothesised that food shortage was the chief natural factor limiting the numbers of many species of bird, particularly through repression of the reproductive rate (Lack 1954). Differences in the abundance of food during the breeding season may, in some species, bring about changes in seasonal productivity, either increasing, or reducing the number of broods it is possible to raise (Holmes *et al.* 1991, Rodenhouse & Holmes 1992), or by causing alterations in clutch size, nest abandonment rates, nestling body condition or mortality rate (Newton 1998). Similarly, long-term changes in the availability of invertebrate food resources may coincide with long-term changes in bird populations (Potts 1986).

Adult flycatchers are reliant on an abundance of large insects when provisioning young. Fewer insects may have reduced the ability of adult birds to successfully rear chicks, or if the adults work harder when provisioning young to compensate for this, lack of invertebrates might affect adult survival rates after the breeding season through a reduction in body condition. Although it seems that the type of prey items taken by flycatchers has not changed during the period of population decline, what may have altered is the relative contribution each of these components makes to the diet as a whole. There is a growing body of evidence that the abundance of invertebrates has declined on farmland (Aebischer 1991, Donald 1998, Sotherton & Self 2000, Benton *et al.* 2002). Although populations of different invertebrate groups in the UK are not monitored to the same extent as birds, declines have nevertheless been recorded for several species of butterfly, moth and bumblebee (Williams 1982, Warren *et al.* 2001, Thomas *et al.* 2004, Conrad *et al.* 2006). Similarly, the scale of the short-term effects of pesticides suggest that they are an important contributory factor in invertebrate declines (Campbell *et al.* 1997, Morris *et al.* 2005). As a result of the consequential reductions in availability of these prey groups, it is possible that flycatchers are finding it increasingly difficult to select such high quality prey items. This in turn may lead to birds, particularly juveniles, being in poorer condition immediately prior to migration or, alternatively, may lead to changes in predation risk as birds reduce vigilance levels by increasing foraging activity.

Beyond effects on food abundance, habitat change may have had a further detrimental effect on breeding Spotted Flycatchers. Recent work on swallows, another obligate insectivore, has shown that there are important interactions between habitat and food abundance that determine food availability. In poorer weather, and more specifically, increased wind speed, swallows *Hirundo rustica* forage preferentially in the lee of hedgerows or woods (Evans *et al.* 2003). In farmland, with the enlargement of fields and removal of hedges, hedgerow trees and scrub, it is possible that simplification of habitat structure (by reducing the availability of perches and open spaces in proximity to each other) has made it harder for Spotted Flycatchers to find suitable areas to forage.

It is therefore possible that habitat structure has an important influence on the availability of insects, beyond the effect of food abundance alone. In woodland, it is possible that some habitat changes may have resulted in a reduction in the abundance of insects, and that this problem is exacerbated by structural changes such as loss of open glades and canopy closure, both of which will have reduced foraging opportunities.

1.4.2.3 Predation

In many open-nesting passerines, predation is the greatest source of nest failure (Lack 1954, Ricklefs 1969, Söderström *et al.* 1998, Donald *et al.* 2002). A number of potential predators, both mammalian and avian, have been implicated in the decline of woodland birds, either through an overall increase in predator numbers or through changes in the vulnerability of nests or adult birds. The introduced Grey Squirrel *Sciurus carolinensis* is often cited as a major potential predator of songbird nests, particularly with respect to its continuing expansion in both range and density. This perception prevails despite the lack of evidence that is anything more than circumstantial or anecdotal (Hewson & Fuller 2003). Similarly, potential avian predators with recent increases in population size, such as the Great Spotted Woodpecker *Dendrocopos major*, have also been suggested as having negative impacts on breeding populations of, particularly, woodland species. In analyses of data from the period 1964-1993, Gregory and Marchant (1996) reported increases in mean corvid densities on farmland Common Bird Census (CBC) plots in both the English regions used in this study, as well as an increased density in woodland plots in the south-west. Corvids, and especially Jays, are widely recognized as nest predators (Angelstam 1986, Møller 1989, Andrén 1992, Götmark 1992a, Groom 1993, Paradis *et al.* 2000, Schaefer 2004). However, as is the case with the Grey Squirrel, there is a dearth of empirical evidence suggesting any strong relationship between the two (Newton 1993, Thomson *et al.* 1998). A species such as the Spotted Flycatcher, which nests in a variety of different landscapes, will be at risk of predation from a wide range of potential predator species. There are several potential mechanisms whereby predation rates may differ between habitats. Habitat characteristics may influence nest concealment and/or predator access to nests, as well as influencing predator type, abundance or distribution (Evans 2004). These two mechanisms may also act in combination to alter the search efficiency of potential nest predators (Bowman & Harris 1980, Tarvin & Smith 1995), allowing predators that rely on visual cues to locate nests more easily. Additionally, predation risk may also be altered by differences in parental behaviour at the nest. Such differences in behaviour may be brought about by other habitat related factors, including differences in the abundance or availability of food for both the adults and chicks. If this was the case, adults may modify their provisioning behaviour, therefore altering the level of activity at or near the nest, thereby varying the overall predation risk of the nest.

1.4.2.4 Weather effects

Weather conditions may have considerable effects on the breeding success of Spotted Flycatchers. Survival of nestlings increases in warm and sunny conditions (O'Connor & Morgan 1982) probably through a combination of effects of temperature on the breeding cycle of the birds themselves, and effects of both temperature and sunshine on the emergence and activity of insects (Taylor 1963). Davies (1977) found that prey activity was very important in influencing the ease with which Spotted Flycatchers could find their prey; in lower temperatures, when fewer insects are flying, Spotted Flycatchers spend less time fly-catching and more time gleaning aphids and small flies in the tree canopy. Additionally, low temperatures may increase the amount of time that the parents need to spend brooding their chicks, with a consequential reduction in time spent foraging.

1.4.2.5 Factors operating outside the UK

The Spotted Flycatcher is a migrant, wintering in sub-Saharan Africa, and so factors on the non-breeding grounds, or on migration routes, may have affected breeding populations. Declines in the breeding population of other sub-Saharan migrants have been linked to conditions on the non-breeding grounds (Winstanley *et al.* 1974, Baillie & Peach 1992). Schaub & Jenni (2000) showed that Spotted Flycatchers have a characteristic migration strategy whereby they do not accumulate fat stores in North Africa in autumn or increase body mass along the migration route. This may require them to stop and fuel up regularly in the Sahara, and indeed Spotted Flycatchers have been observed foraging on insects in the middle of the desert (Bairlein 1992). An expanding Sahara may therefore cause even more problems to Spotted Flycatchers than other species with different migration strategies. There is evidence from BTO analysis of nest record cards and survival data from ringing that the decline in Spotted Flycatcher population may be associated with reduced survival rates of first-year birds (Freeman & Crick 2003), which could be linked to reduced survival on migration routes or non-breeding grounds. Similar demographic analyses of Willow Warbler *Phylloscopus trochilus* data suggests that population declines may have been driven by a decrease in adult survival, potentially resulting from problems in the non-breeding areas (Peach *et al.* 1995).

Although evidence of regional differences in population trends suggests that there may be factors operating in the UK that are contributing to the overall population decline, factors operating on the non-breeding grounds may still need to be taken into account. For instance, similar differences in regional population trends may also have been observed if there were differential over-winter survival of birds within the UK population, possibly as a result of a migratory divide operating at either a regional, or habitat level. Although it would seem unlikely that Spotted Flycatchers breeding in different regions of the UK would migrate to entirely different non-breeding areas, a comparable phenomenon has been observed in a Swedish population of Willow Warblers (Chamberlain *et al.* 2000a), and the possibility nevertheless needs investigation.

1.5 Thesis structure

This thesis examines the breeding ecology of the Spotted Flycatcher in the UK in a comparative study using sites located in two regions of lowland England with contrasting population trends. With the exception of chapters 1, 2 and 8, the thesis has been written as a series of papers, and as such, there is inevitably some overlap between these chapters and the rest. Chapters 3 and 4, and appendices 2 and 3 have either already been published, or are in press.

Following this introductory chapter, I proceed as follows:

Chapter 2 outlines the methodology employed during the study, and provides an overview of the data collected. Subsets of the data are use for subsequent chapters. Although not all of the data collected has been used in the preparation of this thesis, I have nevertheless included information on the nature of additional data that was collected during the course of this study in order to highlight its existence for future analyses.

Chapter 3 considers breeding success, and specifically examines the relationship between nest success and the predominant habitat type around Spotted Flycatcher nests in two contrasting areas of England. The chapter tests the hypothesis that nest survival is associated with region and habitat, and examines whether this may be contributing to the observed population declines. This chapter is published as **Stevens, D.K.**, Anderson, G.Q.A., Grice, P.V. & Norris, K. 2007. Breeding success of Spotted Flycatchers *Muscicapa striata* in southern England – is woodland a good habitat for this species? Ibis 149 (supp. 2): 214-22.

Chapter 4 aims to identify the main causes of Spotted Flycatchers nest failure, and in the case of predation, to identify the species responsible by documenting the fate of nests using purpose-built remote, digital nest cameras. This chapter has been accepted for publication as **Stevens, D.K.**, Anderson, G.Q.A., Grice, P.V., Butcher, N., Allen, D.J. & Norris, K. Predators of Spotted Flycatcher *Muscicapa striata* nests in southern England as determined by digital nest cameras. Bird Study, In Press.

Chapter 5 is concerned with survival estimates based on a model that allowed a more comprehensive investigation of the temporal patterns in daily survival of Spotted Flycatcher nests, thus testing the assumption of constant daily nest survival within nesting stages.

Chapter 6 examines the hypothesis that regional population trends may be related to factors operating outside the UK. Stable isotopic analysis is used to establish whether breeding populations from regions of the UK with contrasting population trends show differences in either geographic location or feeding ecology on the non-breeding grounds.

Chapter 7 uses nest survival estimates based on a model that allows for the temporal patterns in daily survival to formulate a simulation model to derive productivity estimates and hence to examine which demographic factors may be linked to the population decline of Spotted Flycatchers.

Chapter 8 brings together the findings of the previous chapters to explain the observed patterns of population change in Spotted Flycatchers breeding in the UK. The implications for conservation are considered and recommendations for further work are suggested.

The thesis additionally has three appendices, which include supplementary information gathered during the course of the study, but which fall outside the main framework of the study.

Appendix A considers the nestling diet of the Spotted Flycatcher.

Appendix B outlines the manufacture and technological application of the purpose-built nest cameras employed during the study. This appendix has been published as Bolton, M., Butcher, N., Sharpe, F., **Stevens, D.** & Fisher, G. 2007. Remote monitoring of nests using digital camera technology. Journal of Field Ornithology, 78, 213-220.

Appendix C reports on problems associated with colour-ringing several species of flycatcher, and discusses the nature and extent of the issue. This appendix has been published as Pierce, A.J., **Stevens, D.K.**, Mulder, R. & Salewski, V. 2007. Plastic colour rings and the incidence of leg injury in flycatchers (Muscicapidae, Monarchidae and Dicruridae). Ringing & Migration, 23, 205-210.

Chapter 2

Methodology of fieldwork

2.1 Overall methods and approach

With the considerable number of environmental variables that may have contributed to the observed decline in the Spotted Flycatcher population, a comparative approach was employed. Hence, two study sites were selected that would allow comparison of current demography in separate and distinct areas. The areas selected would ideally be distinct both in geographical location and landscape characteristics, as well as having differing population trends. Such an approach was used successfully to determine the causes of population decline in Song Thrushes *Turdus philomelos* in the UK (Gruar *et al.* 2003, Peach *et al.* 2004).

2.2 Establishing the study sites

Data were collected from two study areas; in Devon (southwest England) in 2004, 2005 and 2006, and Bedfordshire and Cambridgeshire (Beds/Cambs; eastern England) in 2005 and 2006.

2.2.1 Evidence for the choice of study sites

Data were obtained from the British Trust for Ornithology (BTO) Common Birds Census (CBC) for the period 1964-2002, the joint BTO/JNCC/RSPB Breeding Bird Survey (BBS) for the period 1994-2003, the Royal Society for the Protection of Birds (RSPB) sites from the Repeat Woodland Bird Survey (RWBS) and the RSPB/English Nature (EN) Core vs. Edge project. Additionally, county reports & avifauna were searched for evidence.

2.2.1.1 CBC data

The CBC was launched by the BTO in 1962, being the first scheme of its kind to monitor populations of common bird species. Initially instigated as a monitoring response following a period of rapid agricultural change in the UK, the CBC was primarily focussed on farmland and woodland sites. The territory-mapping methodology, which was intensive and time-consuming, required the assistance of skilled and dedicated volunteers, thereby indirectly limiting the geographical spread of monitoring plots. Since participants in the scheme were able to choose their own study plots, they varied in size, were not necessarily representative of the wider countryside, and had the added disadvantage that there was a potential for an inevitable bias towards bird-rich areas. Nevertheless, despite these limitations, the CBC has provided a valuable long-term data set (Marchant *et al.* 1990), at the same time as providing the benchmark for bird monitoring schemes worldwide.

Data from long-running CBC sites situated in counties in the E England Government Office Region (GOR) were examined. There were no long-running datasets available in Cambridgeshire and densities of Spotted Flycatchers from long-running Suffolk & Essex sites were consistently low, and showed little in the way of trend information. A farmland site in Norfolk (99.6ha) showed a long-term decline between the years 1964 – 1990. The only long-running site in Bedfordshire (74.5ha of mainly farmland) showed a consistent decline in the number of territorial pairs for the period 1973 – 1993 (Fig. 1).

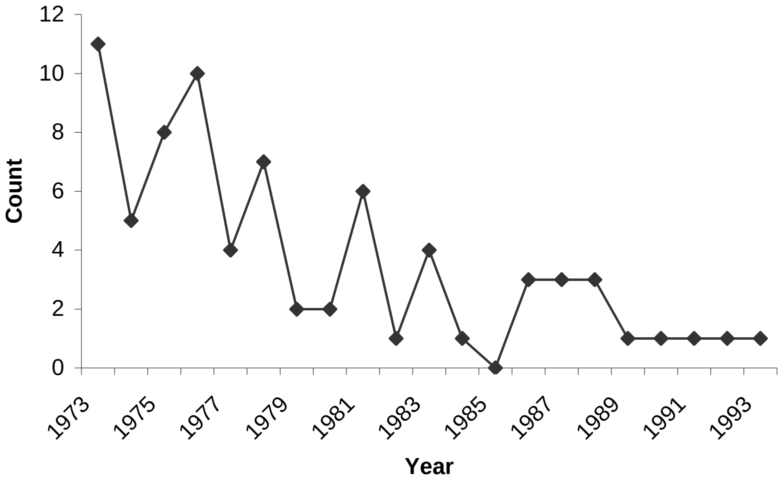

Figure 1. CBC data (counts of Spotted Flycatcher territories) from a site in Bedfordshire (grid ref. TL137454).

2.2.1.2 BBS data

The BBS was launched in 1994 and was designed to improve upon the existing CBC survey methodology by using a random stratified sampling design, thereby increasing geographical, habitat and species coverage. Additionally, by using line transect methodology (unlike the CBC) the BBS was designed so that volunteers could undertake it relatively quickly, thus encouraging maximum participation and national coverage; the target is 2500 1km squares annually.

Since the sampling design allows survey squares to be chosen from within identified regions, indicators of population change between years may be generated either nationally or regionally. For inclusion of a BBS trend in the regional indicators, a mean sample of 30 or more BBS squares must be surveyed annually for that species within the geographic area of interest. Being a relatively scarce species in terms of BBS data recording, particularly in regions with few BBS squares, Spotted Flycatcher has only met this criterion for a few regions. Recent work on BBS regional indicators by the BTO and RSPB (Noble *et al.* 2006) has resulted in the development of a new relaxed rule to include the use of trends for all species counted on at least 20 BBS squares, and using a new protocol in which the trend for each species is generated sequentially from increasingly larger geographic areas. However, this does mean that the individual species trends are less reliable and have larger confidence intervals attached to the estimates.

With this caveat in mind, regional trends for Spotted Flycatcher have been generated for 3 regions (E England, SE England & SW England) based on the 20 sites rule (using data generated solely from that region), and a further 4 regions (NW England, E Midlands, W Midlands & London) using the 20 sites rule and including data from a larger region incorporating adjacent counties. Regional indices for the remaining two regions (Yorks & Humberside and NE England) were based on regions expanded by including adjacent GOR's to increase the sample size to 20 sites (RSPB unpublished data, Table 1).

Regional BBS trends generated in this way for the two regions provided support for our choice of study sites, indicating a relatively stable population in the SW region (for the Devon study site), and a rapidly declining population in the E England region (for the study site on the Bedfordshire & Cambridgeshire border).

Table 1. Regional population indices for the period 1994 – 2003 generated using new criterion (RSPB unpublished data).

Government Office Region	Data source	% Change 1994 – 2003
England	BBS	-38
Wales	BBS	-44
E England	BBS region only	-77
SE England	BBS region only	-39
SW England	BBS region only	-6
NW England	BBS region + adjacent counties	-19
E Midlands	BBS region + adjacent counties	-58
W Midlands	BBS region + adjacent counties	-35
London	BBS region + adjacent counties	-37
Yorkshire & Humberside	BBS region + adjacent GOR	-26
NE England	BBS region + adjacent GOR	-22

2.2.1.3 RWBS data

The Repeat Woodland Bird Survey (RWBS) was a joint project commissioned and funded by Defra, the Forestry Commission, RSPB, BTO, the Woodland Trust and English Nature. The study covered 406 woodland sites to allow comparison of data that was collected at intervals between 1960 and 1980. The aim of the study was to establish a regular national monitoring programme for woodland birds, to analyse population trends in the sites visited and to look for evidence of habitat change or other potential correlates of population change.

Spotted Flycatcher data were obtained from the four regions of the country in which RSPB repeat surveys took place (Table 2, A. Amar, unpublished data); Northamptonshire, Suffolk, Buckinghamshire and Devon & Somerset (data from the latter two counties combined). Data collected in the initial survey carried out in the 1980's were compared to data collected from the repeat surveys, which took place in 2003 & 2004. Counts were converted into densities (derived from Distance), which represented a population index such that zero counts may not actually mean complete absence of birds, just low density (A. Amar, pers. comm.).

Table 2. Densities (territories/ha) and local trends in populations of Spotted Flycatchers at RSPB RWBS sites.

	Devon & Somerset	**Northants**	**Suffolk**	**Bucks**
Year of initial survey	1982	1984	1986	?
Number of sites	13	13	6	12
Mean density start	0.166	0.472	0.778	0
Mean density 2003/2004	1.401	0.348	0	0
Number of sites increasing	11	2	0	-
Number of sites decreasing	2	11	6	-

2.2.1.4 *Core vs. edge project*

The RSPB/EN Core vs. Edge Project was instigated in 2004 with three specific aims. These were to review evidence on biogeographic predictors of abundance and decline, use BBS data for the period 1994-2004 to construct maps of variation in population trends of species across their range in Britain and subsequently to identify biogeographic, climatic, agricultural, and habitat predictors of variation in these population trends.

Maps of Spotted Flycatcher population trends across its range were obtained from the project (Fig. 2, RSPB unpublished data). Although care must be taken to consider the varying degrees of uncertainty in the interpolations whilst interpreting these maps, they nevertheless give an important indication of current Spotted Flycatcher population trends across the UK.

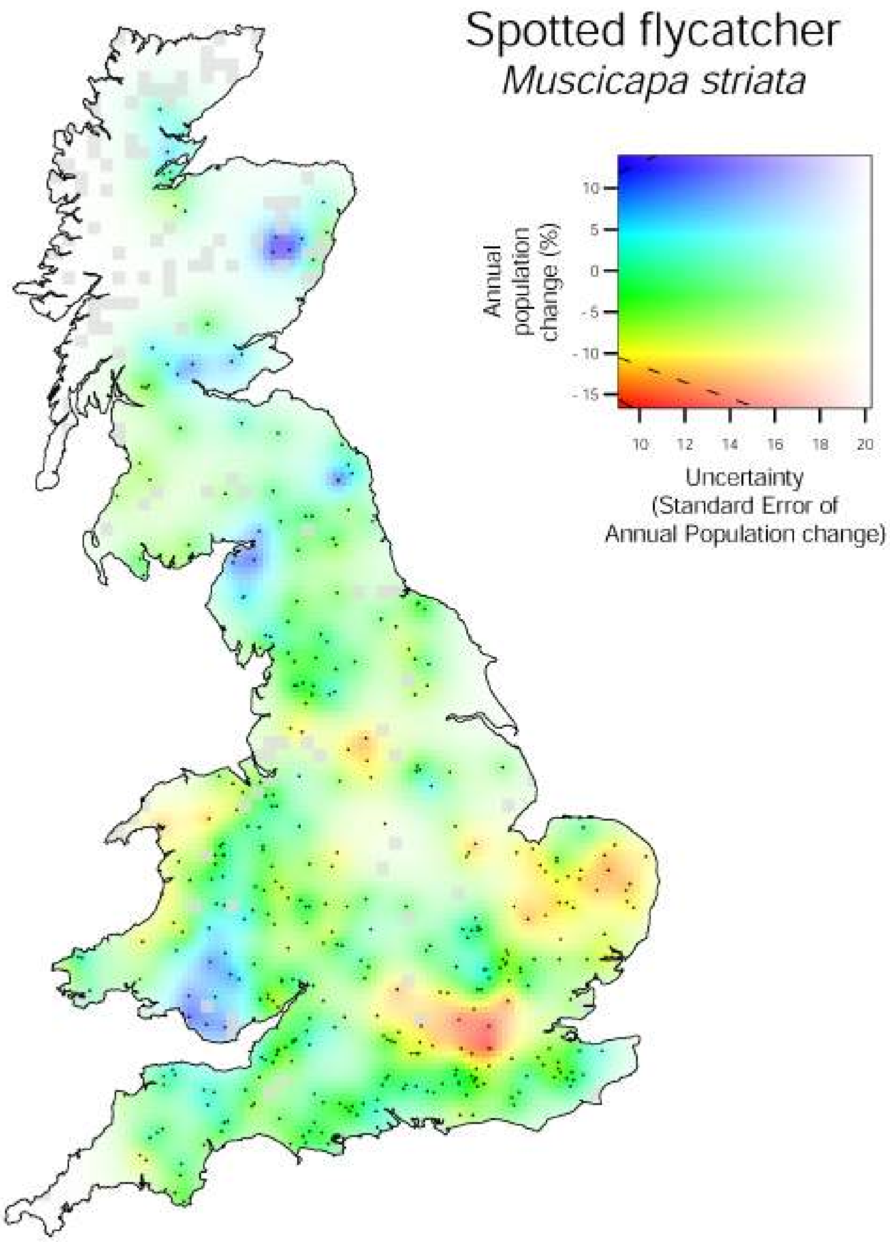

Figure 2. Core vs. Edge Project population trend map for Spotted Flycatcher generated using BBS data for the period 1994 – 2004 (RSPB unpublished data).

2.2.1.5 County reports

Data from County reports and avifauna were examined, but apart from some interesting anecdotal evidence concerning local populations, were difficult to interpret. Data tended to be collected by a relatively small number of observers and search effort between years was often found to be inconsistent. Several individuals assisted by supplying personal data sets, and although these figures provided evidence of local declines, it was difficult to translate these data sets into useful regional trends.

2.2.2 Location and general characteristics of the study sites

Given the growing evidence for stable population trends in southwest England and large declines in eastern England, data extracted from county reports from these two regions were used to assist with the identification of specific study sites that would allow a comparative ecological study of two populations with contrasting trends (Peach *et al.* 2004). Despite the large national decline, the review of county bird reports revealed several potential study sites in Devon where a reasonable sized population was still extant. These included an area around Aveton Gifford, in the South Hams and a site at Yarner Wood, a National Nature Reserve woodland site. Following discussion with local birdwatchers, the site at Aveton Gifford seemed most promising, with consistently high numbers of breeding birds and benefiting from a considerable amount of existing local knowledge (Bone 2002).

The study area in Devon (centred on the parish of Aveton Gifford in the South Hams area, Fig. 3a) covered approximately 3200 ha, of which c. 2670 ha was farmland, 160 ha woodland and 111 ha villages and rural gardens (Fig. 3b). Woodland blocks in the study area were generally small, with only one over 20 ha, or linear in nature (following field edges and water courses) and were primarily deciduous. Grassland (largely used for cattle and sheep grazing, but also some for the production of hay and silage) accounted for over two-thirds of all farmland, with tilled land accounting for less than a third.

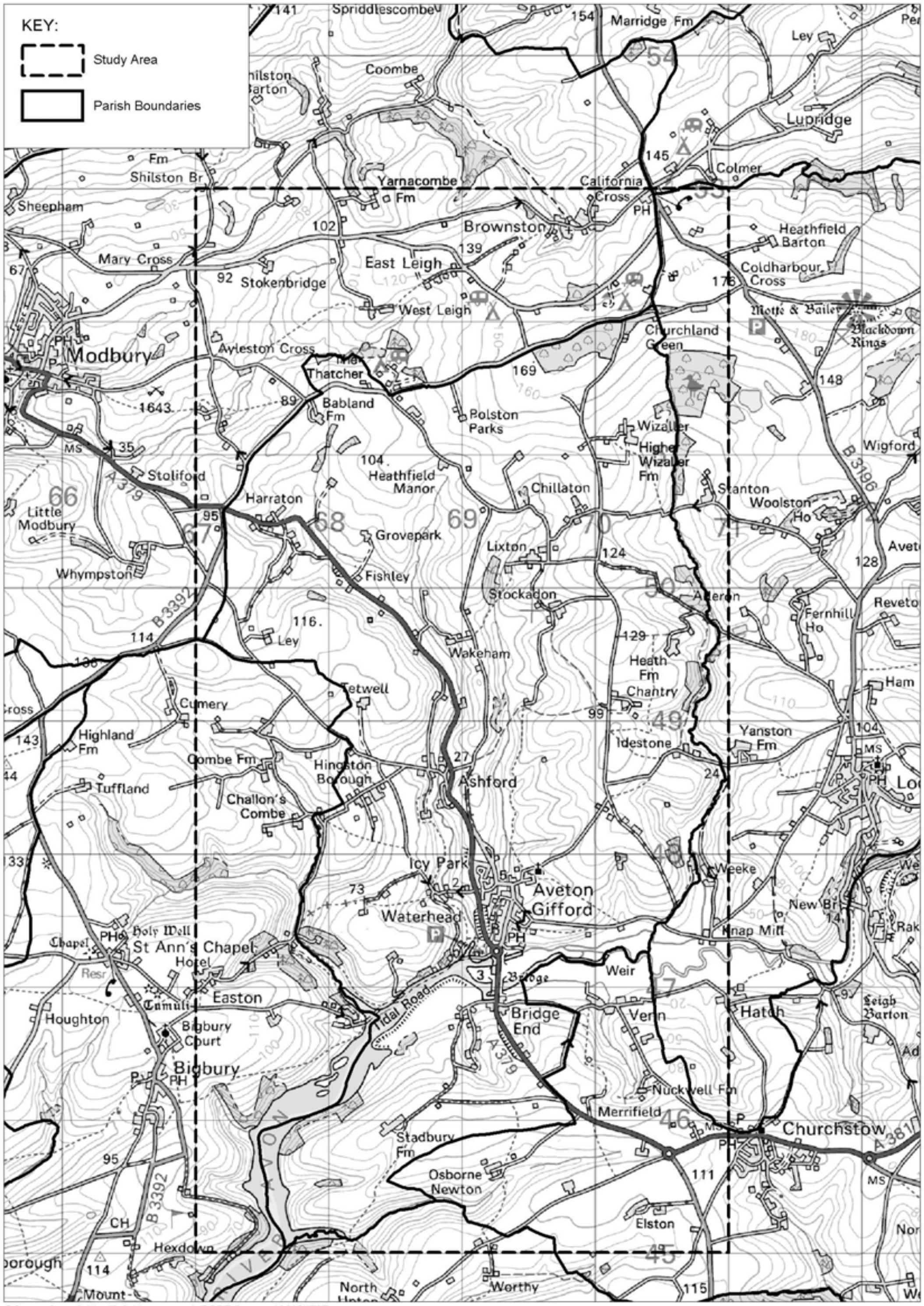

Figure 3a. Map showing the extent of the Devon study area (1km grid).

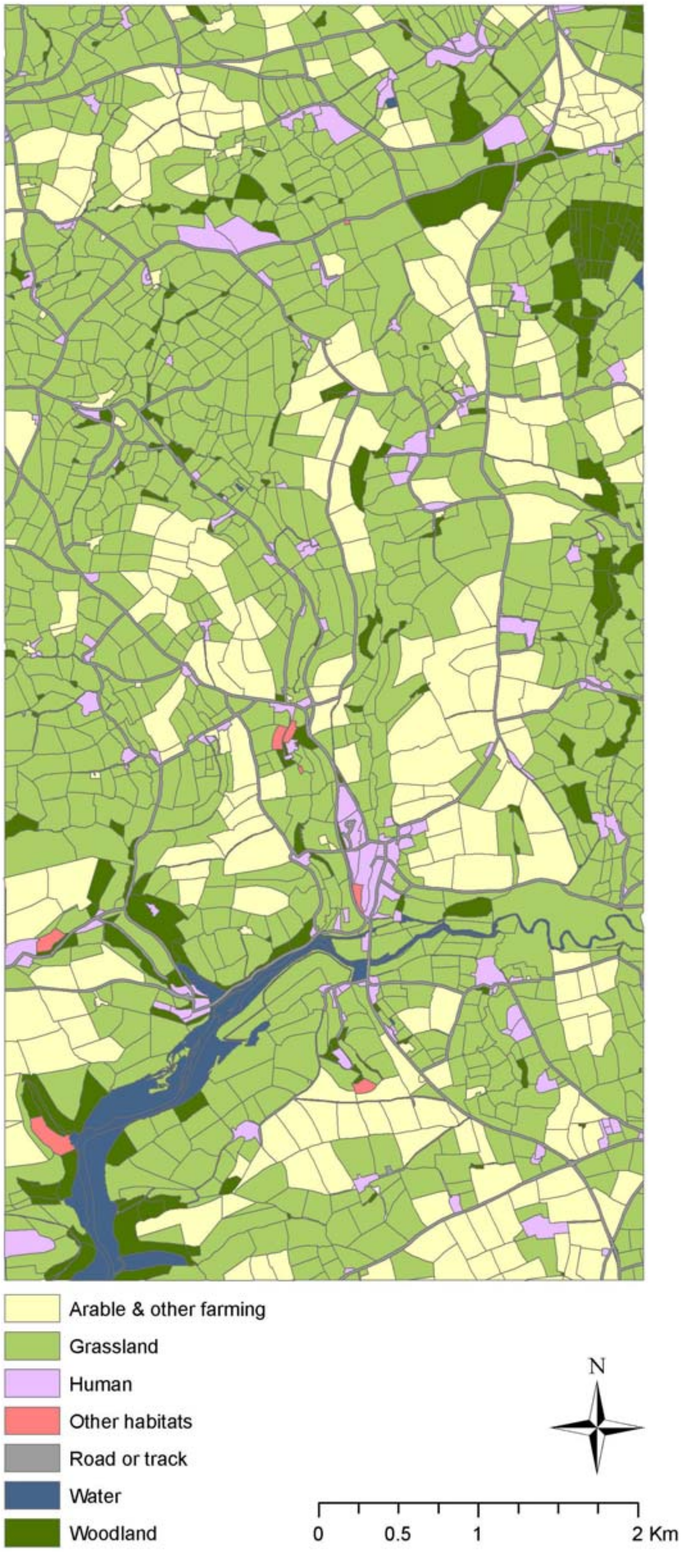

Figure 3b. Thematic habitat map for the Devon study area.

In 2003, the RSPB had undertaken a pilot study to trial research methods that may be utilised when for any future study of Spotted Flycatchers. The pilot project was based largely in northeast Bedfordshire and used existing information on sites collected by members of the Bedfordshire Bird Club during 2002. Eighty occupied sites were initially identified in 2002, with approximately 25 of these, located in the north-east of the county being chosen for re-survey in during the pilot project. Subsequently other sites were added following searches of potentially suitable areas, or where information was received following requests to various interest groups. The pilot project located 26 occupied sites during 2003, and succeeded in trialling field methods and arranging access permission for future work. A study location on the Bedfordshire/Cambridgeshire border was subsequently located that could utilise existing resources from the RSPB headquarters at The Lodge, as well as capitalise on the progress made by the pilot project.

The Beds/Cambs study site (Fig. 4a) covered approximately 3200 ha of which c. 2280 ha was farmland, 440 ha woodland and 123 ha 'human sites' (which included villages and rural gardens). Woodland blocks in the study area ranged in size from less than 1 ha to approximately 92 ha, with 5 blocks being greater than 20 ha in area. Approximately 60% of the woodland in the study area was deciduous and 10% coniferous, the remaining 25% being mixed (i.e. made up of least 10% each of deciduous and coniferous trees). In contrast to the Devon study area, grassland only accounted for about one quarter of the farmed area with the remaining three-quarters being tilled land (Fig. 4b).

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Figure 4a. Map showing the extent of the Bedfordshire/Cambridgeshire study area (1km grid).

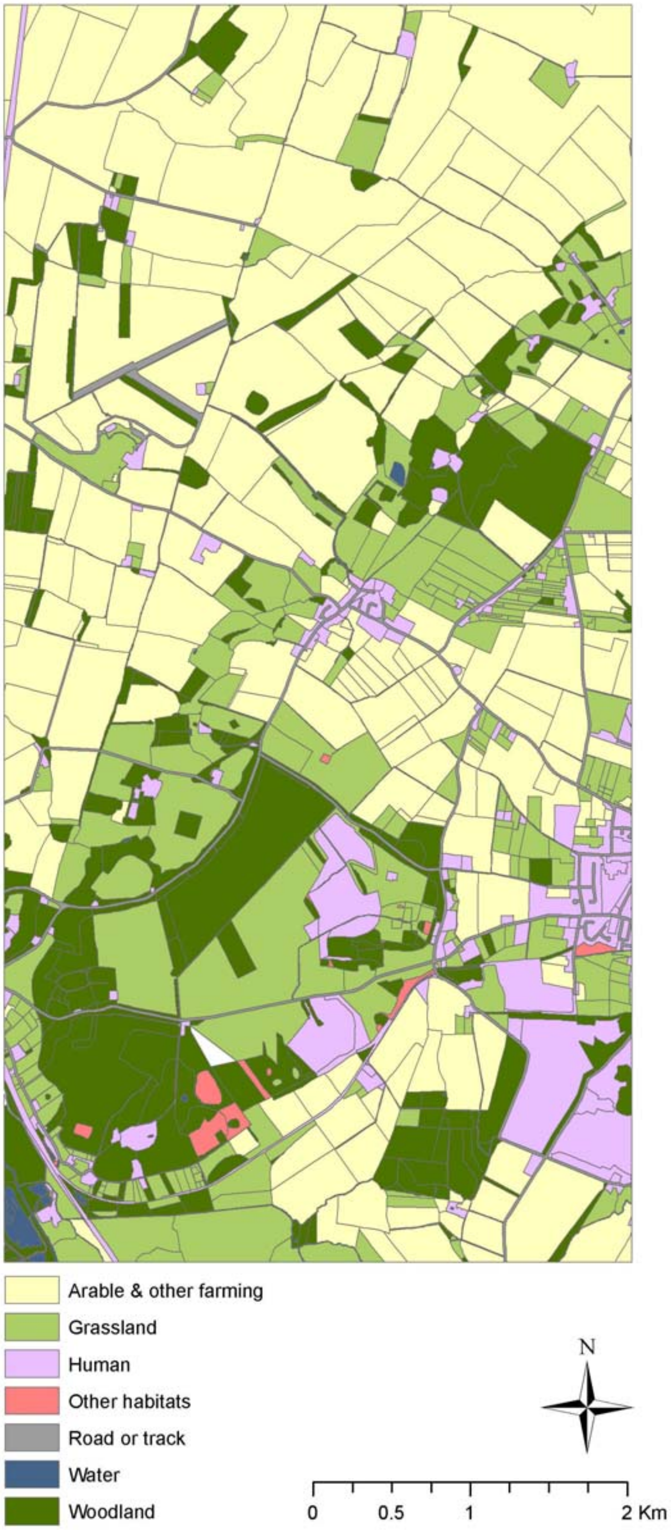

Figure 4b. Thematic habitat map for the Beds/Cambs study area.

Densities of Spotted Flycatchers were twice as high in the Devon study area (mean 2004-2006, 1.8 pairs/km^2) than in the Bedfordshire/Cambridgeshire study area (mean 2005-2006, 0.9 pairs/km^2). The location of the two study areas in relation to each other is shown in Fig. 5.

Figure 5. Map showing Location of the two study sites in lowland England: Devon, 50.31°N 03.84°W and Bedfordshire/Cambridgeshire border, 52.12°N 00.26°W. Study sites are marked on the map as a solid filled rectangle.

2.3 Meteorological data

Daily rainfall and mean daily temperature data were obtained from the Met Office for the duration of each field season (May – Aug inclusive). For the Devon study site, weather data originated from

Plymouth, approximately 20 km north-west of the study site. For the Beds/Cambs study site, the data originated from Wattisham, approximately 80 km east of the study site. Although 2006 was the warmest of the three field seasons, both temperature and rainfall was similar in each (Figs. 6 & 7).

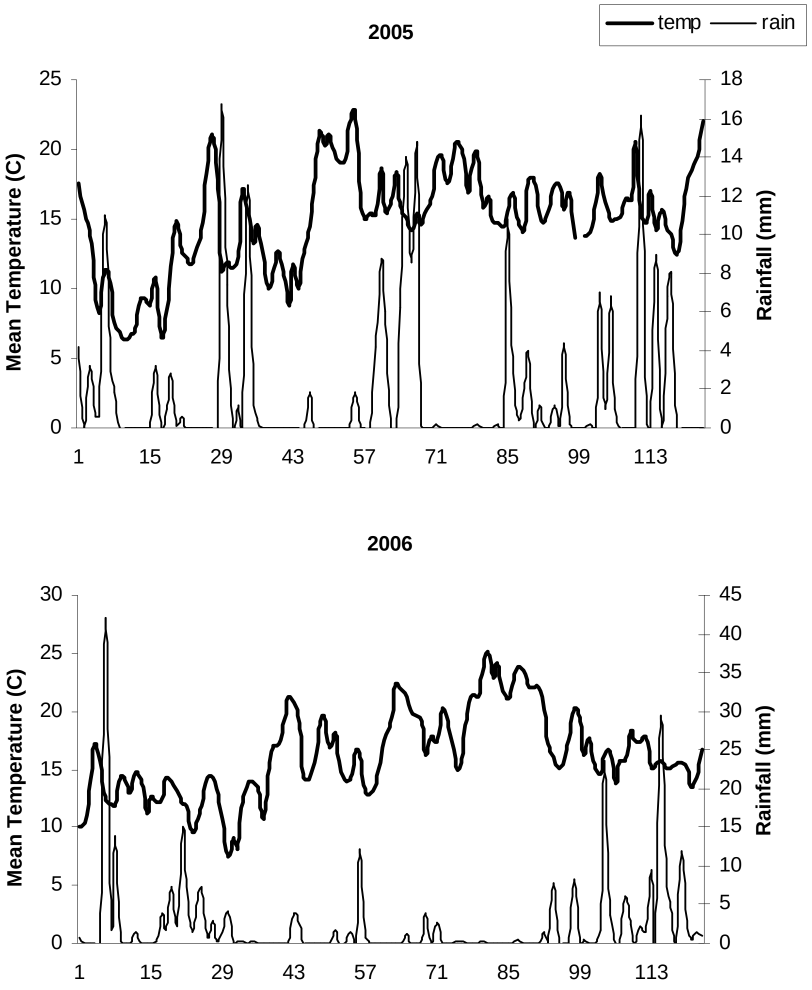

Figure 6. Mean daily temperature and daily precipitation for the two field seasons in the Bedfordshire/Cambridgeshire study site. Data from the meteorological station at Wattisham. X axis represents days from 1st May.

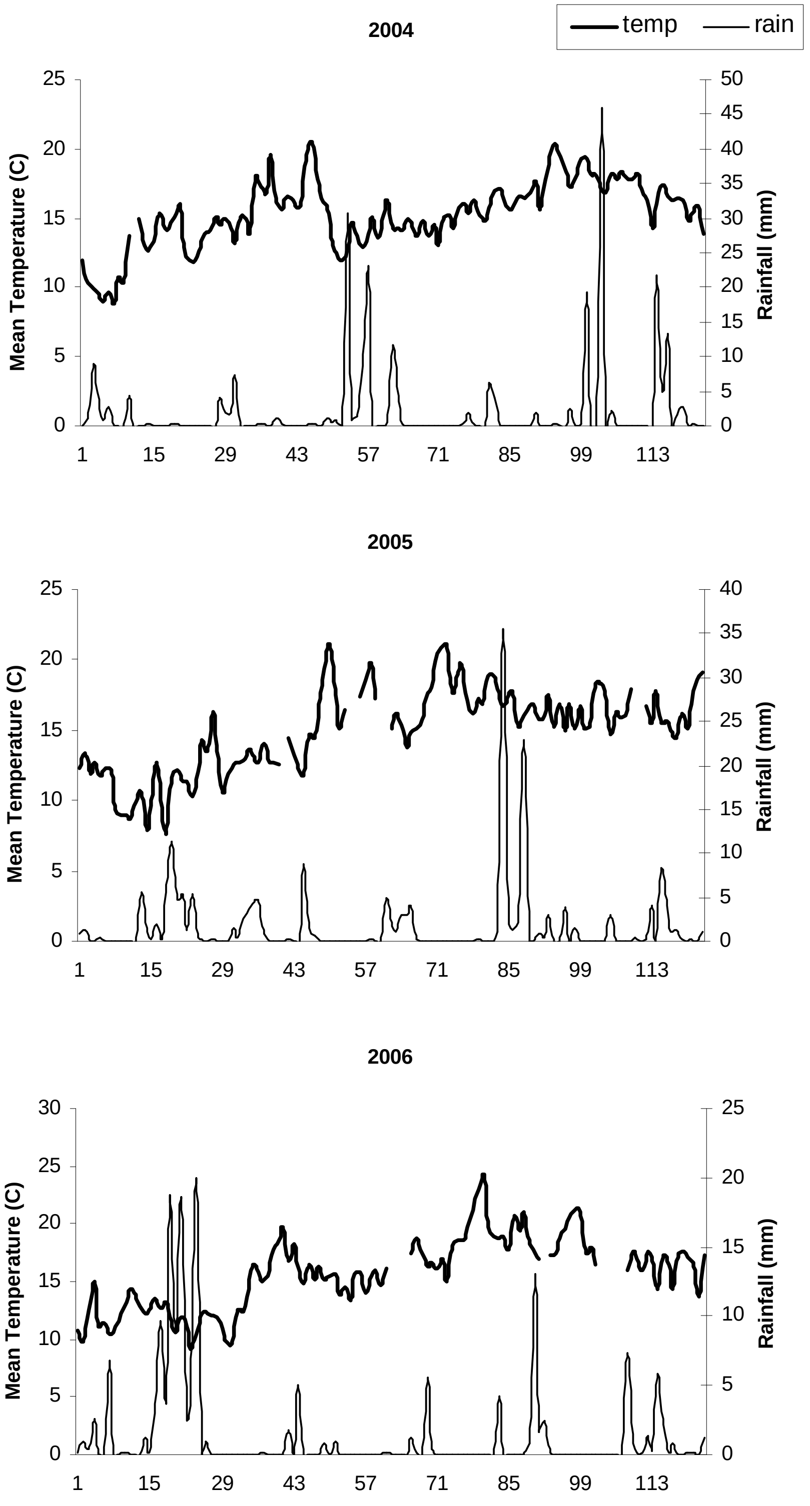

Figure 7. Mean daily temperature and daily precipitation for the three field seasons in the Devon study site. Data from the meteorological station at Plymouth. X axis represents days from 1st May

2.4 Reproductive success

2.4.1 Nest recording and biometric data collected

All potentially suitable flycatcher habitats were regularly searched by observers from early May through to the end of August in each year of the study. Territories were located by observing the behaviour of any birds found. Nests were located either by searching likely locations within a territory, or by observations of the behaviour of the adults. In order to minimise disturbance to nest sites vegetation around the nest was disturbed as little as possible, nests were not visited in poor weather, and time spent at the nest was kept to a minimum. Nests were found at the building stage by observations of nest building behaviour: watching birds collecting nesting material and returning to the nest location. Egg laying and incubation stage nests were found either by watching the female leaving, or returning to the nest after a foraging bout, or by watching the male returning to feed the incubating female. Finally, nests found after hatching were located by observing the adults returning to the nest with prey items, or occasionally, by audible calls of the young within the nest. Once nests had been located, they were visited at regular intervals (usually every three days) to ascertain outcome. Nests were defined as active once the first egg had been laid. If the nest was unattended its contents were checked using a mirror on a telescopic pole, thus allowing access to most nests with heights of 6m or less. Where the first egg date was unknown, it was determined by back calculation from the hatching date assuming an average incubation period of 13 days starting from the date the last egg was laid, and one egg being laid per day (Cramp & Perrins 1993). For nests found at the chick stage where hatch date was unknown, back calculations to determine first egg date were performed after making an estimation of chick age following examination of the degree of feather development and comparing this to known age broods. Hatching date was the first day the eggs hatched, and was considered as the day one of the nestling period. The average nestling period was assumed to last 14 days (Cramp & Perrins 1993). Nest failures were categorised as desertion or predation at either egg or chick stage and predator identity was recorded where known.

In order to be able to identify individuals, all chicks were ringed with a uniquely identifiable BTO aluminium ring (usually around five - six days old), and subsequently, once the tarsus was sufficiently developed (around eight – nine days old), a unique colour combination of three Darvic rings. However, no chicks were colour-ringed during 2006 as potential problems were identified with plastic and PVC (Darvic) colour rings during 2005 (Appendix C, Pierce *et al.* 2007).

Biometric measurements of the chicks were taken at each handling. Since nestling mass is associated with the probability of fledging in several altrical birds species (Hochachka & Smith 1991, Magrath 1991, Brown & Brown 1996, Both *et al.* 1999), as well as being correlated with first year survival, each chick was weighed (to the nearest 0.1g) on each ringing visit using an electronic top pan balance. Maximum tarsus length, measured between the foot and the distal point of the knee (Svensson 1992, Redfern & Clark 2001), was also recorded (to the nearest 0.1mm) using dial-reading callipers.

In multi-brooded species such as the Spotted Flycatcher, reproductive success is linked to subsequent nesting attempts, following either failed or successful nests. In addition to colour marking all young prior to fledging (2004 and 2005 only), attempts were made to individually colour mark as many breeding adults as possible. Adult birds were trapped near to the nest using mist nets, perch traps, or a combination of the two. Sex (using brood patch size), wing length (maximum chord, Redfern & Clark 2001) to the nearest mm and weight (to the nearest 1 g using a 50 g Pesola balance) were recorded before release. In 2004 and 2005 adults were colour-marked with a unique combination of three PVC (Darvic) rings obtained from A.C. Hughes, but following identification of a potential problem with this method, in 2006 birds were marked with a single anodised aluminium colour ring in preference to the continued use of PVC rings (Appendix C, Pierce *et al.* 2007).

2.5 Diet and provisioning

2.5.1 Foraging watches

Although flycatchers will forage up to 200 m from the nest before the eggs hatch, when provisioning young they rarely travel this far, and additionally seem to have a series of favoured perches from which foraging flights after aerial invertebrates are made (Davies 1977). Davies (1977) was able to record the foraging behaviour of provisioning Spotted Flycatchers by using direct observation, this method also being trialled in the RSPB pilot study in 2003 (RSPB unpublished data). Since the rate at which nestlings are provisioned by parent birds may be an important indicator of the availability of prey items in the surrounding habitat, and hence to the condition and subsequent survival of the young, provisioning watches were included in the initial fieldwork design for this study.

In 2004, attempts were made to undertake hour-long foraging watches by direct observation at each nest. These were carried out twice at each active nest (chick age six and nine days), by two observers, each sitting at a point that would allow the clearest view of the nest, yet without causing disturbance. The two observers remained in communication with one another by using two-way radios. For each hour-long watch, the number of visits made by the adults to the nest with food was recorded. At sites where a good view of the nest could be afforded, attempts were made to either identify or at least record the size class of invertebrate prey. Size class was recorded by comparing the size of the prey item delivered to the nest with the length of the adult bill. If the prey item was less than half the adult bill length, it was classed as ‘small’, prey items sized between one-half and one-full bill length were classed as ‘medium’, and any prey longer than the length of the adult bill was classed as ‘large’.

Although Davies (1977) had successfully used a similar method, the study had been conducted in a single large garden and adjoining churchyard in which four pairs of birds were observed. The method was successful because it was conducted in a relatively open and well-defined habitat, with easily observable and identifiable perches. However, the heterogeneous nature of the habitat surrounding the majority of flycatcher nests in this study, and particularly those in woodland, did not allow accurate assessment of the location of the majority of foraging areas, with foraging parents quickly being lost to view. Additionally, and like Davies (1977) had found, it proved impracticable to record either prey identity or size class. Provisioning watches were subsequently dropped from the fieldwork protocol in 2005 and 2006.

2.5.2 *Invertebrate sampling*

During the 2004 field season, Malaise traps were used as the standard sampling method described by Davies (1977) as most suited to capturing the preferred prey of the Spotted Flycatcher. One trap was run for 12 hours per day (0800 – 2000 hrs) every day between 6 June and 27 Aug 2004 at a set location in pastoral farmland/garden habitat just outside the study area. Two further traps were used, each being sited within 50m of the nests, for two 6-hour periods (1000 – 1600hrs) during the chick stage of active nests. Insects collected in the Malaise traps were stored in 40% alcohol before being weighed (wet weight) and sorted into size classes. Since Spotted Flycatchers show a marked preference for larger invertebrates as prey, particularly when feeding chicks (Davies 1977), the number of insects within two size classes (5-10mm & >10mm) was counted for each sample from the Spotted Flycatcher sites.

2.5.3 *Faecal analysis*

Quantitative estimates of the dietary composition of birds are often made through examination of faecal matter (Moreby 1988, Green & Tyler 1989, Brickle & Harper 1999, Deloria-Sheffield *et al.* 2001, Donald *et al.* 2001, Gruar *et al.* 2003). Faecal analysis is an ethically sound method compared to the use of neck ligatures, emetics or examination of the gut contents (Orians 1966, Moore 1986, Major 1990, Kleintjes & Dahlsten 1992, Mellott & Woods 1993, Poulsen & Aebischer 1995, Moreby & Stoate 2000). Additionally, a relatively large number of samples can be collected during other routine practices (e.g. mist netting or colour-ringing nestlings) within a project. Disarticulated prey remains within faecal samples may be identified by reference to features seen on whole specimens. By examining morphological features, insect remains can be identified at least to family, even from the small fragments that are often found in faecal samples. Chitinous exoskeletal remains are, on the whole, resistant to the avian digestive system, but can be quite fragile, consequently disintegrating to the point where they can become almost unidentifiable. However, the more chitinous structures such as mandibles and tarsi, together with some colour patterns and hairs can be well preserved.

In 2005, faecal samples collected during routine handling of Spotted Flycatcher nestlings aged between 3 and 11 days (day of hatching counted as 1 day) were stored in 70% alcohol until laboratory examination.

Following methods developed by Green & Tyler (1989), each sample was decanted into a custom-made glass Petri dish for analysis. Prey remains in each sample were identified and counted using a 30x magnification binocular microscope according to the methods outlined in Gruar *et al*. (2003), so that the relative abundance of each invertebrate group could be scored according to the number of body parts counted.

For the seven most commonly occurring invertebrate groups (Diptera, Hymenoptera, adult Lepidoptera, Coleoptera, Formicidae, Araneae and Aphrophoridae), an additional abundance scoring system was adopted. Using the 36 scored 10° intervals on the underside of the Petri dish, the presence or absence of identifiable body parts from each of these groups was recorded in every sixth interval. This gave a maximum score of six, where the invertebrate group had been recorded in each of the six intervals searched, with a minimum score of zero being where the group had not been recorded in any of the 6 intervals.

In addition to methods already described, any whole wings found in the sample were measured using an eyepiece graticule, and removed for identification as either belonging to Dipteran or Hymenopteran prey.

2.5.4 *Nest cameras*

One measure of habitat quality may be the abundance and/or availability of large flying insects, the favoured prey items delivered to the chicks. The relationship between provisioning rate and habitat quality is most likely not a linear one. Thus, in a poor quality habitat, the parent birds may respond in one of two ways; they may either make very few visits to the nest, but each time may deliver a good quality prey item, or conversely, they may make many more visits, but each time only delivering very poor quality food items (small insects such as aphids). Direct video or camera monitoring of nests has been previously used in order to collect data on the dietary composition of nestlings (Kleintjes & Dahlsten 1992, 1994, Goodbred & Holmes 1996, Nour *et al.* 1998, Tremblay *et al.* 2005), and overcomes many of the uncertainties and limitations of methods involving direct observation by fieldworkers.

Purpose built digital nest cameras (Appendix B, Bolton *et al.* 2007) were used in Devon during 2005 and 2006, and in Bedfordshire/Cambridgeshire in 2006 to record data on provisioning rate and type of prey load delivered. Nests that were accessible were monitored continuously using remote digital photography. Four cameras were used in the Devon study area in 2005 to trial the method, with eight cameras subsequently being used in each study area during 2006. Each camera unit consisted of a surveillance camera (Maplin PH86T monochrome camera, focal length either 3.6 mm or 12mm), surrounded by infrared light-emitting diodes (LEDs) to illuminate the nest and surrounding area at night using a wavelength invisible to birds and mammals (940 nm). Each camera lens (1 x 2 cm) was mounted on a 1 cm diameter aluminium pole with a flexible end section, with the whole unit being painted dark green as camouflage when located in position by the nest. The pole (approx. 30cm in length) was attached to the nesting substrate (tree, wall etc.) using cable ties to firmly attach it to surrounding vegetation (climbers, ivy roots, adjacent branches etc.), such that the (3.6mm) lens itself was positioned approximately 30cm directly above or alongside the nest, pointing downwards into the nest. Cameras with 12mm lenses were positioned on adjacent trees, such that the lens was positioned approximately 2-3m from the nest cup. A camouflaged cable ran back from the mounted lenses and connected the camera to a data recording unit (based on Video Domain Technologies Memocam DVR unit) housed in a waterproof box. The data recording unit contained software which analysed the images captured by the camera. The whole camera unit was powered using a Yuasa cyclic sealed lead acid 12 V 38 Ah battery, and was concealed from view using the surrounding vegetation, several metres from the nest site. A time switch within the case, linked to the camera, switched on the LEDs during the hours of darkness (between approximately 21:00 and 06:00 hours). The data recording unit, which is configured using Windows based software supplied with the unit, incorporates a Memocam Video Motion Detection (VMD) facility, thus allowing cameras to be set up to record images when motion was detected within a pre-determined area around the nest-cup. This area was uniquely specified each time a camera was set up at a nest using a grid system over-laid onto a monitor. This offered the possibility to specify that movement must occur at the nest itself (rather than the surrounding vegetation), before an image is captured The unit was set up so that it would record five images (one pre-alarm and 4 post-alarm frames) each time an event was triggered (an 'alarm'). The time between frames was set to 0.3 seconds, and image recording was suspended between alarms for a period of 5 seconds to reduce the number of duplicated events. Image quality was set to high, allowing many images to be stored on each 256Mb memory card. The image capture unit was set up to be permanently active, and was not allowed to enter stand-by mode, thus maximizing the likelihood of recording events at the nest. The recording units were visited every three days (or more frequently during periods of intense activity at the nest) to change the memory card and battery. Thus, the nest itself was visited only when installing the camera on the first day of recording, and on infrequent occasions when adjustment to the position of the camera or surrounding vegetation had to be made.

All images recorded onto the memory cards were downloaded using a card reader that connected directly into the USB port of a PC or laptop prior to visual analysis. Images were examined in order to determine the time of the visit and the number, size class (three level factor, <5mm, 5-10mm and

>10mm) and, where possible, the identification of prey items brought to the nest throughout the nestling period.

2.6 Habitat

2.6.1 *Landscape scale habitat*

In each study area all discreet habitat patches were identified using 1:10 000 Ordnance Survey maps, and, following field survey, were ascribed to a habitat category according to the habitat coding system developed by Crick (1992). The large size of the area covered ($32km^2$) meant that it could be surveyed only once during the period of the study. Although cropping patterns in individual fields may have changed to some degree on an annual basis, no major land-use changes were observed in either site during the study, and it was assumed that the main habitat classification for each patch (e.g. woodland, farmland, gardens) remained constant. Field survey maps were digitised using MapInfo Professional 7.8 (MapInfo Corporation 1984-2004), so that the extent of each available habitat type in each study area, and around individual nests could be calculated.

2.6.2 *Fine scale habitat*

Detailed habitat data was collected for each nest within a circular plot (50 m radius, 0.785 ha area), centred on the nest. Various measures of habitat were taken within this defined area (Table 3).

Table 3. Independent habitat variables and factors recorded within 50m of each nest.

Variable	Definition
Woodland	2-level factor, present or absent
Water	2-level factor, present or absent
Livestock	5-level factor (cattle, sheep, horses, chickens, pigs)
Manure	2-level factor, present or absent
Human disturbance	2-level factor, frequently disturbed or little/no disturbance
Overhead wires	2-level factor, present or absent
Occupied buildings	Number of occupied buildings present
Unoccupied buildings	Number of unoccupied buildings present
Road	2-level factor, present or absent
Dead wood	2-level factor, present or absent
Field layer	In woodland only, 2-level factor, present or absent
Shrub layer	In woodland only, 2-level factor, present or absent
Grassland	2-level factor, present or absent
Arable	2-level factor, present or absent
Mown grass	2-level factor, present or absent
Flower beds	2-level factor, present or absent
Hedges	2-level factor, present or absent
Fences	2-level factor, present or absent

Additionally, habitat heterogeneity measurements (using methods developed by Kirby *et al.* 2005) were also recorded at eight locations around each nest (Fig. 8).

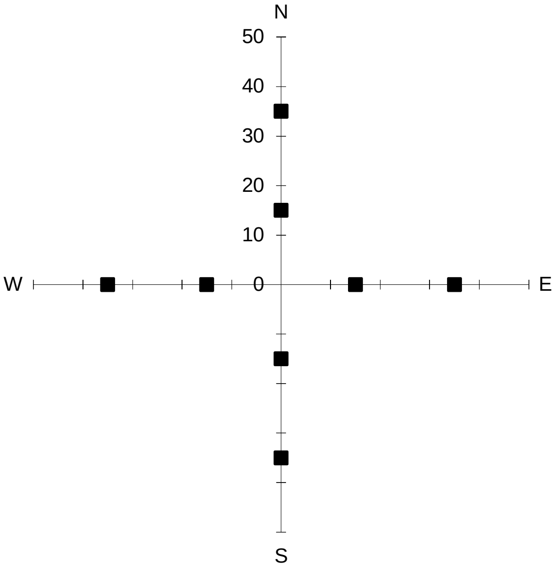

Figure 8. Aerial representation of the sampling protocol used to conduct nesting area habitat assessments. The scale is in metres, and sampling was carried out at each of the 8 points shown, 15m & 35m from the nest site at the centre.

This method involves a 3 x 3 grid of $5m^2$, centred on each of the data points in Fig 8. For the purposes of heterogeneity scoring, this is then extrapolated into three dimensions using three height categories (0-2m, 2-4m and >4m), resulting in a three-dimensional 'grid' of 27 cells. The method then calculates the number of contrasts between the central cell in each of three height categories and those adjacent to it. Each cell is categorized in two ways. Firstly, it is assessed in terms of its 'openness' (>50% open air or not) and secondly it is assessed as either having an available perch or not. Contrasts are scored between adjacent cells in three dimensions, to reflect the choices available to the bird. The number of mature trees in the bottom layer of the three dimensional grid, classified according to size by measuring the diameter of the trunk at breast height (dbh, 2-level factor; dbh < 30 cm = small, dbh > 30 cm = large) was also recorded.

At each of the eight data points a further set of measurements was taken. Wind speed was measured using an anemometer, light intensity was measured using a digital light meter and canopy cover was recorded by taking a vertical looking digital image at each point from a fixed height. Vertical looking canopy images were assessed using Adobe Photoshop (version 8.0) to determine the relative amounts of sky and vegetation (canopy cover) in each image.

2.6.3 Nest location

Each nest was categorised as being in one of three broadly defined habitats: 'garden', 'woodland' or 'farmland', based on the most prevalent habitat within a 50m radius of the nest. This distance was chosen as it has been previously shown that most foraging by provisioning adults is undertaken within 50m of the nest (Davies 1977). A further classification was made based on a visual assessment of the degree of nest exposure. Nests were classified as being 'inside' if the nest was located inside a covered building, 'covered' if the nest was afforded some degree of protection from the elements from either a man-made structure, branches or vegetation, or 'exposed' if the nest was entirely open to the elements. The aspect of each nest was measured using a compass to assess the mean angle of view from the nest cup and measurements were also taken to assess the ability of the sitting female to view the surrounding area (the vertical angle of view of the (assumed) sitting bird was measured using a clinometer, and the horizontal angle was assessed using a compass). The height of each nest was measured using calibrated sectional poles, to the nearest 25cm, from the lip of the nest to the ground.

At woodland nest sites only, the horizontal visibility of the woodland around the nest was measured. A 2.4m pole (22.5mm diameter), marked off in alternate black and orange 10cm bands, was placed in the ground, at four primary points, one each north, south, east and west, 15m from the nest tree. The pole was placed such that the first of the 12 orange bands started 10cm above ground level. The pole was then viewed from four secondary points 12.5m to the north, south, east and west of the primary point. At each of these points, the number of orange bands that were at least 50% visible through the vegetation was recorded (range 0-12). A horizontal visibility score for each of the four primary points was calculated by taking the mean of the score from the secondary points. A horizontal visibility score for each woodland nest location was then calculated by taking the mean of the four primary point scores.

Chapter 3

Breeding success of Spotted Flycatchers *Muscicapa striata* in southern England – is woodland a good habitat for this species?

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Breeding success of Spotted Flycatchers *Muscicapa striata* in southern England – is woodland a good habitat for this species?

Ibis 149 (supp. 2): 214-22.

3.1 Introduction

The Spotted Flycatcher *Muscicapa striata* is one of the UK's most rapidly declining birds: in the twenty-five year period 1978-2003, the breeding population fell by an estimated 82% (Baillie *et al.* 2006). The species was placed on the 'Red' list of birds of conservation concern in the UK (Gibbons *et al.* 1996) and was included on the list of 26 priority bird species in the UK Biodiversity Action Plan, with a species action plan being published in 1998 (Anon. 1998b). This action plan identified a specific requirement for a study of the summer ecology and habitat use of the species.

Throughout their range, Spotted Flycatchers are dependent on a landscape that provides both accessible space for catching flying insects and raised perches from which to make foraging flights or 'sallies' (Cramp & Perrins 1993). They occur in a range of habitats that comprise a mix of trees and open space, including parkland, gardens, orchards, woodland edge, open woodland and lines or copses of mature trees on farmland. In the UK, the species has shown similar population declines in both woodland and farmland (Freeman & Crick 2003). Potential causes of decline during the breeding season include reduced abundance and availability of invertebrate food, loss of foraging habitat, and reduced nest survival, which in some open nesting passerines is known to be affected by surrounding habitat (Martin & Roper 1988, Kelly 1993, Tarvin & Smith 1995).

However, a dearth of recent published research into the breeding ecology of Spotted Flycatchers hinders our ability to evaluate the potential causes, and problems may also exist in staging and/or overwintering areas. Population declines have been linked to reduced survival of first-year birds (Freeman & Crick 2003) and there has also been an indication of a reduction in breeding productivity as a result of reductions in brood size and chick stage nest survival rate (Baillie *et al.* 2006). Analyses of BTO/JNCC/RSPB Breeding Bird Survey and other census data have highlighted potential regional differences in population trends, suggestive that there may be factors operating at a regional scale that are contributing to the national population decline. Small-scale, recent autecological studies of birds breeding in the UK have suggested that nests in trees may be more likely to fail than those placed either on or in buildings (Kirby *et al.* 2005), which concurs with the findings of Stoate & Szczur (2006), who reported lower survival of nests in woodland when compared to those within gardens. However, the relatively small-scale of these studies did not make it possible for the authors to compare breeding success in different regions or across the range of habitats in which Spotted Flycatchers breed. If the population decline of Spotted Flycatchers is associated with factors operating at a regional level, an understanding of the causal factors affecting breeding success at a regional scale may therefore be an important pre-requisite to developing a recovery plan for this species.

This paper presents results from a study of Spotted Flycatchers breeding in three broad habitat types; garden, farmland and woodland, in two regions of England with contrasting landscapes and Spotted Flycatcher population trends. It tests the hypothesis that nest survival is associated with region and habitat and examine whether this may be contributing to the observed population declines.

3.2 Methods

3.2.1 Study sites

Data were collected from two study areas; in Devon (southwest England) in 2004, 2005 and 2006, and Bedfordshire and Cambridgeshire (Beds/Cambs; eastern England) in 2005 and 2006. There is evidence for recent population decline in eastern England, compared to stability or increase in southwest England (Noble *et al.* 2001, Noble & Raven 2002, Amar *et al.* 2006).

The study area in Devon (centred on the parish of Aveton Gifford in the South Hams area) covered approximately 3200 ha, of which c. 2670 ha was farmland, 160 ha woodland and 111 ha villages and rural gardens. Woodland blocks in the study area were generally small, with only one over 20 ha, or linear in nature (following field edges and water courses) and were primarily deciduous. Grassland (largely used for cattle and sheep grazing, but also some for the production of hay and silage) accounted for over two-thirds of all farmland, with tilled land accounting for less than a third.

The Beds/Cambs study site covered approximately 3200 ha of which c. 2280 ha was farmland, 440 ha woodland and 123 ha ‘human sites’ (which included villages and rural gardens). Woodland blocks in the study area ranged in size from less than 1 ha to approximately 92 ha, with 5 blocks being greater than 20 ha in area. Approximately 60% of the woodland in the study area was deciduous and 10% coniferous, the remaining 25% being mixed (i.e. made up of least 10% each of deciduous and coniferous trees). In contrast to the Devon study area, grassland only accounted for about one quarter of the farmed area with the remaining three-quarters being tilled land.

3.2.2 Data collection

All potentially suitable flycatcher habitats were regularly searched by observers from early May through to late August in each year of data collection. Territories were located by observing territorial bird behaviour (singing, territorial disputes, strong alarm calling in response to observer, carrying food or nesting material). Nests were located either by searching likely locations within a territory, or by observations of bird behaviour (following adults to or from nests, or occasionally hearing calls of begging chicks). Once nests had been located, they were visited at regular intervals (usually every three days) to ascertain outcome, following methods described in Crick *et al.* (1994, 2003). Contents of accessible nests (nest height approx 6m or less) were checked using a mirror on a telescopic pole. Activity at higher nests was observed using binoculars or telescope, thus allowing data to be gathered from most nests. Nests were deemed to have been successful if chicks had reached fledging age and the nest showed signs of success (well-trodden lining, droppings and/or feather scale present), if fledged young were seen nearby, or if adult activity indicated fledged chicks in the vicinity (alarm calling or feeding). Cause of nest failure (abandonment or predation) was determined either directly using evidence recorded by remote digital nests cameras following methods described by Bolton *et al*. (Appendix B, 2007), or by interpretation of signs at, or around the nest, based on experience gained from the camera evidence. Presence of a camera at Spotted Flycatcher nests had no significant effect on nest survival (egg stage $\chi^2 = 0.03$, $P = 0.8612$; chick stage $\chi^2 = 0.55$, $P = 0.4575$, DKS unpublished data). This was based on a comparison of nests with cameras (n=49 egg stage; n=53 chick stage), and nests without (n=129 egg stage; n=140 chick stage), using the modelling method as described below for nest survival (total exposure days egg stage n=1731, chick stage n=2035; total nest failures nest without cameras n=63, nest with cameras n=25). Nests were recorded as predated if found empty (of either eggs or chicks that were too young to fledge) or if there were signs of nest damage with remains of eggs or chicks in the vicinity. Nests were considered to have been abandoned if (in the absence of parental activity) intact eggs remained in the nest beyond the expected hatching period, or dead nestlings (without any signs of aggressive injury) were found in the nest. Whilst it is acknowledged that in some cases such determination of the cause of nest failure may be equivocal, given the frequency of nest visits it is believed that in the majority of cases it was possible to ascribe nest failures correctly.

3.2.3 Habitat classification

In each study area all discreet habitat patches were identified using 1:10 000 Ordnance Survey maps, and, following field survey, were ascribed to a habitat category according to the habitat coding system developed by Crick (1992). Habitats were surveyed once during the period of the study. Although cropping patterns in individual fields may have changed to some degree on an annual basis, no major land-use changes were observed in either site during the study, and it was assumed that the main habitat classification for each patch (e.g. woodland, farmland, gardens) remained constant. Field survey maps were digitised using MapInfo Professional 7.8 (MapInfo Corporation 1984-2004), so that the extent of each habitat type around individual nests could be calculated; each nest was categorised as being in one of three broadly defined habitats: ‘garden’, ‘woodland’ or ‘farmland’, based on the most prevalent habitat within a 50m radius of the nest. This distance was chosen as it has been previously shown that most foraging by provisioning adults is undertaken within 50m of the nest (Davies 1977). In each of these broad habitat categories flycatchers were found nesting in a range of locations. Since it has previously been suggested that higher nests have increased survival probability (Kirby *et al.* 2005), height was also recorded using a calibrated measuring stick for lower nests and a Bushnell Yardage Pro™ laser rangefinder for higher nests.

3.2.4 Analyses

Nests were defined as active once the first egg had been laid. First egg date (the day the first egg was laid) was determined either by direct observation or by back calculation from either hatching date, assuming an average incubation period of 13 days starting from the date the last egg was laid, (Cramp & Perrins 1993), or an estimate of chick age. Hatching date was the day the first egg hatched, and was considered as day one of the nestling period. The average nestling period was assumed to last 14 days (Cramp & Perrins 1993). Successful nests were defined as those fledging at least one offspring. Nest survival rates were estimated using methods described by Mayfield (1975), with exposure days being calculated from the first egg date (for nests found before egg-laying started) or the date of finding for an active nest. For failed nests, the date of failure was estimated as the mid-point between the date the nest was last known to be active and the date it was found to have failed. Analyses were carried out using the GENMOD procedure of SAS (SAS Institute Inc. 2002-2003) and following Aebischer (1999), using a generalised linear model with binomial error term and logit link function with success/failure as the response and exposure days as the binomial denominator. Significance was assessed by comparing the likelihood ratio statistic to the χ^2 distribution with the appropriate degrees of freedom. Separate models were constructed for the egg and chick stages to determine whether factors affecting nest survival differed between these two phases of the nesting period. Categorical variables entered into each model were habitat type (three level factor: farmland, garden or woodland), region (two level factor: Devon or Beds/Cambs), and year (three level factor: 2004, 2005, 2006). The interaction effect habitat*region was also included in the initial model to test for regional differences in nest success between habitats. Since it has previously been suggested that higher nests have increased survival (Kirby *et* *al.* 2005), linear and quadratic height terms were included in the model, and linear and quadratic terms for first egg date (measured as days from 1 May) were included to control for seasonal effects. Within the three different habitats considered here, flycatchers nest in a variety of locations. In garden and farmland habitats, nests will frequently be located in or on buildings. Using a subset of the data from these two habitats only, models were also constructed with an additional categorical variable, nest location (two level factor: building or tree) to test whether location is an important predictor of nest survival. The interaction effect habitat*location was also included in the initial model to test for any habitat related differences in survival between the two nest locations.

Initially full models were fitted, including all the predictor variables, and these results are presented to support the minimal models as recommended by Whittingham *et al*. (2006). Subsequently, minimum adequate models were selected using a backwards deletion process (Crawley 1993), with each variable being removed and replaced sequentially. Following each iteration, the variable explaining the least amount of variance was removed until only significant variables were retained. Mayfield logistic regression assumes that nests are independent samples. Since Spotted Flycatchers occasionally re-use previously used nests (either within or between seasons), data from such nests were only included for the first time the nest was used – any subsequent re-use of the nest site was excluded from the analyses. All other nesting attempts were considered independent since they were located at a different site and at a different time (Hatchwell *et al.* 1996, Cresswell 1997). This resulted in a reduced data set being used for the purposes of the statistical modelling. Models were checked for over-dispersion using the ratio of the residual deviance to the remaining degrees of freedom (Crawley 1993, Aebischer 1999). Daily nest survival estimates, s, expressed as a proportion, were derived from back-transformation of the least squares means estimates generated by the minimum adequate models. Mayfield survival estimates for each nest stage were calculated as $100(s^x)$, where x is the approximate length of the appropriate nest stage in days (16 and 14, egg and chick stage respectively). Estimates of overall nest survival were then generated simply by multiplying the survival probabilities for egg and chick stages.

A crude estimate of nest productivity (*p*) was calculated in relation to habitat based on methods described in Donald *et al.* (2002), using the formula:

$$p = ch\,(1-l)\,(se^{16})(sc^{14})$$

where *p* is defined as the number of chicks leaving the nest, *c* is mean clutch size, *h* is the proportion of eggs hatching, *l* is the proportion of chicks dying before fledging (excluding whole nest failures), and *se* and *sc* are the egg stage and chick stage daily survival estimates respectively (with 16 and 14 being the length of these two stages in days).

3.3 Results

In total, 248 nests were monitored during the course of the study (Table 1). In Devon, 171 nests provided sufficient data for analysis (Table 1), with 74 categorized as in farmland, 60 in gardens and 37 in woodland habitat.

In Beds/Cambs 77 nests were located and provided sufficient data for analysis (Table 1). Of these nests, seven were categorized as farmland, 54 as garden and 16 as woodland habitat.

Table 1. A summary of the nest data collected during the study.

			Devon		Beds/Cambs
	2004	2005	2006	2005	2006
No. of nests found	67	54	50	40	37
(Farm/Garden/Wood)	(29/26/12)	(21/18/15)	(24/16/10)	(5/29/6)	(2/25/10)
Median 1st egg date	9 Jun	5 Jun	11 Jun	12 Jun	11 Jun
Median hatch date	26 Jun	22 Jun	27 Jun	29 Jun	27 Jun
No. of successful nests (%)	40 (59.7)	29 (53.7)	35 (70.0)	30 (75.0)	26 (70.3)
No. of abandoned nests (%)	8 (11.9)	7 (13.0)	2 (4.0)	3 (7.5)	1 (2.7)
No. of depredated nests (%)	19 (28.4)	18 (33.3)	13 (26.0)	7 (17.5)	10 (27.0)

Within the three habitat categories, birds nested in a variety of locations. In gardens however, nests were predominantly located either on, or in built structures (76%), whereas in woodland the majority of nests (89%) were located in trees. In farmland, nests were found in reasonably equal numbers in trees (39%) and built structures (61%).

Clutch initiation (date of first egg) followed a bi-modal pattern (Fig. 1) and clutch size decreased as the season progressed (Fig. 2; Spearman rank-order correlation $r_s = -0.646$, $P = <0.001$).

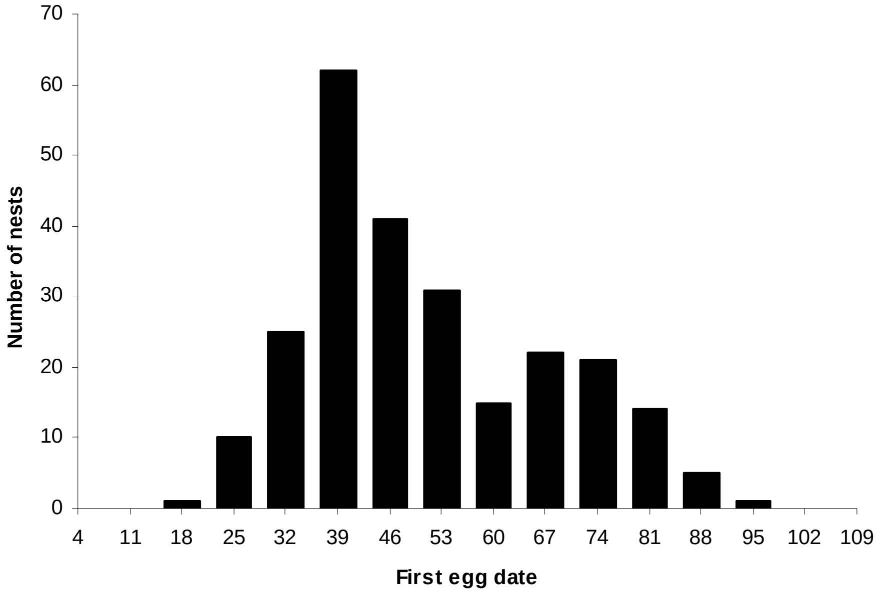

Figure 1. The distribution of clutch initiation dates (first egg dates day 1 = May 1). Data from both study areas and all years combined with nests grouped by seven-day period.

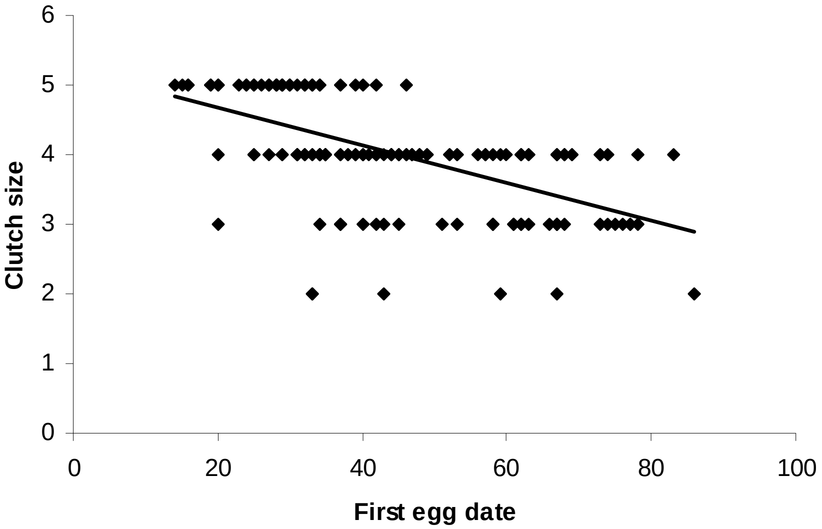

Figure 2. Clutch size in relation to first egg date (day 1 = 1 May). Data from all years and habitats combined. The continuous line indicates the linear regression of clutch size v. first egg date.

In Devon, the earliest first egg date was 15 May and the latest 25 July. Nest height ranged from 0.9 to 20.0m (mean 3.34 ± 0.16m). In Beds/Cambs, the earliest first egg date was 14 May and the latest 17 July and nest height ranged from 1.1 to 15.0m (mean 3.59 ± 0.25m). Using data from complete clutches only, mean clutch size was 4.06 ±0.09 in farmland (n=50), 4.05 ±0.08 in gardens (n=93) and 3.89 ±0.16 in woodland (n=28). For nests that survived the egg stage, the proportion of eggs that hatched was 0.951 in farmland, 0.934 in gardens and 0.908 in woodlands. Using data from nests that were successful, of those eggs that hatched, the proportion of chicks that died before fledging was 0.050 in farmland nests (n=37), 0.103 in gardens (n=85) and 0.182 in woodland nests (n=20).

Predation of eggs or chicks was the most frequently observed cause of nest failure, with only a small number of nests being abandoned (Table 2). Predation accounted for 71.4% of nest losses in gardens, 75.0% in farmland and 83.3% in woodland. However, whilst over a third (35%) of woodland and farmland nests were predated, only 17% of garden nests were (Table 2).

Table 2. The overall causes of nest failure in relation to the habitat of the breeding site.

	Farm	Garden	Woodland
No. of nests found	81	114	53
No. of abandoned nests (%)	9 (11.1)	8 (7.0)	4 (7.5)
No. of depredated nests (%)	27 (33.3)	20 (17.5)	20 (37.7)

To ensure statistical independence, a reduced data set was used for the modelling procedure comprising data from 218 nests (Devon: n=146, 64 farmland, 50 garden and 32 woodland; Beds/Cambs: n=72, seven farmland, 50 garden and 15 woodland). When full models were fitted, habitat type was the only variable influencing daily nest survival rates significantly at the egg stage (Table 3), and was almost significant at the chick stage.

Table 3. Full models of daily nest survival rates during the egg and chick stages incorporating categorical and continuous variables. The significant result is shown in bold.

Independent variable		Egg stage		Chick stage	
	df	χ2	P	χ2	P
Categorical					
Habitat	2	**6.64**	0.0362	5.41	0.0669
Region	1	0.12	0.7338	0.04	0.8457
Year	2	2.66	0.2650	1.23	0.5403
Continuous					
Height	1	1.66	0.1974	0.00	0.9611
$(\text{Height})^2$	1	3.14	0.0766	0.05	0.8182
First egg date	1	1.57	0.2107	0.08	0.7776
$(\text{First egg date})^2$	1	3.10	0.0783	0.71	0.4006
Habitat*Region	2	1.16	0.5601	0.34	0.8452

For nests at the egg stage, the minimum adequate model retained habitat type, the linear effect for first egg date and height (linear and quadratic terms) as significant predictors of daily nest survival (Table 4). Daily nest survival rates during egg stage nests in woodlands and farmland did not differ significantly (Fig. 3a; $\chi^2 = 0.02$, P=0.90), but nests in both of these habitat types had a significantly lower daily survival than those in gardens (Fig. 3a; for woodland nests $\chi^2_1 = 7.97$, P=0.0047: farmland nests $\chi^2_1 = 10.97$, P=0.0009). The retention of the quadratic term for height indicates a curvilinear relationship with nest survival (Table 4). The minimum adequate model for chick stage nests retained both habitat and the linear effect for first egg date (Table 4). As in egg stage nests, daily nest survival at chick stage did not differ significantly between nests in woodland and farmland (Fig. 3b; $\chi^2_1 = 0.62$, P=0.43), but nests in both these habitats had significantly lower survival than those in gardens (Fig. 3b; for woodland nests $\chi^2_1 = 3.92$, P=0.048: farmland nests $\chi^2_1 = 9.68$, P=0.0019). The linear effect for first egg date was retained in both models, indicating that nest survival increases as the season progresses (Table 4).

Table 4. Variables retained in the minimum adequate models of daily nest survival rate.

Independent variable	df	Parameter estimate	$\chi 2$	P
Egg stage				
Intercept	1	1.0549	2.88	0.0896
Habitat	2	-	13.99	0.0009
First egg date	1	0.0260	7.66	0.0056
Height	1	0.2769	2.21	0.1370
$(\text{Height})^2$	1	-0.0296	3.92	0.0477
Chick stage				
Intercept	1	2.1579	12.49	0.0004
Habitat	2	-	10.64	0.0049
First egg date	1	0.0410	10.03	0.0015

Based on the daily nest survival estimates for the egg and chick stages from the minimum adequate models the Mayfield estimates for nest survival over the entire nesting period were 22.4% for farmland nests, 58.8% for garden nests and 24.2% for woodland nests. The models produced over-dispersion estimates of 1.23 and 0.78 (for egg and chick stages respectively), indicating a good fit to the data (Crawley 1993).

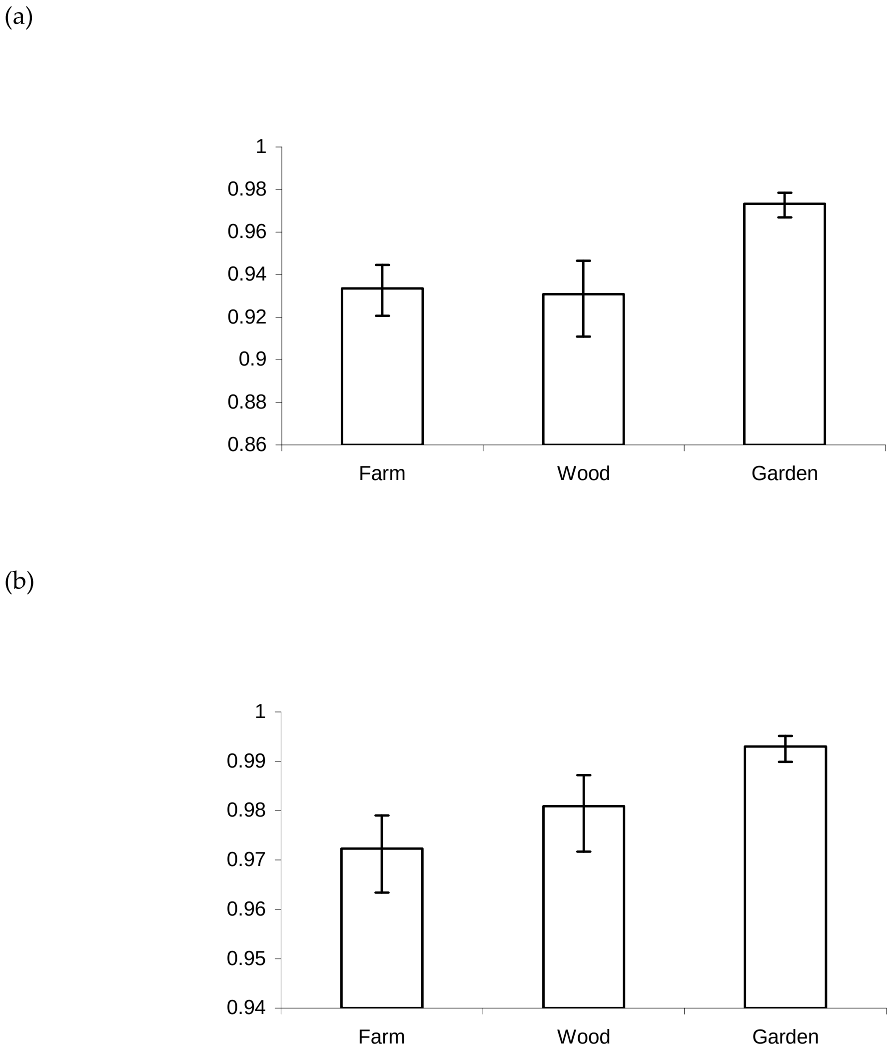

Figure 3. Daily nest survival estimates for habitat type (based on the back-transformed least squares mean estimates from the minimum adequate models) for (a) egg stage and (b) chick stage nests. Sample sizes for egg and chick stages respectively: Farmland, n=51 & n=51; woodland, n=28 & n=34; garden, n=75 & n=85.

Construction of models to test for an effect of nest location, using a subset of the data from farmland and garden nests (farmland: n=71, 41 building, 30 tree; garden: n=100, 73 building, 27 tree), resulted in minimum adequate models that retained only habitat and the linear effect for first egg date for both egg and chick stage nests (Table 5).

Table 5. Variables retained in the minimum adequate models of daily nest survival rate for farmland and garden data only. A nest location variable was included in the full model, but was not retained in the MAM.

Independent variable	df	Parameter estimate	χ2	P
Egg stage				
Intercept	1	2.3994	30.97	<0.0001
Habitat	1	-0.9434	10.80	0.0010
First egg date	1	0.0304	7.72	0.0055
Chick stage				
Intercept	1	3.0090	22.51	<0.0001
Habitat	2	-1.4198	9.99	0.0016
First egg date	1	0.0457	8.05	0.0046

Estimates of productivity per nesting attempt were lower in both woodland (0.70 fledglings/nesting attempt) and farmland (0.82 fledglings/ nesting attempt) than in garden nests (1.99 fledglings/nesting attempt).

3.4 Discussion

The main finding of this study is that nest success of Spotted Flycatchers is closely associated with the habitat in which they breed, with birds breeding in woodland and farmland habitats having significantly lower nest success than those nesting in gardens. Moreover, productivity estimates also reflect this trend, suggesting that the number of young fledged per nesting attempt is also particularly low for birds nesting in woodland and farmland.

Although Kirby *et al*. (2005) suggested that higher nests were more successful than those lower down, results from this study indicate that the relationship is curvilinear in nature and may therefore not be as simple as previously suggested. Further analyses at the nest-site scale, including incorporation of more detailed nest location variables, such as level of nest concealment, for example, would be required to more fully establish the effect of nest height on survival. In common with many other open-nesting passerines (Lack 1954, Ricklefs 1969, Söderström *et al.* 1998, Donald *et al.* 2002), predation was the greatest source of nest failure in each of the study areas, and differences in nest success between the habitats in this study most likely reflect differences in predation rates. Since the presence of a predator or predation of an adult bird may also be a cause of desertion, total nest loss to predation is likely to be underestimated. There are several potential mechanisms whereby predation rates may differ between habitats. Habitat characteristics may influence nest concealment and/or predator access to nests, as well as influencing predator type, abundance or distribution (Evans 2004). These two mechanisms may also act in combination to alter the search efficiency of potential nest predators (Bowman & Harris 1980, Tarvin & Smith 1995), allowing predators that rely on visual cues to locate nests more easily. Additionally, predation risk may also be altered by differences in parental behaviour at the nest. Such differences in behaviour may be brought about by other habitat related factors, including differences in the abundance or availability of food for both the adults and chicks. If this was the case, adults may modify their provisioning behaviour, therefore altering the level of activity at or near the nest, thereby varying the overall predation risk of the nest. Additionally, hungry chicks often call continuously (Davies 1977), possibly making them more susceptible to predation (Evans *et al.* 1997), although this would not have been a factor during the egg stage.

Although there was an indication from Kirby *et al.* (2005) that birds breeding in trees may have reduced nest survival, the results presented here suggest that nest survival is influenced by the habitat surrounding the nest, rather than the fact that the nest is in a building or a tree. In contrast to most woodland, farmland and mature gardens typically include both trees and buildings, and birds are able to utilise both of these as nest sites. However, within these two habitats, the choice of nest location does not appear to influence survival. Results from this study support those of Stoate & Szczur (2006), who reported a reduced survival of birds breeding in woodland compared to those breeding in gardens. Additionally, this study shows that the association of nest success with habitat appears to be comparable between regions with differing population trends. Low productivity in farmland and woodland habitats suggested by this study supports similar recent evidence from the British Trust for Ornithology (BTO) Nest Record Scheme of reduced productivity driven by lower brood sizes and increased chick stage nest failure rates (Baillie *et al.* 2006). Low nest survival rates and, hence, productivity in woodland and farmland provide evidence of a problem on the breeding grounds for this species, in at least these two habitats. Differences in annual productivity play a large role in determining changes in population size in short-lived species (Sæther & Bakke 2000). The bi-modal pattern of clutch initiation date in this study most likely reflects peaks in nesting activity associated with first and second nesting attempts. In the case of failed first attempts, replacement clutches are normally laid (Cramp & Perrins 1993). Following successful first attempts, Summers-Smith (1952) estimated that only 20% of Spotted Flycatchers are double-brooded, with Kirby *et al.* (2005) estimating this same figure to be 14%. A negative correlation between clutch size and first egg date such as found in this study is often indicative of a single-brooded, rather than a multi-brooded species (Klomp 1970, Crick *et al.* 1993), although Crick *et al*. (1993) additionally showed that multi-brooded long-distance migrants also have seasonal declines in clutch size. In migratory species, such as the Spotted Flycatcher, the length of the breeding season is often constrained by the date that adults return from the wintering quarters, and birds that breed early are more likely to attempt second broods (Ogden & Stutchbury 1996). Development of models that include renesting (covered subsequently in Chapter 7) may be required in order to understand more fully how the variation in productivity per nesting attempt reported in this study relates to individual fecundity and the observed population declines.

The lack of a significant difference between nest success in farmland and woodland habitats is consistent with earlier analyses (Freeman & Crick 2003), which suggested that population declines have been similar in these two habitat types, hence leading them to conclude that some broad-scale factor was probably driving population declines. However, since gardens are not adequately represented by Common Bird Census data, Freeman & Crick (2003) were unable to construct separate models for this habitat type. Interestingly, however, the results reported here suggest that habitat-specific differences may exist in breeding success. In order to support the generality of these findings, analyses of national data sets, such as that collected as part of the BTO Nest Record Scheme, may be required in order to explore whether similar habitat related differences in breeding success exist at a national scale.

Regardless of low fecundity, Spotted Flycatchers still nest in good numbers in woodland and farmland habitats in Devon. Although nests were still found in these habitats in Beds/Cambs, the majority of birds nesting in this region are found in gardens, this probably being a true reflection of the breeding distribution in this region since both study areas were thoroughly searched for breeding birds and it is unlikely that nesting attempts would have been missed. Given the differential usage of the three habitats, the overall productivity is higher in Beds/Cambs than in Devon (weighted mean 1.62 fledglings per nest in Beds/Cambs compared with 1.20 in Devon). This is surely a paradox, given the population trends in the two regions. Aside from the possibility, albeit unlikely, that there may be differential over-winter survival, possibly as a result of a regional migratory divide, reasons why the Devon population is stable whilst that in Beds/Cambs is declining are numerous. Current estimates of per nest productivity suggest that recent population trends in these two regions are not dependent on this particular aspect of demography. One possibility is that there may be subtle differences in renesting probability resulting from differences in habitat quality as yet not explored, such that individual nest estimates do not reflect whole season fecundity. Alternatively, there may be density dependent processes operating, with the higher breeding density in Devon resulting in some birds utilising sub-optimal habitats for nesting.

No regional differences in nest success were detected during this study, despite the increasing evidence for differing regional population trends (Noble *et al.* 2001, Noble & Raven 2002, Amar *et al.* 2006), but habitat specific differences were clear. It is possible that the population in Devon is now undergoing the same processes that have already led to the decline in Eastern England, but why this should be the case remains unclear. In contrast to Devon, woodland and farmland appear to be relatively unimportant breeding habitats for the species in Beds/Cambs. This cannot have been the case historically, and indeed, anecdotal evidence suggests that Spotted Flycatchers were once found commonly in both woodland and farmland in Bedfordshire and Cambridgeshire, and that they have now disappeared from many 'traditional' sites. Data from the BTO's Common Bird Census for the period 1962 to 1988 shows consistent declines in both farmland and woodland populations, with the most notable declines being in farmland populations in western, eastern and southern England (Marchant *et al.* 1990). It is possible, therefore, that the severe population decline suggested for the East of England region is at least partly attributable to the loss of birds from these two key habitats. This may be the case if the habitat preference of Spotted Flycatchers has changed, or if the relative availability, absolute abundance or quality of one or more of the habitats has changed unequally between the two regions.

Population modelling, carried out by Freeman and Crick (2003), suggested that declines in first year, and possibly post-fledging survival were the most likely demographic causes of population decline for this species, further stating that changes in annual fecundity were unlikely to be important drivers. Although found in several habitats, the Spotted Flycatcher is often regarded as a woodland species and it is included in the suite of birds contributing to the composite index of woodland bird populations which forms part of the UK Government's wild bird indicator (Anon. 1998a, 1999, Gregory *et al.* 2003). Results presented here suggest that the species may not be doing well in this habitat, and that this pattern may be general across regions with differing population trends. Whatever the reasons behind the decline of Spotted Flycatchers in the UK, demographic factors that cause population decline may not always be the same as those that must be manipulated to achieve population recovery. In woodlands, for example, the potential exists, given suitable conditions, for breeding productivity to increase from its current low level, with the ultimate goal for land managers being to bring about this change in such a way as to engender population recovery. However, further research is required to investigate the mechanisms responsible for the habitat related differences in breeding success reported here before recommendations on effective conservation measures can be made.

Chapter 4

Predators of Spotted Flycatcher *Muscicapa striata* nests in southern England as determined by digital nest cameras

This chapter has been accepted for publication as follows:

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Bird Study, In press.

4.1 Introduction

Many formerly abundant species of birds have shown dramatic population declines in recent years, and in the United Kingdom, these trends have been particularly apparent for woodland and farmland specialists, being especially so for long-distance migrants (Sanderson *et al.* 2006). Understanding the causes of changes in the populations of migrant species requires knowledge of events operating throughout the annual cycle. Although populations of migratory passerines may be regulated by processes that impact on survival in the non-breeding season (Baillie & Peach 1992), many studies have demonstrated that factors affecting fecundity play an important role (Böhning-Gaese *et al.* 1993, Holmes *et al.* 1996, Browne & Aebischer 2004).

The UK population of Spotted Flycatchers declined by 82% during the period 1979 – 2004 (Baillie *et al.* 2007), and whilst, being a long distance migrant, there are many factors that may impact upon survival during the non-breeding period, a knowledge of the factors affecting its breeding biology could be vital to our understanding of population change. In the UK, the species is found in a wide variety of habitats, but it is traditionally regarded as a woodland species, being included in the composite index of woodland bird populations which forms part of the UK Government's wild bird indicator (Anon. 1998a, 1999, Gregory *et al.* 2003). Recent work in the UK examining breeding success in different habitats has identified differences in nesting success, with daily nest survival rate of birds breeding in highly modified habitats such as gardens, being higher than those breeding in woodland and farmland habitats with which the species is more traditionally associated (Chapter 3, Stevens *et al.* 2007). In common with many other bird species (Lack 1954, Ricklefs 1969, Martin 1995), nest predation was the main proximal cause of nest failure (Chapter 3, Stevens *et al.* 2007).

A number of potential predators, both mammalian and avian, have been implicated in the decline of woodland birds, either through an overall increase in predator numbers or to changes in the vulnerability of nests or adult birds. The introduced Grey Squirrel is commonly regarded as a major potential predator of songbird nests, particularly with respect to its continuing expansion in both range and density. This perception prevails despite the lack of evidence that is anything more than circumstantial or anecdotal (Hewson & Fuller 2003). Similarly, potential avian predators with recent increases in population size, such as the Great Spotted Woodpecker, have also been suggested as having negative impacts on breeding populations of, particularly, woodland species. However, as is the case with the Grey Squirrel, there is a dearth of empirical evidence suggesting any strong relationship between the two (Newton 1993, Thomson *et al.* 1998). A species such as the Spotted Flycatcher, which nests in a variety of different landscapes, will be at risk of predation from a wide range of potential predator species. Both the type, and the relative importance, of each potential predator may vary between habitats (Donovan *et al.* 1997). Therefore, in order to understand the processes influencing the predation risk of Spotted Flycatcher nests, it is first necessary to identify the predators involved.

A variety of techniques have been employed to identify predators responsible for nest failure. Artificial nests containing model eggs have been widely used to investigate both the processes affecting predation risk (Götmark *et al.* 1995, Jokimäki & Huhta 2000, Santisteban *et al.* 2002, Martin & Joron 2003, Muchai & du Plessis 2005, Remes 2005b) and the identity of the predators responsible (Söderström *et al.* 1998, Grégoire *et al.* 2003, Remes 2005a). However, many studies have reported on the limitations or weaknesses of the technique (Martin 1987, Major & Kendal 1996, Wilson *et al.* 1998, Thompson & Burhans 2004, Robinson *et al.* 2005), and results obtained from such studies must therefore be interpreted with caution. To overcome many of the potential biases inherent in studies involving artificial nests, the use of nest cameras is becoming increasingly common as an investigative tool in nesting studies. Such techniques have enabled researchers to directly identify nest predators (Major & Gowing 1994, Purcell & Verner 1999, Thompson *et al.* 1999, Pietz & Granfors 2000, Liebezeit & George 2002, Renfrew & Ribic 2003, Schaefer 2004), thus providing valuable information on which investigations of predator-prey relationships can be based. However, although such techniques are becoming increasingly common, they are less often used in the study of European bird species, particularly passerines, with the exception of Schaefer (2004), who successfully employed the technique to monitor predators of Blackcap *Sylvia atricapilla* nests in shrub habitats.

Using a purpose-built digital camera system (see Appendix B, Bolton *et al.* 2007 for further details), we deployed cameras at a sample of Spotted Flycatcher nests during the 2005 and 2006 nesting seasons in order to identify causes of nest failure, and in the case of those nests lost due to predation, to identify the predators responsible.

4.2 Methods

4.2.1 Study areas

Data were collected from two study areas: in the South Hams area of Devon (southwest England) in 2005 and 2006 (subsequently referred to as 'Devon' here), and Bedfordshire and Cambridgeshire (eastern England) in 2006 (subsequently referred to as 'Beds/Cambs'). Both study areas covered approx 3200 ha, comprising a mix of habitats, including farmland, woodland, villages and rural gardens (Chapter 3, Stevens *et al.* 2007).

4.2.2 Camera system

Sixteen purpose-built digital camera systems, as described in Bolton *et al*. (Appendix B, 2007), were used, with eight systems being deployed in each study area. Images of nest activity were recorded by means of a video motion detection (VMD) facility, which enabled selection of specific parts of the image to trigger image capture, allowing each camera setup to be tailored to individual nest locations. Units were configured such that any movement event near the nest would trigger the system, but to minimise the chance of recording images by movement such as vegetation swaying in the wind. As well as recording a pre-event frame 0.5 sec before the trigger event occurred (Appendix B, Bolton *et al.* 2007), the units were configured to capture five images (with 0.3 sec intervals) each time the VMD facility was activated. A five second delay between trigger events was programmed into the units, to reduce the chance of the units being continually triggered by small movements of vegetation around the nest, or movement of chicks within the nest, whilst at the same time not compromising the ability to record failure events. The camouflaged cameras (3 x 2 x 2 cm) were mounted on a suitable support and placed near nests so that as clear a view as possible was achieved. By using a combination of lenses (Appendix B, Bolton *et al.* 2007), units were sited between 30cm and 4m from the nest. Cameras were connected to the recording unit and 12V battery power by means of a cable (minimum of 10m), thereby allowing the systems to be serviced (batteries and memory cards changed) some distance from the nest, minimising disturbance to the nest.

4.2.3 Data collection

Spotted Flycatcher breeding territories were identified by searching study areas from early May through to late August in each year of the study, with nests being subsequently located by observation of adult behaviour (strong alarm calling in response to observer, carrying food or nesting material). Cameras were deployed at a sample of the nests, ensuring that nests were monitored from an early a stage in the nesting cycle as possible, thus reducing the potential for bias resulting from nests only be monitored by cameras during the later stages of incubation. Cameras were deployed in a variety of habitats across both study areas, with the predominant habitat type around each nest being determined following the methods described in Stevens *et al.* (Chapter 3, 2007). All nests were visited at regular intervals (approximately every 3 days), to ascertain outcome (Crick *et al.* 1994, 2003). If it was possible to do so without disturbing a sitting female, nest contents were checked using a mirror on telescopic pole (in the case of nests without camera), or monitored by means of a portable monitor (for nests with cameras). Once away from the nest site, activity at nests with cameras was also monitored by viewing images recorded on the memory cards. This enabled a complete record of activity to be collected for these nests, thus allowing outcome to be ascertained directly. Once nests were empty, or were no longer attended by adults, the nest location was checked for signs of either success or failure. Success was recorded if adult activity indicated the presence of recently fledged young in the vicinity, or if the nest had a well-trodden lining, with droppings and/or feather scale present. Failure was recorded if the nest was found empty of either eggs or chicks that were too young to fledge, showed signs of nest damage (with or without remains of eggs or chicks), or abandonment (intact eggs remaining in the nest beyond the expected hatching period, or dead nestlings without any signs of aggressive injury). Any visible nest damage following a predation event was recorded in order to determine whether or not this was a useful indicator of predator identity. Nest height was measured (to the nearest 0.1 m).

4.2.4 Analysis

To compensate for the differing lengths of observation intervals between nests monitored with and without cameras we used the logistic exposure method as described by Shaffer (2004) to estimate daily survival of nests. An information-theoretic approach (Burnham & Anderson 1998) was used to evaluate the *a priori* hypothesis that cameras had no effect on nest success. In order to control for other factors that may affect nest survival (Chapter 3, Stevens *et al.* 2007), we compared support for a null model that contained habitat type (3-levels: farmland, garden and woodland), date (at midpoint of observation interval), nesting stage (laying, incubation or brood rearing) and a quadratic term for nest height, with a full model that contained all these effects plus camera (presence or absence). The overdispersion parameter of the full model was examined to check for lack of fit (Burnham & Anderson 1998). Models were ranked according to their Akaike Information Criterion (AIC) for small sample size (AICc) values (Burnham & Anderson 1998). When computing AICc values, we used the effective sample size as described by Rotella *et al.* (2004). The highest ranking (most parsimonious) model was that with the lowest AICc value and highest Akaike weight w_i (Burnham & Anderson 1998). Models were fitted using the PROC GENMOD procedure of SAS (SAS Institute Inc. 2002-2003).

4.3 Results

141 nests were monitored: 104 in Devon during the 2005 and 2006 breeding seasons, and 37 in Beds/Cambs in 2006. The majority of nests (83%) were found at, or before hatching (27 were found during the building stage, 27 during egg laying, 42 during the incubation period, 21 at hatching and 24 during brood-rearing). Cameras were deployed at 65 nests, in a range of habitats: 21 in farmland, 25 in gardens and 19 in woodland. Most cameras were deployed at nests early in the nesting cycle: 12 nests had cameras present at egg stage only, 17 at chick stage only, with 36 nests having cameras in place at both egg and chick stages. On average, cameras were deployed at nests 3.4 days (±0.563 days) after the nest was first found, with the mean nest age at deployment being 5 days (day 1 being the first egg date). Mean nest age at the start of monitoring for non-camera nests was 4 days. No nests were abandoned as a direct result of the cameras being deployed. At nests where it was possible to measure the time the adult took to return to the nest after the camera was set up (n = 22), the mean return time was 14 min 16 s (range 2 min 7 s – 45 min 55 s). There was a marginal non-significant difference in the heights of nests with cameras (mean 3.403 ± 0.20 m), or without (mean 4.143 ± 0.36 m, analysis of variance, $F_{1,140}$ =2.92, *P* = 0.090). Of the 141 nests monitored, 90 were successful (non-camera nests, 49 out of 76 successful, camera nests, 41 out of 65, $◎^2$ = 0.03, *P* = 0.86). The null model (without camera effects) had more support than the model with camera effects (Table 1). Although a ΔAICc of 1.551 indicated some degree of uncertainty, when the significance of the terms in the full model were assessed (by comparing the likelihood ratio statistic to the χ^2 distribution with the appropriate degrees of freedom), the camera effect was not significant (χ^2 = 0.46, *P* = 0.498). There was no evidence of model lack of fit; the overdispersion parameter for the full model with camera effect (c = 1.004) indicated a good fit to the data. Daily nest survival rates were similar for nests with and without cameras in each of the three habitat types (Table 1).

Table 1. Ranked models with (Full) and without (Null) camera effects and daily survival rates. Daily survival rates are calculated using parameter estimates derived from the full model, with camera effect, using an observation period mid-point date of 40.

Model	K	AICc	ΔAICc	w_i	Daily survival rate		
					Farm	Garden	Wood
Null	4	394.287	0.000	0.685	0.962	0.981	0.927
Full (camera)	5	395.828	1.551	0.315	0.969	0.985	0.940

The exact fate of eggs and nestlings was determined for 63 of the 65 nests monitored by camera. Twenty predation events were documented on camera (four partial and 16 complete), more than half in woodland habitat (Table 2). Avian predators were responsible for 85% of the predation events recorded, with the only mammalian predator being the Domestic Cat. Of the avian predators, the Eurasian Jay was the most commonly recorded, being responsible for 60% of all nest predation events, and 71% of the avian predations. Jays were recorded predating both egg and chick stage nests with equal frequency, with nest age at predation ranging from five days (day one being 1st egg date) through to 31 days (with chicks ready to fledge). The mean date for the Jay predations was 18 June (range 29 May- 7 Jul).

All predation events occurred during daylight hours (earliest 05:57 hrs, latest 18:03 hrs). On average, the time between parent bird departure and predator arrival was 8 min 03 s. It is possible that during this period the adult may have been involved in some form of active defence or distraction behaviour. Although the cameras were not positioned to record adult behaviour, fieldworkers observed nest defence on a number of occasions. Most avian predators, but particularly the corvids (Jay and Jackdaw *Corvus monedula*), left no visible signs of damage to the nest cup. The Common Buzzard *Buteo buteo* caused a small amount of damage to the rim of the nest cup when its curved claws became entangled as it perched alongside. The partial predation of chicks by the Great Spotted Woodpecker also caused some damage to the rim of the nest cup, but in this case, it was due to the repeated stabs at the chicks by the bird's beak and the subsequent dragging of one chick from the nest. In all three cases of cat predation, the nest was partially destroyed as the cat pawed at the nest whilst removing the chicks. It was not possible to safely determine signs left by the Eurasian Sparrowhawk *Accipiter nisus,* as the predated nest was located at height.

In Jay predations, the bird would land close to (but not on) the nest and, using its beak, pick out the nest contents. When egg stage nests were predated, Jays would either remove the eggs one at a time, consuming them at the nest in one sitting, or remove eggs one at a time and carry them away (this technique was also employed in the case of the Jackdaw predation). When chicks were predated, they were always carried away from the nest, with the Jay making return visits to take subsequent chicks. When nest contents (either eggs or chicks) were carried away from the nest, return visits for remaining nest contents could be several hours apart. Predation by Jays was typically a very speedy event – on average each predation visit by a Jay lasted for only 17 seconds (range 1 s – 1 min 39 s). In the case of the Buzzard predation, three 6-day old chicks were taken from the nest, but whilst they were removed one at a time, in contrast to the Jay, they were consumed at the nest.

Partial predations were recorded on four occasions (Table 2) with the nest subsequently failing completely in two out of the four cases. In one instance a Jay took one egg from a nest, leaving two eggs intact which the parent bird continued to incubate for a further four days before the remaining eggs were predated by a Jay (it is not known whether this was the same bird or not). In another case, a cat took two eight-day old chicks from a nest, leaving two chicks in the nest. It was not clear whether these chicks had sustained a physical injury, but both their level of activity, and that of the provisioning parents were much reduced after the predation event. Both chicks subsequently perished when the (surviving) female failed to brood them during a rainstorm in the night following the predation. Instances of partial predation involving Great Spotted Woodpecker were recorded at two nests (one at egg stage and one at chick stage). At one nest, despite the loss of one egg, the female continued to incubate the remaining four eggs and the nest went on to successfully fledge two chicks. At the chick stage nest, a woodpecker removed one chick from the nest, and although the remaining three chicks had sustained some superficial physical injury from the stabbing attack of the woodpecker's beak, they went on to fledge successfully.

Several other species were also recorded at nests, but were not involved in predation events. Most noticeably, Grey Squirrels visited nests that were (ultimately) successful during both the building stage and after the chicks had fledged, but were not recorded at nests with eggs or young. Both Common Shrew *Sorex araneus* and Bank Vole *Clethrionomys glareolus* were recorded at nests containing eggs, albeit briefly, but did not take or damage the eggs.

Two non-predation events resulting in failure were also recorded. In the first instance, four 11-day old young fell from a nest (located amongst ivy against the trunk of a tree) when it collapsed due to a combination of the growing weight and increased activity of the young. In the second instance, four 3-day old young were abandoned as they became increasingly less responsive to adult provisioning. Upon further examination, it was discovered that the nest contained a heavy parasite loading (primarily mites), and the chicks were consequently in very poor condition. By viewing earlier images, it was noticed that the female exhibited extreme and increasing restlessness during the incubation period, it being highly likely that this was also due to the excessive number of mites present.

Table 2. Predators of Spotted Flycatcher nests in two English study areas, identified using nest cameras.

Predator identification	Number of predation events							Total
	Egg stage		Chick stage		Habitat			
	Partial	Complete	Partial	Complete	Farmland	Garden	Woodland	
Eurasian Jay	1	5	-	6	3	1	8	12
Domestic Cat	-	-	1	2	1	2	-	3
Great Spotted Woodpecker	1	-	1	-	-	1	1	2
Common Buzzard	-	-	-	1	-	-	1	1
Eurasian Sparrowhawk	-	-	-	1	-	-	1	1
Jackdaw	-	1	-	-	-	1	-	1
Total	2	6	2	10	4	5	11	20

4.4 Discussion

The overall predation rate of camera-monitored nests in this study (31%) is comparable with that observed in other passerine nesting studies (Halupka 1998, Schaefer 2004), indicating that predation rates observed for Spotted Flycatchers were within normal limits. The results reinforce those of earlier studies (Pietz & Granfors 2000, Liebezeit & George 2002, Schaefer 2004) in demonstrating that nest cameras can be useful tools in the identification of nest predators. Furthermore, this study provides further evidence that cameras can be successfully deployed at nests with minimal disturbance and no subsequent effect on nest survival. Although the nests with cameras were marginally lower than those without in this study, this difference was due to constraints on accessibility when erecting cameras.

In analyses of data from the period 1964-1993, Gregory and Marchant (1996) reported increases in mean corvid densities on farmland Common Bird Census (CBC) plots in both the English regions used in this study, as well as an increased density in woodland plots in the south-west. Corvids, and especially Jays, are widely recognized as nest predators (Angelstam 1986, Møller 1989, Andrén 1992, Götmark 1992a, Groom 1993, Paradis *et al.* 2000, Schaefer 2004), so the findings of this study, with 65% of documented predation events by this group alone, are supportive of numerous previous studies. Jay was by far the principal nest predator recorded, predating both egg and chick stage nests in equal numbers. The peak nesting period for Jay is the end of April, with young fledging by the end of May (Joys & Crick 2004). Since most of the Jay predations recorded during this study occurred during June, it is unlikely that nests are being predated by Jays in order to provision their own young, but more likely coincides with the period when Jays are most abundant in the landscape. Jays are visually, rather than olfactory-oriented predators, and have been known to react to mobbing calls of passerines by commencing active searches of nearby trees and bushes (Goodwin 1986). During the latter part of the 19th century and into the early 20th century, the UK Jay population was intensely persecuted, and, as a consequence, became relatively scarce in many parts of England (Holloway 1996). Subsequently, and particularly after the 1914-1918 war, numbers increased steadily through to the early 1960's. Since then, and importantly, throughout the period of decline in Spotted Flycatcher numbers, the Jay population has apparently stabilised, albeit with slight annual fluctuations in numbers (Baillie *et al.* 2006). Although there seems to be no apparent link, a large-scale spatial analysis would be required to test whether BBS trends in Jay numbers are in some way related to population trends in Spotted Flycatchers.

Although Jays are often regarded as woodland specialists, in the absence of persecution they have become more generalist in their choice of habitat. Additionally, when woodland is fragmented and interspersed with agricultural land, Jays are often found at a higher density than in purely wooded landscapes (Andrén 1992), with consequential increases in the nest predation risk of birds breeding in the same landscape (Andrén *et al.* 1985, Andrén 1992). Similarly, predation risk is often higher near to habitat edges (Andrén & Angelstam 1988), an effect that impacts not just on the edge itself, but also some distance beyond (Brand & George 2000). Where small patches of different habitat types form a mosaic within the landscape, as is the case in the area of south Devon used as part of study, interfaces between habitats are frequent. In landscape such as this, potential predator species with large home ranges regularly move between habitats, and edge effects would be ubiquitous. There are several potential mechanisms whereby predation rates may differ between habitats. Habitat characteristics may influence nest concealment and/or predator access to nests, as well as influencing predator type, abundance or distribution (Evans 2004). These two mechanisms may also act in combination to alter the search efficiency of potential nest predators (Bowman & Harris 1980, Tarvin & Smith 1995), allowing predators that rely on visual cues to locate nests more easily. Additionally, predation risk may also be altered by differences in parental behaviour at the nest. Such differences in behaviour may be brought about by other habitat related factors, including differences in the abundance or availability of food for both the adults and chicks. If this was the case, adults may modify their provisioning behaviour, therefore altering the level of activity at or near the nest, thereby varying the overall predation risk of the nest.

It is not surprising that the carnivorous species recorded as predators in this study all involved chick-stage nests, with nestlings representing a potentially valuable source of protein for such top-level predator species. Predation of nestlings by species of both *Accipiter* (McCallum & Hannon 2001, Liebezeit & George 2002) and *Buteo* (Picman & Schriml 1994, Thompson *et al.* 1999, Small 2005) have previously been recorded, whilst records of nest predation by Domestic Cat, although largely anecdotal, are numerous (Woods *et al.* 2003, Baker *et al.* 2005). What is surprising, however, is that despite being recorded by nest cameras, squirrels were not documented predating nests during the course of this study. Squirrels are widely recognized as nest predators (Leimgruber *et al.* 1994, Willson *et al.* 2003) and in the UK, nest predation by the Grey Squirrel is often cited as a potential contributory factor in the population declines of several species of woodland birds (Hewson *et al.* 2004, Fuller *et al.* 2005). However, the results from this study provide no evidence to support this belief, at least with respect to Spotted Flycatchers. The only other mammalian species recorded at nests during this study (Shrew and Vole), also did not take notice of nest contents, despite both groups being reported as nest predators elsewhere (Darveau *et al.* 1997, Sieving & Willson 1998).

Without the use of nest cameras in this study, it would not have been possible to identify correctly those predators responsible for nest failure. Examination of the nest after a predation event provided few clues that would be helpful for anything other than a crude classification of predator type. The identification of specific nest predators serves to enhance studies of breeding productivity and provides useful information for the interpretation of results when looking at factors that may influence the risk of predation. Furthermore, it can serve to identify and inform potential management solutions that may directly or indirectly reduce rates of predation, hence assisting the design of effective conservation plans. However, in the case of the Spotted Flycatcher, the next step would be to assess the population level impact of Jay predation, which would require more data and further analyses before any recommendations on effective conservation measures could be considered.

Chapter 5

Investigating temporal trends in nest survival of Spotted Flycatchers *Muscicapa striata* in lowland England

5.1 Introduction

Annual population trends for many species of birds in the UK have revealed worrying declines in recent years, thus forming the basis for autecological studies designed to diagnose potential causes (Evans *et al.* 1997, Bradbury *et al.* 2000, Brickle *et al.* 2000, Donald *et al.* 2002). Where there is potential for problems to exist during the breeding season, nest survival estimates are often used as indicators of reproductive success and in subsequent calculations of annual fecundity (Bradbury *et al.* 2000, Brickle *et al.* 2000, Browne & Aebischer 2004). Analyses of daily nest survival frequently involve the use of the Mayfield method (Mayfield 1961), or at least one of the more recent expansions of this technique (Johnson 1979, Aebischer 1999). Ideally, estimates of nest survival should be unbiased, yet achievement of this is rarely straightforward. One such source of bias that should be accounted for are temporal trends that may impact upon nest survival within a breeding season, such as first egg date or nesting stage. In the derivation of such estimates of nest survival, data are often grouped to stratify according to season (early/late), or stage (egg/nestling), but grouping of data leads to reduced sample sizes and hence statistical power. Such grouping of data however, even if biologically significant, does not remove the problem related to the supposition of constant daily nest survival within these 'groups', inherent in Mayfield-based techniques. If this assumption is violated, as must often be the case in nesting studies, derived survival estimates may be biased (Klett & Johnson 1982). Therefore, it is critically important to test the assumption implicit in Mayfield-based techniques that nest survival rates are constant over time. With this in mind, several techniques have recently been developed that specifically allow more detailed exploration of temporal and age-dependent variation in daily nest survival (Dinsmore *et al.* 2002, Rotella *et al.* 2004, Shaffer 2004).

The once familiar Spotted Flycatcher is now perhaps better known as one of the UK's most rapidly declining birds: in the twenty-five year period 1979-2004, the breeding population fell by an estimated 82% (Baillie *et al.* 2007). The current UK population estimate is now only 63,700 pairs (BirdLife International 2004, Baker *et al.* 2006). Spotted Flycatchers nest in a variety of habitats in the UK, including parkland and gardens, open woodland and woodland edges, and lines or copses of mature trees on farmland. However, notwithstanding this, nest survival has been shown to be significantly lower in both farmland and woodland habitats than in gardens, with the proximal cause of poor nest survival being predation (Chapter 3, Stevens *et al.* 2007).

Through the deployment of purpose built digital nest cameras (Appendix B, Bolton *et al.* 2007), it has been established that the majority of Spotted Flycatcher nest predators, at least in lowland England, are avian rather than mammalian, with the Eurasian Jay being the species responsible for the majority of documented predation events (Chapter 4, Stevens *et al.* In press). Since avian predators rely on visual, rather than olfactory cues, it is probable that the predation risk, and hence daily survival rate, of a nest may vary temporally, either due to alterations in the level of nest exposure resulting from seasonal changes in vegetational cover, or due to changes in adult behaviour at different stages in the nesting period. Nest age may effect daily nest survival in two contrasting ways. Firstly, open-cup nests in more exposed locations may have a greater risk failure due to predation by predators that rely on visual cues during the laying period, before the incubating female affords crypsis to the nest. Additionally, this may be confounded by the search patterns of visual predators allowing earlier location of more conspicuous nests (Klett & Johnson 1982, Cresswell 1997, Weidinger 2001). Alternatively, predation risk, and hence survival, may be greater when nests are older, due to the increased levels of activity at the nest whilst young are being provisioned (Skutch 1949).

Although seasonal differences in nest survival have been previously investigated for this species by taking into account first egg date (see Chapter 3, Stevens *et al.* 2007), temporal trends associated with the age of the nest have not. The primary aim of this paper therefore, was to formulate survival estimates based on a model that allowed a more comprehensive investigation of the temporal patterns in daily survival of Spotted Flycatcher nests, thus testing the assumption of constant daily nest survival within nesting stages on which previous analyses of this data set have been based. Additionally, since a primary cause of nest failure in this species has been linked to avian predation, such methods allow examination of the pattern of daily nest survival to explore the possibility that this may indicate periods of increased predation risk from a predator with a visual search strategy.

5.2 Methods

5.2.1 Study sites and data collection

Data were collected from two study areas as described in Stevens *et al.* (Chapter 3, 2007); in Devon (southwest England) in 2004, 2005 and 2006, and Bedfordshire and Cambridgeshire (Beds/Cambs; eastern England) in 2005 and 2006.

Between early May and late August in each year of data collection, all potentially suitable habitat within each of the 3200 ha study sites was regularly searched for the presence of flycatchers. When territories were located, nests were found either by searching likely locations within a territory, or by observations of bird behaviour (strong alarm calling in response to observer, carrying food or nesting material). Once located, nests were visited at three-day intervals to ascertain age (where the day the first egg is laid = 1 day) and outcome (Crick *et al.* 1994, Crick *et al.* 2003). For nests of uncertain age (i.e. those not located during the laying period), first egg date was estimated by back-calculation from either the hatching or fledging date, assuming an egg laying interval of one day, an incubation period of 13 days (starting from the date the last egg was laid), and nestling period of 14 days (Cramp & Perrins 1993). Whilst it is acknowledged that in some cases the estimation of nest age by this method may be equivocal, it is believed that in the majority of cases it was possible to ascribe nest age to within ± 2 days. Nests were considered successful if at least one young fledged and as failed if found empty (of either eggs or chicks that were too young to fledge) or if (in the absence of parental activity) intact eggs remained in the nest beyond the expected hatching period, or dead nestlings (without any signs of aggressive injury) were found in the nest.

In each study area, all discreet habitat patches were identified using 1:10 000 Ordnance Survey maps, and, following field survey, were ascribed to a habitat category according to the habitat coding system developed by Crick (1992). Each nest was then categorised as being in one of three broadly defined habitats: 'garden', 'woodland' or 'farmland', using criteria described in Stevens *et al.* (Chapter3, 2007). The height of each nest was recorded using a calibrated measuring stick for nests up to 7 m, and a Bushnell Yardage Pro™ laser rangefinder for nests higher than this.

5.2.2 Nest survival

Although some nests may have represented repeat nesting attempts by the same pair, all nests were considered to be statistically independent since these analyses investigated the effects of temporal variation in nest survival, and each nest was active at a different time (Hatchwell *et al.* 1996, Cresswell 1997). Each row of data used in the analysis comprised information for one observation interval (the length of time between successive visits) for a given nest, including nest fate for the interval (1=success, 0=fail). Thus, each nest could have one or more observation interval, and each interval be one or more days long. PROC NLMIXED (SAS Institute Inc. 2002-2003) was used to fit a logistic-exposure model to the data, with a binomial likelihood and logit link function, modelling daily nest survival as a function of both nest- and time-specific covariates (Rotella *et al.* 2007). Since nest survival of Spotted Flycatchers is influenced by the habitat surrounding the nest (Chapter 3, Stevens *et al.* 2007), this effect was controlled for by including a categorical variable, habitat type (three level factor: garden, farmland or woodland) as a fixed effect in each model. Through the use of polynomial models, previous studies have shown that daily survival rates may vary with nest age in a non-linear manner (Grant *et al.* 2005). Hence, differences in survival during the egg laying, incubation and brood-rearing periods may conceivably create a cubic response (Grant *et al.* 2005). Similarly, differential survival during the breeding season - reported by some studies to be higher mid-season that at the beginning or end (Burhans *et al.* 2002) - could potentially having a quadratic effect of age-related survival. Thus, as well as a linear effect of nest age (at the start of the interval; Age, 1-31 d), both quadratic and cubic effects were included as continuous covariates in the modelling process. Other temporal covariates included in the modelling procedure were the continuous variable, Date (at start of interval, measured as days from 1 May), and a categorical variable, Year (three level factor: 2004, 2005, 2006). By using an iterative process for each day of an observation interval, programming statements within NLMIXED avoid the need to average values of covariates across these periods (Stephens 2003, Rotella *et al.* 2004, Shaffer 2004, Rotella *et al.* 2007). Since it has previously been suggested that the height of a nest may influence its survival (Kirby *et al.* 2005, Chapter 3, Stevens *et al.* 2007), linear and quadratic height terms were also included. The global model included habitat, year and date as well as a quadratic effect of height, and a cubic effect of age. All higher order polynomial models also included the relevant lower order polynomial terms.

By taking into account the potential effects of the covariates considered, a set of *a priori* biological hypotheses were developed to compare 48 candidate models of daily nest survival using information theoretic methods (Burnham & Anderson 1998), in addition to a model that assumed constant daily survival. The value for Akaike's Information Criterion for small sample size (AICc), by which models were compared, was computed using the effective sample size (Rotella *et al.* 2004). The highest ranking (most parsimonious) model was that with the lowest AICc value and highest Akaike weight, w_i, and where no simpler model had a Delta AICc of 2.0 or lower (Burnham & Anderson 1998). Nest survival rates were subsequently calculated as the product of daily survival rates for the 30-day nesting period. Interactions between Habitat and Age (including the polynomial effects of Age) were subsequently also investigated by fitting these terms in sequence to the most parsimonious model to see if model fit (as tested by AICc value and Akaike weight, w_i) was improved.

5.3 Results

In total, 248 nests were monitored during the course of the study, with 114 categorized as in gardens, 81 as farmland and 53 as woodland. Nest fate was determined in all but four cases.

5.3.1 Nest survival

To avoid bias associated with the treatment of nests of unknown fate (Manolis *et al.* 2000), four nests of uncertain fate were excluded from the data set used for the modelling procedure. Although bias could also have been introduced by excluding such nests, this was thought to be negligible given that they represented only a small fraction of the available data. The data set used for analysis therefore comprised data from 244 nests (113 garden, 79 farmland and 52 in woodland), and had an effective sample size of 3627. For nests that were both located and failed during the incubation period (n = 23), nest age was determined by taking a mid-point between the minimum and maximum possible age for the nest, based on the clutch size, the length of the observation period and a total incubation period of 13 days. Length of the observation intervals ranged from 1 – 19 days (mean 1.9 d ± 0.03), with 89% being 3 days or less and only 2% being longer than 5 days. As well as habitat, the best model (and nearly all the top ranked models) included an effect of date and a cubic effect of nest age (Table 1). The top ranked model was considerably better than that which assumed constant daily survival either within each habitat (ΔAICc = 23.443), or across all habitats (ΔAICc = 39.778). Support for models that included either a linear or quadratic effect of nest height was also found. There was no support for models that included a year effect. Nest survival increased during the egg-laying period and through the early part of incubation, reaching a peak on the sixth day of the incubation period (Fig. 1). Subsequently, daily survival gradually decreased to a low when the young were approximately six days old, followed by an increase in survival to fledging. Interaction effects between nest age and both habitat and region were tested but were not significant and did not improve the model (Age*Habitat *P* = 0.9924, Age^2*Habitat *P* = 0.9451, Age^3*Habitat *P* = 0.8949, Age*Region *P* = 0.9967, Age^2*Region *P* = 0.8954, Age^3*Region *P* = 0.9475), indicating that the age-related daily survival patterns were consistent across habitats and between regions. Model estimates of nest survival over the 30 d average nesting period in all habitats increased as season progressed, with survival of nests in gardens being consistently higher than that of nests in woodland or farmland (Fig. 2; $F_{2,8}$ = 5.68, P = 0.041, Fisher's LSD test).

Table 1. Summary of model selection results for the top seven logistic-exposure models (including the global model) of nest survival of Spotted Flycatchers in Bedfordshire, Cambridgeshire and Devon 2004-2006. Forty-nine candidate models were considered, including a constant survival model, and one that assumed survival was constant between habitats. Models are ranked by ascending ΔAICc. *K* is the number of parameters, AICc is Akaike's Information Criterion for small sample sizes and w_i is the Akaike weight. HAB is the categorical habitat effect, DATE is the linear effect of date, AGE^3 is the cubic polynomial effect of age, YR is the categorical year effect, HT is the linear effect of nest height, and HT^2 is the quadratic polynomial effect. The global model included habitat, year, date, a quadratic effect of height and a cubic effect of age.

Model	K	*AICc*	ΔAICc	w_i
HAB + DATE + AGE^3	7	616.820	0.000	0.374
HAB + DATE + AGE^3 *+ HT*	8	618.259	1.440	0.182
HAB + DATE + AGE^3 + HT^2	9	619.223	2.404	0.112
HAB + DATE + AGE^3 + YR	9	619.423	2.604	0.102
HAB + DATE + AGE^3 + YR + HT	10	620.959	4.139	0.047
GLOBAL MODEL	11	621.938	5.119	0.029
HAB + DATE + AGE	5	622.301	5.481	0.024

Table 2. Parameter estimates for the two top-ranked logistic exposure models of daily survival rate of Spotted Flycatchers in Bedfordshire, Cambridgeshire and Devon 2004-2006.

Parameter	Estimate	95% confidence limits	
		Lower	Upper
Best model			
Intercept	0.4858	-0.6745	1.6461
HAB-Garden	0.9147	0.3957	1.4337
HAB-Wood	-0.1948	-0.7453	0.3557
DATE	0.0212	0.0064	0.0360
AGE	0.4734	0.1794	0.7674
AGE2	-0.0348	-0.0579	-0.0117
AGE3	0.0007	0.0002	0.0013
Second-best model			
Intercept	0.3875	-0.8073	1.5824
HAB-Garden	0.9298	0.4091	1.4506
HAB-Wood	-0.2468	-0.8128	0.3193
DATE	0.0202	0.0053	0.0352
AGE	0.4684	0.1742	0.7626
AGE2	-0.0345	-0.0576	-0.0114
AGE3	0.0007	0.0002	0.0013
HT	0.0532	-0.0910	0.1974

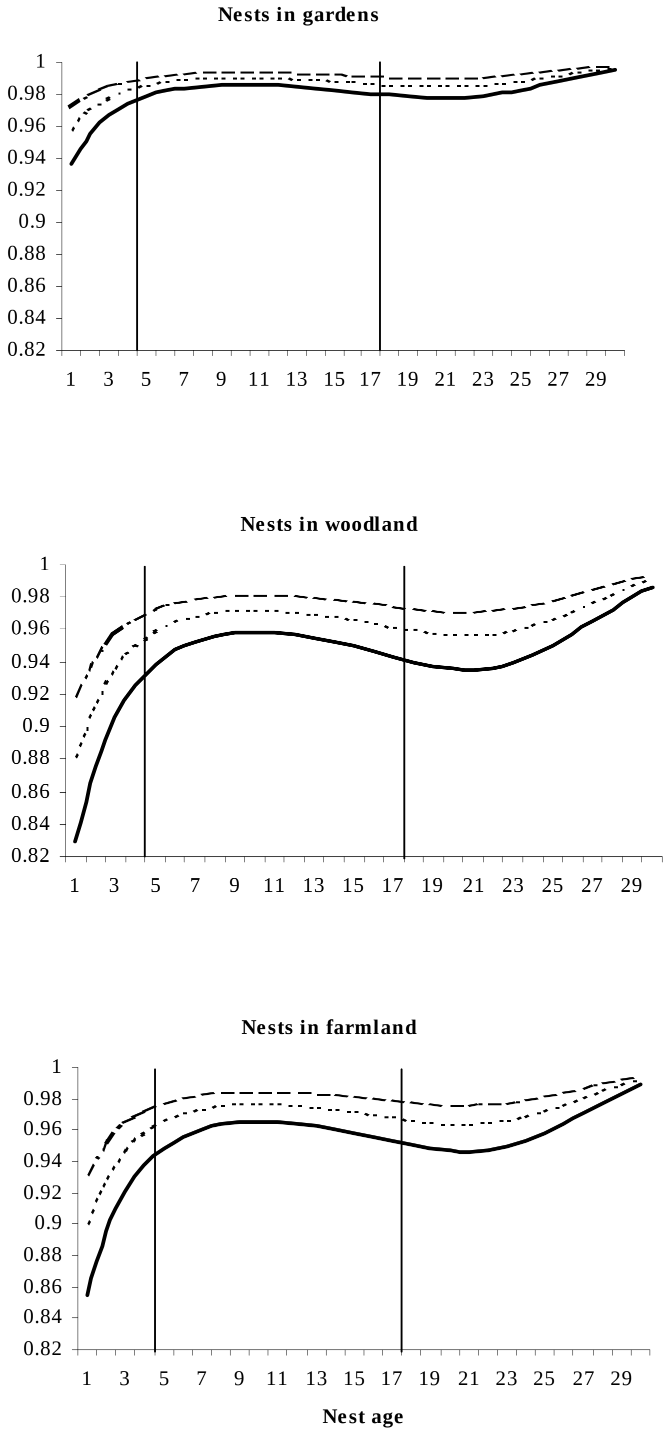


Figure 1. Model estimates of the average relationship of daily survival rate of nests situated in gardens, farmland and woodland with age (days) in Bedfordshire, Cambridgeshire and Devon 2004-2006. Solid line, represents early season nests (Date = 9 Jun), dotted line mid season (Date = 29 Jun) and dashed line late season (Date = 19 Jul). Vertical lines at nest age 4 and 17 days represent average values for the end of the laying period/beginning of incubation and the hatch date/beginning of the chick period respectively.

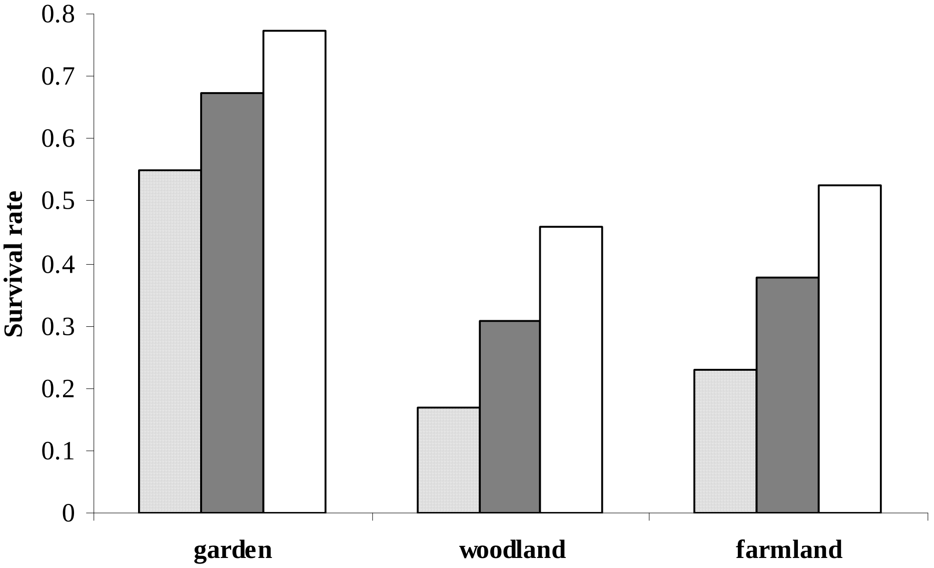


Figure 2. Model estimated survival rates for the entire 30-day nesting period of early (Date = 9 Jun, shaded bars), mid (filled bars, Date = 29 Jun) and late season (open bars, Date = 19 Jul) nests in gardens, woodland and farmland. Survival rates shown are the product of the daily survival rates for the 30-day nesting period.

5.4 Discussion

The results show that there are clear temporal patterns in the daily survival of Spotted Flycatcher nests, and confirm previous work showing that overall survival is higher for nests in gardens when compared to those in either farmland or woodland (Chapter 3, Stevens *et al.* 2007). The temporal patterns of daily nest survival are related to both the age of the nest and the date on which it was initiated, thus indicating that any analysis for this species based on an assumption of constant survival, even when data was grouped by nesting stage, would not be appropriate.

However, although there were clear temporal patterns in daily nest survival, there was no evidence of any differences in the patterns between either region or habitats. Comparable patterns have been previously described for other passerines (Grant *et al.* 2005), indicating that such patterns are not necessarily site- or species-specific. Aside from Grant *et al.* (2005), many previous studies only allow for temporal differences by calculating separate period-specific nest survival, egg- and chick-stage being the more commonly used (Pietz & Granfors 2000, Chapter 3, Stevens *et al.* 2007). However, although widely used, this approach may mask any subtle differences in daily survival within these periods. For instance, Stevens *et al*. (Chapter 3, 2007) reported egg-stage survival values that were always lower than chick-stage values, a fact that may seem counter-intuitive given that the majority of predators are visual-oriented, and that activity around the nest would be higher during the chick stage. However, since only those nests that are less easily located by predators are likely to survive to hatching, it is probable that nestling survival rates of this sample nests would be relatively high. Based on the same data, the age-dependent survival model reported here suggests that the low overall 'egg-stage' value is a combination of high survival rates during incubation, but very low rates during the egg-laying period. Hence, like Grant *et al*. (2005), this would encourage a more thorough exploration of age- and date-specific temporal effects.

That survival increases during the first third of the nesting period is perhaps not surprising. The proximate cause of failure of Spotted Flycatcher nests is predation (Chapter 3, Stevens *et al.* 2007), with avian predators, and predominantly the Eurasian Jay, being chiefly responsible (Chapter 4, Stevens *et al.* In press). During the laying period, eggs are left uncovered and relatively exposed, with a consequential higher risk of predation, particularly to predators that rely on visual cues. Similarly, nests in more exposed locations will have an increased risk of mortality in the early stages, as they are more easily located than those situated within cover and benefiting from increased concealment. Although small sample sizes of nests located in the earlier stages may result in survival estimates being less precise during this period, this is not likely to be the case in this study as 44% of nests were discovered before egg laying was complete, and 60% within the first 10 days. Once incubation begins, the sitting female may not only afford additional crypsis, but since there is a greater level of investment in the nest, may also offer a more active defence against predators, and hence increase the likelihood of the nest surviving.

The middle third of the nesting period (the latter half of incubation through hatching to 6-day old chicks) reflects a period of decrease in the daily survival rate. This may suggest changes in the behaviour and/or increased activity of the adults around the nest, since it is hypothesized that this may be related to predation risk (Skutch 1949, Conway & Martin 2000b). However, this result seems counter-intuitive if the female becomes more attentive as hatching approaches as suggested by Ryves (1943), although a similar decrease in survival during this period was reported for both Clay-colored Sparrow *Spizella pallida* and Vesper Sparrow *Pooecetes gramineus* (Grant *et al.* 2005), with the authors suggesting that this corresponded with an increase in adult activity at the nest during late incubation. The onset of hatching would clearly bring about changes in adult activity at the nest, as provisioning behaviour commences, increasing the visual cues available to predators, and potentially making nests more vulnerable to predation. Clearly, further work is required to investigate temporal patterns of adult activity associated with both the incubation and chick rearing periods before assumptions can be made concerning any correlations between these two factors.

Finally, daily nest survival increased during the final third of the nesting period, with nestlings from 6-days old to fledging, with all nests having similar daily survival rates during the final three days of the nesting period, irrespective of habitat or season. Nests that have survived until this stage may be those located in the most favourable sites, with those in suboptimal locations having failed during the first two thirds of the nesting period. Additionally, older nestlings may be less exposed to adverse environmental conditions, and more able to defend themselves in instances of predation, even if this results in premature fledging.

Low nest survival rates for birds breeding out-with mature garden habitats is suggestive of evidence of a problem on the breeding grounds for this species, and since nest failure is predominantly due to predation, the age-specific survival patterns described in this study may help to facilitate our understanding of predator-prey interactions. The fact that Spotted Flycatchers still breed in relatively good numbers in habitats, which, if judged by nest survival, appear to be of poor quality, may lead to a misinterpretation of what constitutes good quality habitat for this species. Similarly, despite the fact that flycatchers do well in gardens, it is clear that not all gardens would be suitable for breeding flycatchers. Although it seems likely that habitat heterogeneity provided by a mixture of mature trees and open spaces may be important predictors of site occupancy (Kirby *et al.* 2005), further work would be required to identify key features within gardens that fulfill the breeding requirements of the species before recommendations on effective conservation measures could be made.

Chapter 6

Is there any evidence of a migratory divide within the UK population of the Spotted Flycatcher *Muscicapa striata*?

6.1 Introduction

The populations of many species of birds, once abundant in the UK, have shown dramatic declines in recent years, being particularly noted for long-distance Afro-Palearctic migrants, and especially so for those wintering in dry, open habitats (Sanderson *et al.* 2006). This may encourage the belief that the population declines of our migratory passerines may be regulated by processes that impact on survival in the non-breeding season (Baillie & Peach 1992), but understanding the causes of changes in the populations of migrant species requires knowledge of events operating throughout the annual cycle.

The UK population of Spotted Flycatchers declined by 82% during the period 1979 – 2004 (Baillie *et al.* 2007). Recent work has suggested population declines may be linked to reduced survival of first year birds, possibly in the period immediately post-fledging (Freeman & Crick 2003), and there has also been an indication of a reduction in breeding productivity as a result of reductions in brood size and chick stage nest survival (Baillie *et al.* 2006). More recent work has highlighted potential differences in population trends at a regional scale (Noble & Raven 2002, Amar *et al.* 2006) and differences in seasonal fecundity between nesting habitats (Chapter 3, Stevens *et al.* 2007). Based on our understanding of the species breeding ecology, such regional differences in population trends appear to be explicable by known land-use changes, for instance agricultural intensification, and hence suggest that there may be factors operating in the UK that are contributing to the overall population decline. However, similar trends may also have been observed if there were differential over-winter survival of birds from different regions within the UK population. Such a scenario may be possible if there were a migratory divide operating at either a regional, or habitat level, such that the different population groups either migrate along different routes and/or spend the non-breeding season in different areas.

Currently, little information exists on specific links between breeding and wintering areas for many populations of Afro-Palearctic migrants. Although migratory divides have traditionally been identified through analyses of ringing recoveries (Baillie 2001, Bairlein 2001, 2003), this process may be relatively imprecise for species for which large data sets do not exist, either due to low recovery rates or rarity. Although the use of satellite telemetry has improved our understanding of migratory connectivity, body weight considerations, among other factors, restrict this option to larger species (Berthold *et al.* 1992, Kjellen *et al.* 1997, Higuchi *et al.* 2004, Lindberg & Walker 2007). Development of techniques involving Stable Isotopic Analysis (SIA) has more recently enabled a more refined approach to the determination of non-breeding areas and investigations of migratory connectivity without the requirement for large data sets based on ringing recoveries (Webster *et al.* 2002, Rubenstein & Hobson 2004, Hobson 2005). Through the analysis of naturally occurring stable isotopes in tissues such as feathers, this approach has been successfully used to aid delineation of geographically distinct populations (Chamberlain *et al.* 2000a, Bensch *et al.* 2006), or to constrain the winter range of afrotropical migrants (Pain *et al.* 2004).

Whilst there is a paucity of ring recovery data for the Spotted Flycatcher, patterns have nevertheless emerged. Based upon recoveries of birds ringed across Europe, a migratory divide is thought to operate between populations either side of a line of longitude approximately 12°E (Cramp & Perrins 1993, Baker & Baker 2002). Thus it appears that the majority of birds breeding to the west of this line (therefore including the UK population) spend the non-breeding period in sub-Saharan west Africa, whereas those breeding eastwards follow a route which takes them into east Africa. Whilst field records confirm that Spotted Flycatchers are found throughout sub-Saharan Africa during the non-breeding period (Cramp & Perrins 1993, Urban *et al.* 1997), precise information concerning the non-breeding areas of different populations of Spotted Flycatchers is lacking. Although it appears that the east/west migratory divide operates, it is possible that some degree of mixing may occur in the non-breeding area, and particularly around the Congo Basin, as a proportion of birds from both eastern and western populations appear to spend the non-breeding period in this region (Cramp & Perrins 1993). However, it has previously been shown that Spotted Flycatchers show site fidelity on the non-breeding grounds (Salewski *et al.* 2000), exposing the possibility that birds may regularly migrate between the same two areas. In a study of Aquatic Warblers *Acrocephalus paludicola*, Pain *et al*. (2004) demonstrated that discrete breeding populations of Aquatic Warblers also have discrete wintering areas. In this scenario, rather than a migratory divide operating, birds from different regions simply exhibit specificity of both breeding and non-breeding sites.

Since the Spotted Flycatcher exhibits a moult strategy that involves undergoing a complete moult away from the breeding area (Jenni & Winkler 1994), SIA of feathers grown in the non-breeding area therefore has the potential to highlight geographical differences between birds during this period. If breeding populations within the UK with contrasting population trends show differences in either geographic location or feeding ecology on the non-breeding grounds (as detected by SIA), this is consistent with the hypothesis that this link may be causal, thus supporting the hypothesis that regional population trends may be related to factors operating outside the UK.

6.2 Methods

6.2.1 Sample collection

Feather samples were collected from breeding adult flycatchers at known nest sites in two study areas in 2005 and 2006 (Fig 1); Devon (southwest England) and Bedfordshire and Cambridgeshire (Beds/Cambs; eastern England). Study sites were chosen based on evidence for recent population decline in eastern England, compared to stability or increase in southwest England (Noble *et al.* 2001, Noble & Raven 2002, Amar *et al.* 2006). Despite undergoing a limited partial moult before migration, both adult and first year Spotted Flycatchers from the UK undertake moult of remiges and rectrices on their non-breeding grounds after completion of the autumn migration (Jenni & Winkler 1994, Salewski *et al.* 2002). Once birds had been trapped (using either perch type spring traps or mist nets), R5 (i.e. second outermost tail feather) on the right hand side was routinely sampled by cutting near to the base (under licence from English Nature), storing each sample in a self-sealing polythene bag prior to analysis. Since only female Spotted Flycatchers incubate, the sex of each bird sampled was determined by the presence of a brood patch (Svensson 1992).

Figure 1. Location of the two study sites in lowland England: Devon, 50.31°N 03.84°W and Bedfordshire/Cambridgeshire border, 52.12°N 00.26°W. Study sites are marked on the map as a solid filled rectangle.

6.2.2 *Analytical methods*

Each feather was washed in 0.25M sodium hydroxide solution followed by two separate washes in purified water before being transferred to a clean screw top vial. The clean feathers were then further prepared by drying overnight at 50 °C, followed by being cut into fine sections (0-2 mm in length) in the sample vials using surgical scissors. For hydrogen isotope analysis, the exchangeable hydrogen in the feather keratin was equilibrated with the moisture in the laboratory air by weighing out 1mg of the feather sample and placing in a silver capsule before leaving open for a period of not less than 4 days, sealing just prior to analysis.

$\delta^{13}C$ and $\delta^{15}N$ were analysed using EA-IRMS (elemental analyser - isotope ratio mass spectrometry). Feather samples (each 0.5 mg) were analysed with 20 % duplication in a batch process, using NBS-1577B (powdered bovine liver) supplied by the US National Bureau of Standards as a reference material due to its close matches of both the isotopic and elemental makeup of the samples. NBS-1577B has a $\delta^{13}C_{V\text{-}PDB}$ value of -21.60 ‰ and a $\delta^{15}N_{Air}$ value of +7.65 ‰, being calibrated against IAEA-CH-6 Sucrose ($\delta^{13}C_{V\text{-}PDB}$ = -10.43 ‰) for $\delta^{13}C$ and IAEA-N-1 Ammonium Sulphate ($\delta^{15}N_{Air}$ = +0.4 ‰) for $\delta^{15}N$, both of which are International Atomic Energy Agency (IAEA), Vienna reference standards. Samples of NBS-1577B, IA-R038 L-Alanine with a $\delta^{13}C_{V\text{-}PDB}$ value of -24.99 ‰ and a $\delta^{15}N_{Air}$ value of -0.65 ‰ and an egg shell membrane standard were also analysed as quality control checks.

The $\delta^{2}H$ analysis (using feather samples, each 1.0 mg and analysed with 20 % duplication in a batch process) also employed EA-IRMS, but used IA-R002 (mineral oil) with a $\delta^{2}H_{V\text{-}SMOW}$ value of -111.2 ‰ as the reference material. IA-R002 has been calibrated against NBS-22 (mineral oil, IAEA isotope reference standard) with a $\delta^{2}H_{V\text{-}SMOW}$ value of -118.5 ‰. Samples of IAEA-CH-7 (polyethylene foil, $\delta^{2}H_{V\text{-}SMOW}$ = +100.3 ‰) were also analysed as quality control checks. In addition, we analysed samples of BWB-II (whale baleen) with a known non-exchangeable $\delta^{2}H_{V\text{-}SMOW}$ value of -108 ± 4 ‰ and an eggshell membrane standard (independently measured $\delta^{2}H_{V\text{-}SMOW}$ = -93.8 ± 2.3 ‰), within each batch of feather samples. The measured $\delta^{2}H_{V\text{-}SMOW}$ value for BWB-II in each batch was used to apply a correction for exchangeable hydrogen to the $\delta^{2}H_{V\text{-}SMOW}$ data for the feather samples.

$\delta^{13}C$ and $\delta^{15}N$ analyses were performed on a Roboprep-CN sample preparation module and 20-20 IRMS (Europa Scientific) and $\delta^{2}H$ analyses were performed on an ANCA-GSL sample preparation module and GEO 20-20 IRMS. All analysis was performed at Iso-Analytical, Sandbach, Cheshire.

6.2.3 Data analysis

Multivariate general linear models (GLM) were used to test the null hypothesis that there was no difference in the non-breeding (moulting) regions (and hence isotopic signals) of birds from different subpopulations within lowland England. Analyses were carried out using the GENMOD procedure of SAS (SAS Institute Inc. 2002-2003), with separate models being constructed for each isotopic signal ($\delta^{2}H$, $\delta^{13}C$ and $\delta^{15}N$). Significance was assessed by comparing the likelihood ratio statistic to the χ^2 distribution with the appropriate degrees of freedom. Categorical variables entered into each model were region (two level factor: Devon or Beds/Cambs), sex (two level factor: male or female), and year (two level factor: 2005, 2006). Initially full models were fitted, including all the predictor variables, and these results are presented to support the minimal models as recommended by Whittingham *et al*.(2006). Subsequently, minimum adequate models were selected using a backwards deletion process (Crawley 1993), with each variable being removed and replaced sequentially. Following each iteration, the variable explaining the least amount of variance was removed until only significant variables (P < 0.05) were retained. Interactions between the main effects were also tested.

All data were tested for normality using the Anderson-Darling test (Anderson & Darling 1952). Following Pain *et al*. (2004) ANOVA ws used to test for equality of variances. The relationship between individual stable isotopic values was investigated using bivariate scatter plots.

6.3 Results

Fifty birds were sampled, 25 from each of the two regions (Table 1 and Fig. 1). Values for δ²H, δ¹³C and δ¹⁵N were normally distributed (Anderson-Darling test, *P* > 0.05).

Table 1. Mean isotopic ratios (δ¹⁵N, δ¹³C & δ²H) in adult Spotted Flycatcher retrices from two breeding sites in lowland England in 2005 & 2006.

Sample	Sex		δ¹⁵N (‰)		δ¹³C (‰)		δ²H (‰)	
		n	Mean	SE	Mean	SE	Mean	SE
Devon	M	9	12.01	0.71	-16.79	0.40	-55.72	4.65
Devon	F	16	11.45	0.28	-17.80	0.54	-53.90	3.15
Beds/Cambs	M	9	11.42	0.44	-17.34	0.65	-62.42	3.11
Beds/Cambs	F	16	11.64	0.33	-17.79	0.40	-56.50	3.59
Devon	Both	25	11.65	0.31	-17.44	0.38	-54.56	2.57
Beds/Cambs	Both	25	11.56	0.26	-17.62	0.34	-58.63	2.58
Males	-	18	11.71	0.41	-17.07	0.38	-59.07	2.83
Females	-	32	11.54	0.21	-17.79	0.33	-55.20	2.36
2005	Both	27	11.63	0.31	-16.923	0.39	-48.55	2.01
2006	Both	23	11.57	0.23	-18.248	0.24	-66.04	1.73

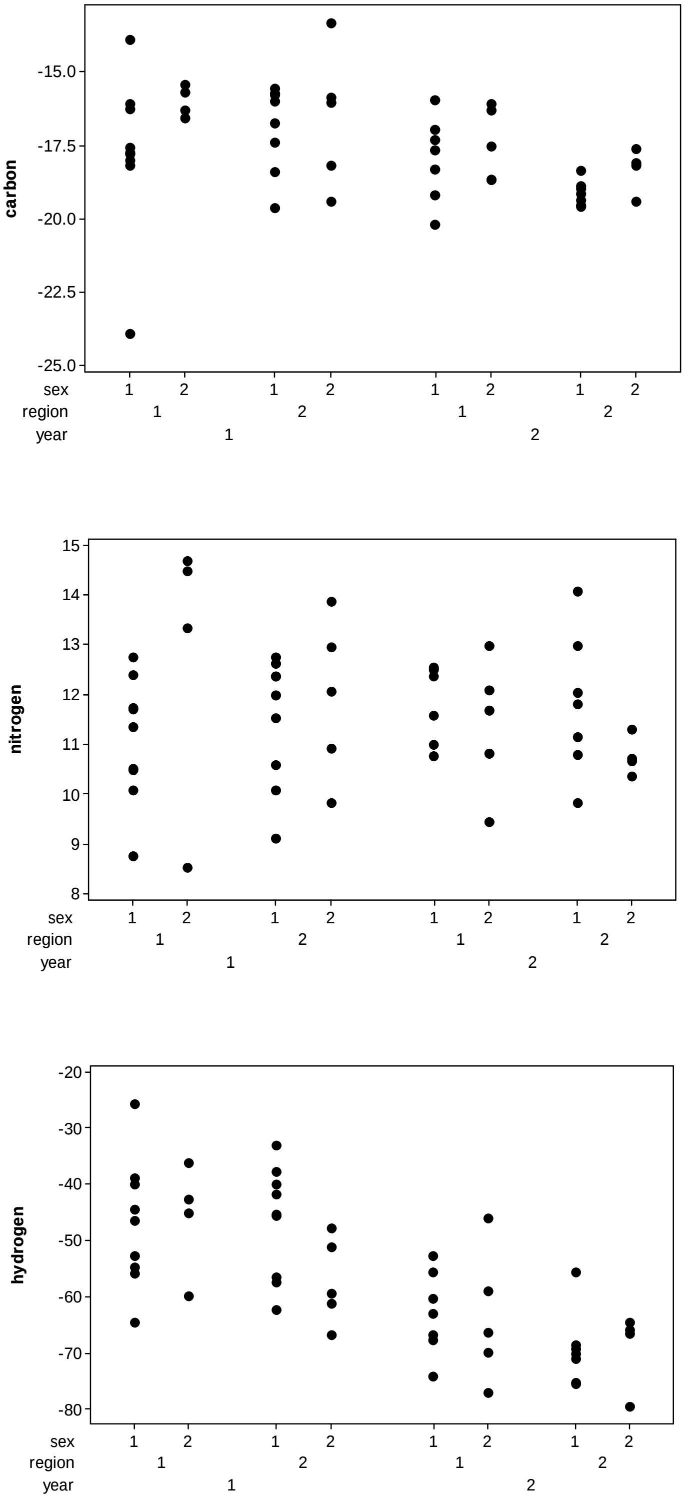


Figure 2. Individual δ¹³C, δ¹⁵N and δ²H values from feathers of Spotted Flycatchers, grouped by year (1=2005, 2=2006), region (1=Devon, 2=Beds/Cambs) and sex (1=Female, 2=Male).

Mean stable-carbon, nitrogen and hydrogen values were comparable across regions and between sexes, although values of $\delta^{2}H$ and $\delta^{13}C$ (but not $\delta^{15}N$) showed significant year effects (Table 2), with year being the only effect retained in the minimum adequate models (MAM) for both these two isotope ratios. There were no significant interactions. $\delta^{2}H$ also showed a near significant effect of region in the full model (model estimates: -55.30 ± 1.90 Devon, -60.07 ± 1.90 Beds/Cambs; *P* = 0.0695), although this was not retained in the MAM for this stable isotope.

Table 2. Full models of stable isotopic ratios ($\delta^{15}N$, $\delta^{13}C$ & $\delta^{2}H$) from two breeding sites in lowland England in 2005 & 2006. There was no significant interaction effects. Significant results are shown in bold.

Independent variable		$\delta^{15}N$		$\delta^{13}C$		$\delta^{2}H$	
	df	$\chi2$	*P*	$\chi2$	*P*	$\chi2$	*P*
Region	1	0.06	0.8138	0.26	0.6110	3.30	0.0695
Year	1	0.03	0.8554	8.42	**0.0037**	43.96	**<0.0001**
Sex	1	0.17	0.6844	2.72	0.0991	1.02	0.3121

6.3.1 Differences in variances of isotopic signatures

Since the data were normally distributed ANOVA was used as a comparison of the variances of the different subpopulations (Brown & Forsythe 1974). A significant difference was found for $\delta^{13}C$ (Bartlett's test statistic = 23.13, *P* = 0.002), with a near significant difference for $\delta^{15}N$ (Bartlett's test statistic = 12.54, *P* = 0.084). No significant difference was found for $\delta^{2}H$ (Bartlett's test statistic = 3.52, *P* = 0.833). An *F*-test was used in order to examine where the differences lay for both $\delta^{13}C$ and $\delta^{15}N$. Samples taken from birds in 2005 had significantly higher variance in $\delta^{13}C$ than those taken in 2006 (*F* = 3.00, *P* = 0.011). For $\delta^{15}N$, near significant results were obtained for both year (samples from 2005 showed greater variance than those from 2006; *F* = 2.15, *P* = 0.073) and sex (samples from males had greater variances than those from females; *F* = 0.47, *P* = 0.069).

6.4 Discussion

The results reported here provide support that Spotted Flycatchers from two populations in areas of England with contrasting trends may not winter in different areas, suggesting that the differing population trends probably cannot be explained by factors operating on the non-breeding areas. The results reinforce those of earlier studies (Pain *et al.* 2004, Bensch *et al.* 2006) in demonstrating that the analysis of stable isotopic ratios within feather samples can be a useful tool in studies seeking to identify the non-breeding range of afrotropical migrants at a spatial scale that would not be possible using data from ringing recoveries.

The normal distribution of the data for each of the stable isotopic signatures would suggest that samples were taken from birds that were more or less continuously distributed in a single region, rather than occupying more than one discrete region. Since within biomes there is $\delta^{15}N$ enrichment with trophic level (Hobson 1999a), the lack of any differences between samples from different regions of the UK in this particular isotopic signature suggests that birds from both populations are feeding at similar trophic levels during the non-breeding period. Flycatchers feed almost exclusively on aerial invertebrates, although in adverse weather they have been recorded both taking food from ground (Kovshar 1966) and gleaning prey items from vegetation (Davies 1977). Whilst Spotted Flycatchers may take advantage of food sources that may be ephemeral and local on their non-breeding grounds (Thiollay 1970), prey items taken during this period are not dissimilar to those taken at other times of the year (Urban *et al.* 1997).

The annual variation observed in $\delta^{2}H$ and $\delta^{13}C$ ratios may be due to annual variation in the local values of these two stable isotopes at the non-breeding (moulting) sites of birds. Alternatively, between year differences may be due to annual variation in the choice of non-breeding, and hence moulting, location. $\delta^{2}H$ ratios in feathers have been shown to vary in relation to $\delta^{2}H$ ratio in the rainwater in the area where the feathers were grown (Chamberlain *et al.* 1997), and so annual variation in these values would not be surprising if annual differences in atmospheric circulation patterns had occurred. The difference, albeit non-significant and small, between δ2H values from birds from different regions might at least imply a small difference in the average non-breeding location between the two sub-populations.

$\delta^{13}C$ ratios are linked to photosynthetic pathways, and are therefore regularly used as habitat indicators (Hobson 1999b), although they also exhibit latitudinal and altitudinal differences. Within specific regions $\delta^{13}C$ can be used to indicate the degree to which terrestrial habitats are mesic or otherwise (Hobson 1999b). Consequently, the between-year differences identified in this study suggest that birds may have wintered in a more mesic habitat in 2006 than in 2005. Although this could be due to either a distributional shift, or in-situ changes in the habitat, both of these possibilities could have survival consequences, especially in sub-Saharan Africa. However, the small range of $\delta^{13}C$ ratios reported here, even when annual variation is taken into account, does not provide any evidence for a latitudinal difference in moulting location, either between the sexes or the regional breeding populations within this study.

In a study of Aquatic Warblers, Pain *et al*. (2004) found that different breeding populations had markedly different variances in stable isotopic signatures, implying that some populations spread out over large regions during the non-breeding season, while others must have been extremely localised. The variances of at least the $\delta^{13}C$, and possibly to a lesser extent the $\delta^{15}N$ isotopic signatures in the present study differed between years. Although such differences between years are difficult to interpret, it is possible that in 2005, when there was a high variance in both these signatures, there may have been a reduced food supply, with birds consequently having to occupy a wider, and possibly less optimal, niche. Further work looking at how means and variances of data differed over a number of years and how this related to survival would be required to help examine this in more detail and it could be a powerful tool to determine whether survival is linked to conditions on the non-breeding grounds.

Collection of feather samples from birds across a range of non-breeding sites would increase our understanding of migratory connectivity in Spotted Flycatchers and similarly, samples from birds on active migration may help us to establish whether isotopically distinct birds (which must therefore come from different wintering areas) use different migration routes. However, since between year variation in the ratios of both δ^2H and $\delta^{13}C$ may bias analyses, comparisons between different geographical regions would be better served by the collection of samples from a single year.

Chapter 7

Using current habitat-specific demographic parameters to investigate the recent population decline of Spotted Flycatchers *Muscicapa striata* in lowland England

7.1 Introduction

Recent declines in the UK populations of many species of both farmland and woodland birds, both resident and migrant, are now well documented, with many likely causes being identified, varying by the autecology of the species concerned (Siriwardena *et al.* 1998a, Vanhinsbergh *et al.* 2003, Gregory *et al.* 2004, Fuller *et al.* 2005, Amar *et al.* 2006, Donald *et al.* 2006).

In the 19th, and for much of the 20th century, the Spotted Flycatcher was distributed throughout England, and although numbers showed small annual fluctuations, they were thought to be one of the commonest summer migrants (Holloway 1996). In 1968, when fieldwork for the first *Atlas of Breeding Birds* began, few long-term changes in either numbers or distribution had been recorded (Sharrock 1976). However, by the time the *Atlas* was published in 1976, data from the BTO/JNCC Common Bird Census (CBC) had revealed a 50% decline in the population from a peak in 1965 (Marchant *et al.* 1990). Subsequently, declines have been rapid and consistent: in the twenty-five year period 1979-2004, the breeding population fell by an estimated 82% (Baillie *et al.* 2007), and the species is on the 'Red' list of birds of conservation concern in the UK (Gibbons *et al.* 1996).

Although population declines were previously thought to be similar between different regions and habitats within the UK (Freeman & Crick 2003), recent analyses of BTO/JNCC/RSPB Breeding Bird Survey (BBS) and other census data has highlighted potential regional differences in population trends (Noble *et al.* 2001, Noble & Raven 2002, Amar *et al.* 2006). There is evidence for recent population decline in eastern England, compared to stability or even increase in southwest England, suggesting that there may be factors operating at a regional scale that are contributing to the national population decline. Identifying regional differences in population trends potentially provides a basis for diagnosing the cause(s) of decline by using comparative studies of both breeding ecology and environmental disparities in regions with contrasting trends. Such an approach has previously been used successfully to identify region-specific environmental causes of demographic differences for several species (Peach *et al.* 2004, Both *et al.* 2006, Wretenberg *et al.* 2007).

Spotted Flycatchers nest in a variety of habitats in the UK, including parkland and gardens, open woodland and woodland edges, and lines or copses of mature trees on farmland. Aside from an abundance of their aerial invertebrate prey, a key requirement of nesting habitat is a mix of mature trees and other features that can be used as perches, and open spaces into which foraging flights can be made (Davies 1977, Cramp & Perrins 1993, Kirby *et al.* 2005). Since Spotted Flycatchers are readily able to utilize a range of nesting locations within different habitats, with nests located both in trees and on, or in buildings, the availability of nest sites does not appear to be limiting. However, notwithstanding this, nest survival has been shown to be significantly lower in both farmland and woodland habitats than in gardens, with these differences being consistent between regions with contrasting population trends (Chapter 3; Stevens *et al.* 2007).

However, although previous work (Chapter 3; Stevens *et al.* 2007) determined basic nest survival data, with this concept being further extended to take into account the temporal trends uncovered in the age-dependant nest survival modelling explored in Chapter 5, neither of these approaches allowed for multiple nesting attempts, other than by incorporation of a seasonal effect. Whilst most Spotted Flycatchers are single brooded in Britain, second broods are not infrequent (Witherby *et al.* 1958, Cramp & Perrins 1993). In multi-brooded species reproductive success is linked to subsequent nesting attempts, following either failed or successful nests, and undoubtedly this requires consideration when examining annual fecundity. The habitat in which birds choose to breed may not only affect the success of individual nesting attempts, but, through increased adult effort, may influence the ability of the adult to re-nest. The primary aim of this Chapter therefore was to formulate a simulation model that would allow examination of how multiple nesting attempts influence seasonal fecundity. Although it is acknowledged that information is scant for some of the parameters necessary and that some will have to be estimated, this approach allows a more detailed assessment of region- and habitat-specific productivity estimates from regions with contrasting population trends. Additionally, the output of the age-dependant nest survival models were incorporate into the analyses to examine which demographic factors may be linked to the population decline of Spotted Flycatchers.

7.2 Methods

7.2.1 Study sites, data collection and estimation of breeding parameters

Data were collected from two study areas; in Devon (southwest England) in 2004, 2005 and 2006, and Bedfordshire and Cambridgeshire (Beds/Cambs; eastern England) in 2005 and 2006. The study area in Devon (centred on the parish of Aveton Gifford in the South Hams area) covered approximately 3200 ha, of which c. 2670 ha was farmland, 160 ha woodland and 111 ha villages and rural gardens (Fig.3b, Chapter 2). Woodland blocks in the study area were generally small, with only one over 20 ha, or linear in nature (following field edges and water courses) and were primarily deciduous. Grassland (largely used for cattle and sheep grazing, but also some for the production of hay and silage) accounted for over two-thirds of all farmland, with tilled land accounting for less than a third. The Beds/Cambs study site also covered approximately 3200 ha of which c. 2280 ha was farmland, 440 ha woodland and 123 ha 'human sites' (which included villages and rural gardens). Woodland blocks in the study area ranged in size from less than 1 ha to approximately 92 ha, with 5 blocks being greater than 20 ha in area. Approximately 60% of the woodland in the study area was deciduous and 10% coniferous, the remaining 25% being mixed (i.e. made up of least 10% each of deciduous and coniferous trees). In contrast to the Devon study area, grassland only accounted for about one quarter of the farmed area with the remaining three-quarters being tilled land (Fig. 4b, Chapter 2).

Between early May and late August in each year of data collection, all potentially suitable habitat within each of the 3200 ha study sites was regularly (at least twice-weekly) searched for the presence of flycatchers. When territories were located, nests were found either by searching likely locations within a territory, or by observations of bird behaviour (strong alarm calling in response to observer, carrying food or nesting material). Once located, nests were visited at three-day intervals to ascertain age (where the day the first egg is laid = 1 day) and outcome (Crick *et al.* 1994, Crick *et al.* 2003). For nests of uncertain age (i.e. those not located during the laying period), first egg date was estimated by back-calculation from either the hatching or fledging date, assuming an egg laying interval of one day, an incubation period of 13 days (starting from the date the last egg was laid), and nestling period of 14 days (Cramp & Perrins 1993). Whilst it is acknowledged that in some cases the estimation of nest age may be equivocal, we believe that in the majority of cases it was possible to ascribe nest age to within ± 2 days. For all nests found during the egg stage, maximum clutch size was recorded when laying was complete. Nests were considered successful if at least one young fledged and as failed if found empty (of either eggs or chicks that were too young to fledge) or if (in the absence of parental activity) intact eggs remained in the nest beyond the expected hatching period, or dead nestlings (without any signs of aggressive injury) were found in the nest.

In order to determine the nest replacement period following failed nesting attempts, and the double-brooding period following successful attempts, efforts were made to individually colour mark as many breeding adults as possible in each year. Adult birds were trapped near to the nest using mist nets, perch traps, or a combination of the two, with the sex of each bird being determined according to brood patch size before release. From 2004 to 2006, adults were marked with a unique combination of three colour rings obtained from A.C. Hughes. For details of the colour-ringing procedure see Appendix C (Appendix C; Pierce *et al.* 2007).

In each study area, all discreet habitat patches were identified using 1:10 000 Ordnance Survey maps, and, following field survey, were ascribed to a habitat category according to the habitat coding system developed by Crick (1992). Each nest was then categorised as being in one of three broadly defined habitats: ‘garden’, ‘woodland’ or ‘farmland’, using criteria described in Stevens *et al.* (Chapter 3; 2007).

7.2.2 *Estimates of nest survival for different regions and habitats*

Since nest survival of Spotted Flycatchers is influenced by the habitat surrounding the nest (Chapter 3; Stevens *et al.* 2007), for simplicity, this effect was controlled for by analysing habitat-specific data, separated into three distinct habitat categories (garden, farmland and woodland), and repeating the modelling procedure for each habitat type. The procedure took the most parsimonious model identified in previous nest-survival modelling (a model containing terms for both date and a polynomial (cubic) effect of nest age), in addition fitting a term for Region as a co-variate (two-level factor; Devon or Beds/Cambs). Although it is acknowledged that Region would not improve model fit (Chapter 5), including this factor enables both region- and habitat-specific model parameter estimates to be generated, thus allowing the investigation of ecological, rather than statistical differences between regions with contrasting population trends. PROC NLMIXED (SAS Institute Inc. 2002-2003) was used to fit a logistic-exposure model to the data, with a binomial likelihood and logit link function, modelling daily nest survival as a function of both nest- and time-specific covariates (Rotella *et al.* 2007). Although some nests may have represented repeat nesting attempts by the same pair, all nests were considered statistically independent since these analyses controlled for the effects of temporal variation in nest survival, and each nest was active at a different time (Hatchwell *et al.* 1996, Cresswell 1997). Each row of data used in the analysis comprised information for one observation interval (the length of time between successive visits) for a given nest, including nest fate for the interval (1=success, 0=fail). Thus, each nest could have one or more observation intervals, and each interval be one or more days long. By using an iterative process for each day of an observation interval, programming statements within NLMIXED avoid the need to average values of covariates across these periods (Stephens 2003, Rotella *et al.* 2004, Shaffer 2004, Rotella *et al.* 2007).

7.2.3 Productivity estimates

Flycatcher breeding productivity was estimated by developing simulation models that allowed for re-nesting following failed nesting attempts and double brooding after successful attempts (Green *et al.* 1997, Ratcliffe *et al.* 2005, Gilbert *et al.* 2007). Models were run separately for each of the main three nesting habitats (garden, farmland and woodland; Chapter 3; Stevens *et al.* 2007). Within each region, the proportion of clutches of different size was determined for each habitat at nests for which the complete clutch size could be accurately determined. Similarly, for successful nests, the proportion of eggs that did not result in fledged young was also calculated, thus allowing for infertile or addled eggs and partial brood reductions through starvation or predation. The final simulation models incorporated region- and habitat-specific parameters for clutch size, probability of eggs failing to fledge and nest survival, as well as parameters for the length of breeding season, the re-nesting interval and the double-brooding interval, which were constant between regions and habitats and were based on data collected during this study. Average start and stop dates (date for incubation of first clutch and date after which no more clutches are started) were defined by iteratively varying these parameters (and their standard deviations) in the model until the frequency of distribution of laying dates created by the model were analogous to observed values. Clutch size in the simulation was determined by comparing a randomly generated probability to the observed probability of a clutch containing 2, 3, 4 or 5 eggs for the given combination of region and habitat. The likelihood of an egg in a clutch surviving the nesting period to fledging was similarly estimated, by comparing a randomly generated probability to that observed in each region and habitat, such that nest productivity could be subsequently calculated by dividing the number of chicks fledged by the number of pairs. Having allocated each female a start date, for each day of the nesting period, the simulation models compared randomly generated probabilities with a likelihood of failure produced using the parameter estimates from the daily nest survival model for each region and habitat. Re-nesting/double brooding attempts were allowed if the date of failure/success, together with the observed replacement or double-brooding interval was earlier than the stop date. The model also allowed the number of nesting attempts per female to be calculated, thus allowing seasonal productivity to be estimated. The mean and standard deviation of these parameters were calculated by running the simulation models 999 times using a bootstrapping process. Simulation models were performed by using a program written in Microsoft Visual Basic 6.0.

The use of empirical data from this study on the proportion of pairs nesting in the three habitats in both study areas allowed estimates of productivity to be derived for each of the two study areas, weighted by the proportion of birds nesting in each habitat.

7.2.4 Population modelling

A simple deterministic population model (Thomson *et al.* 1997, Peach *et al.* 1999, Siriwardena & Vickery 2003) was used, incorporating both previously described values for demographic rates and those from this study, following the format:

$$N_{t+1} = (N_t \text{ x } Sa) + (N_t * P * 0.5 * \mathrm{Spf} * S_1)$$

Where N_t and N_{t+1} is the population available for breeding in one year and the next, *Sa*, Spf and S_1 are the annual survival rates of an adult, fledgling (fledging to independence) and first-year (independence to second summer) respectively and P is the productivity in chicks per pair.

The model incorporated independent estimates of adult survival (0.493±0.033, n = 94) and first-year survival (0.465±0.057, n = 78), suggested by Siriwardena *et al.* (1998b), and estimates of seasonal productivity resulting from the simulation models. Previous studies examining post-fledging survival in passerines have shown that survival during this period may be particularly low (Dhondt 1979, Anders *et al.* 1997). For Spotted Flycatchers, it is therefore likely that the highest mortality of first year birds occurs during the 18-day interval between leaving the nest and the development of independent feeding (Davies 1976). Since the Siriwardena *et al.* (1998b) estimate for first-year survival specifically excludes birds ringed as pulli and immediately after fledging, a term for post-fledging survival was additionally included. Following Bradbury *et al*. (2000), an estimate of post-fledging survival (0.561, range 0.428 – 0.734) was derived based on daily post-fledging survival estimates obtained from a range of other passerines, and given that the period from fledging to independence in young Spotted Flycatchers lasts approximately 18 days (Davies 1976). Since both the availability, and use by nesting Spotted Flycatchers, of the three main habitat types in the two study areas is probably reasonably representative of the both eastern (Beds/Cambs) and western (Devon) England, mean productivity estimates (weighted by the proportion of birds in each habitat) were used for each study area in the population model. However, it is acknowledged that this simplistic approach relies on the assumption that there is no dispersal between the three breeding habitats and that they are distinct and closed populations (this model termed the "closed population model" hereafter). This is unlikely to be the case, and indeed anecdotal evidence (DS unpublished data) suggests that birds move between habitats between seasons, if not within. Consequently, an alternative approach was also considered whereby rather than weighting productivity by region, as in the "closed" model, individual region- and habitat-specific productivity estimates were used in a population model that took into account the potential for dispersal between habitats between seasons. This was based on the assumption that birds probably select a breeding area based on cues related to the structure of the habitat, rather than by distinguishing between farmland, garden and woodland *per se*. Hence, the second population model (termed the "open population model") used a random distribution of birds within the study area, based on the availability of each habitat. Additionally, the model allowed for birds that survived to return to breed (both adult and first-year) to randomly distribute between habitats for each year that the model was run. The asymptotic population multiplication rate (λ) was then calculated for each population model following Lebreton & Clobert (1993).

7.3 Results

In total, 248 nests were monitored during the course of the study, with 114 categorized as in gardens (60 in Devon, 54 in Beds/Cambs), 81 in farmland (74 in Devon, 7 in Beds/Cambs) and 53 in woodland (37 in Devon, 16 in Beds/Cambs), allowing the proportion of nests in each habitat to be calculated for both study areas (Table 3). Clutches were initiated between 14 May and 25 July (Fig. 1).

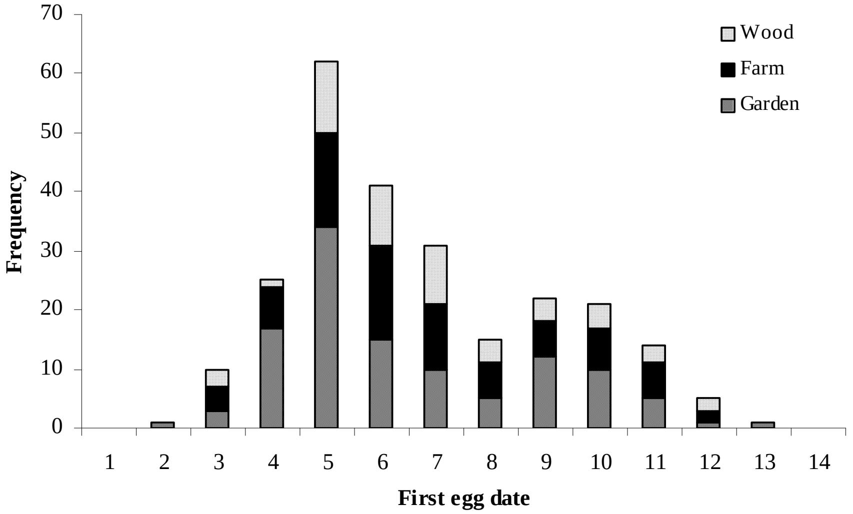


Figure 1. The distribution of clutch initiation dates for nests in gardens (n = 114), farmland (n = 81) and woodland (n = 53). Data from both study areas and all years combined with nests grouped by seven-day period (period 1= seven-day period starting 1 May).

The mean nesting period was 29 days (range 28 – 32, based on data from n = 21 nests where both the first egg date and fledging date were known with certainty). Following colour-marked individuals allowed determination of the replacement and double-brooding period for a small number of pairs. For pairs with failed nests, the mean replacement period was 9 days (range 5 – 16, n = 4), whereas for those with successful first attempts, the mean double-brooding period was 12 days (range 2 – 19, n = 7). Maximum clutch size could be accurately determined for 171 nests that survived the laying period, and the likelihood of an egg producing a fledgling was determined using data from the 142 of these nests that were subsequently successful (Table 1).

Table 1. Likelihoods of clutch size and egg fledging failure for nests in farmland, garden and woodland habitats in Devon and Beds/Cambs, with respective sample sizes.

	Clutch size likelihood				n	Likelihood of egg failure	n
	2	3	4	5			
Devon							
Farmland	0.000	0.178	0.578	0.244	45	0.116	32
Garden	0.063	0.104	0.563	0.271	48	0.139	43
Woodland	0.059	0.118	0.588	0.235	17	0.256	11
Beds/Cambs							
Farmland	0.000	0.000	1.000	0.000	5	0.000	5
Garden	0.022	0.222	0.422	0.333	45	0.187	42
Woodland	0.091	0.364	0.273	0.273	11	0.313	9

Combining data from different habitats and regions, clutch size decreased as the season progressed (Spearman rank-order correlation r_s = -0.646, P = <0.001).

7.3.1 Nest survival

Four nests of uncertain fate were excluded from the data set used for the modelling procedure, which therefore comprised data from 244 nests: 113 in gardens (60 in Devon, 53 in Beds/Cambs), 79 in farmland (73 in Devon, 6 in Beds/Cambs) and 52 woodland (36 in Devon, 16 in Beds/Cambs), and for calculation of AICc, had an effective sample size of 3627 (Rotella *et al.* 2004). Length of the observation intervals ranged from 1 – 19 days (mean 1.9 d ± 0.03), with 89% being 3 days or less and only 2% being longer than 5 days. Parameter estimates (Table 2) derived for each habitat-specific model were used in the re-nesting simulation model.

Table 2. Parameter estimates for each habitat-specific logistic exposure model of daily survival rate of Spotted Flycatchers in the Beds/Cambs and Devon study areas 2004-2006. These parameter estimates were used in the habitat- and region-specific re-nesting simulation models.

Parameter	Habitat type		
	Garden	Farmland	Woodland
Intercept (DEVON)	0.3966	-0.1332	2.401
BEDS/CAMBS	0.2397	-0.6909	0.5981
DATE	0.02003	0.03289	-0.00456
AGE	0.8017	0.5414	0.05386
AGE2	-0.06053	-0.04204	-0.00081
AGE3	0.001317	0.000927	0.000028

7.3.2 Productivity

The average dates on which incubation of the first clutch commenced and that after which no more were started were 31 May (± 6.5 d) and 23 July (± 5.5 d) respectively, resulting in a laying season of approximately 54 days duration. The simulation models allowed estimates of the number of nesting attempts, annual productivity and the proportion of pairs that successfully double-brooded (i.e. raised two successful broods in a season) to be derived for each habitat within the two regions (Table 3, and also annual productivity shown in Fig. 2).

Estimates of productivity for the two study areas, weighted by the proportion of pairs nesting in the three habitats in both study areas, were 3.80 chicks pair^{-1} in Devon and 4.26 chicks pair^{-1} in Beds/Cambs.

Table 3. Productivity estimates (± 1 S.E.) for Spotted Flycatchers breeding in different habitats in two regions with contrasting population trends. Based on data collected in study areas in Devon (stable population, southwest England) and Bedfordshire/Cambridgeshire (declining population, eastern England).

	Proportion of habitat available	Proportion of nests within each habitat	No. nesting attempts per pair	Productivity per pair	Proportion of pairs double-brooding
Devon					
Farmland	0.908	0.433	2.749 ± 0.082	3.989 ± 0.229	0.231 ± 0.041
Garden	0.038	0.351	2.383 ± 0.066	4.907 ± 0.232	0.456 ± 0.050
Woodland	0.054	0.216	3.099 ± 0.093	1.621 ± 0.188	0.048 ± 0.020
Beds/Cambs					
Farmland	0.802	0.091	3.398 ± 0.118	2.868 ± 0.248	0.057 ± 0.026
Garden	0.043	0.701	2.278 ± 0.070	4.968 ± 0.266	0.530 ± 0.059
Woodland	0.155	0.208	2.568 ± 0.088	2.489 ± 0.226	0.186 ± 0.048

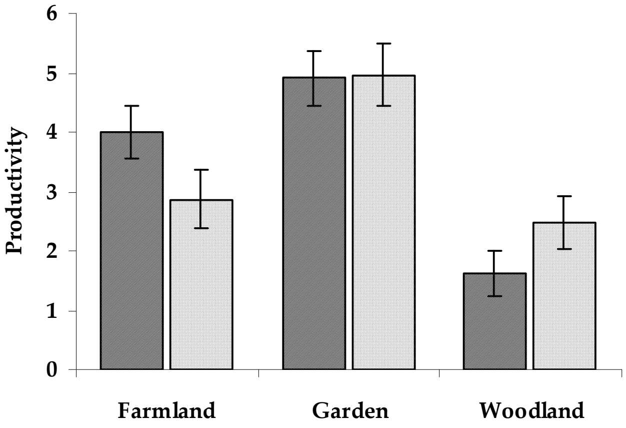


Figure 2. Simulated estimates of seasonal productivity (chicks pair^{-1}, ± 95% CI) of birds nesting in different habitats in the Devon (hatched bars) and Beds/Cambs (shaded bars) study areas.

7.3.3 Population modelling and demographic predictions

7.3.3.1 Closed population model

Population models were developed that encompassed the period of CBC and BBS monitoring data for England (1966 – 2005, CBC/BBS data, Fig. 3a and 1994 - 2005, BBS data, Fig. 3b). The modelled population trend for Devon showed an overall decline of –36% during the period 1966 to 2005 (Fig. 3a, asymptotic population multiplication rate λ = 0.988), whereas the modelled trend for the Beds/Cambs study area increased exponentially by 600% overall (λ = 1.049). The CBC/BBS trend for England during the same period showed a decline of -84% (λ = 0.954). For the period 1994 – 2005, during which regional BBS trends are available, the trajectory of the modelled population trend for the Devon study area was very similar to that observed on BBS plots within the same region (Fig. 3b: modelled trend for Devon -12%, BBS trend for South-west region -0.5%). The modelled trend for Beds/Cambs showed an overall increase of 70%, whereas the BBS trend for East of England region was -67%. Based on the available figures for adult, first-year and post-fledging survival, the level of seasonal productivity required for population stability was 3.887 chicks pair^{-1}.

7.3.3.2 Open population model

Population models for both study areas were developed that encompassed the CBC monitoring period for England (1966 – 2005, Fig. 4a). Using a model that allowed for dispersal between habitats, with settlement based on the availability of each habitat, indices were generated that showed a period of relative stability (or slight increase) for the Devon population (λ = 1.001), compared with a dramatic decline for the Beds/Cambs study area (λ = 0.871). The population trend for the observed CBC data for England falls midway between the regional variation of the modelled trends. For the period 1994 – 2005, during which regional BBS trends are available, the trajectory of the modelled population trend for both study areas was very similar to that observed on BBS plots within the same regions (Fig. 4b).

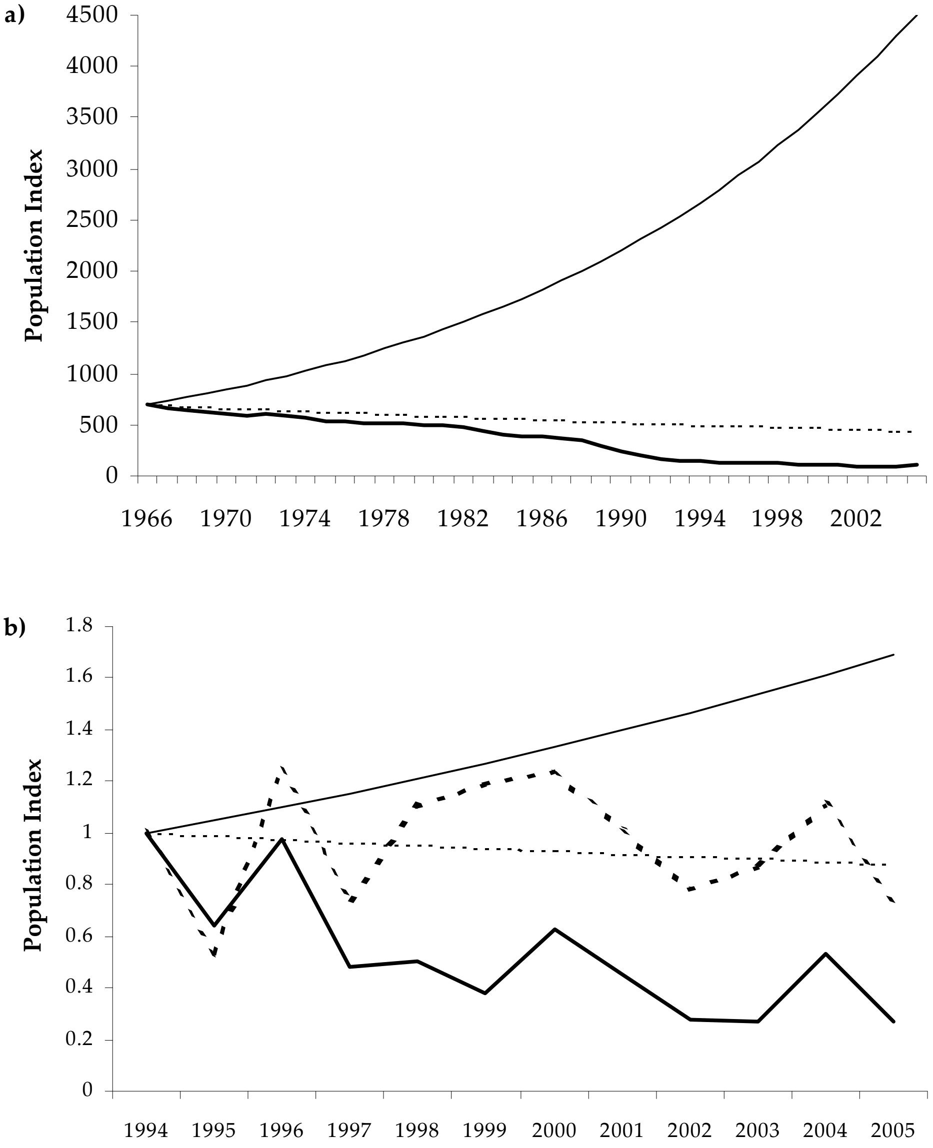
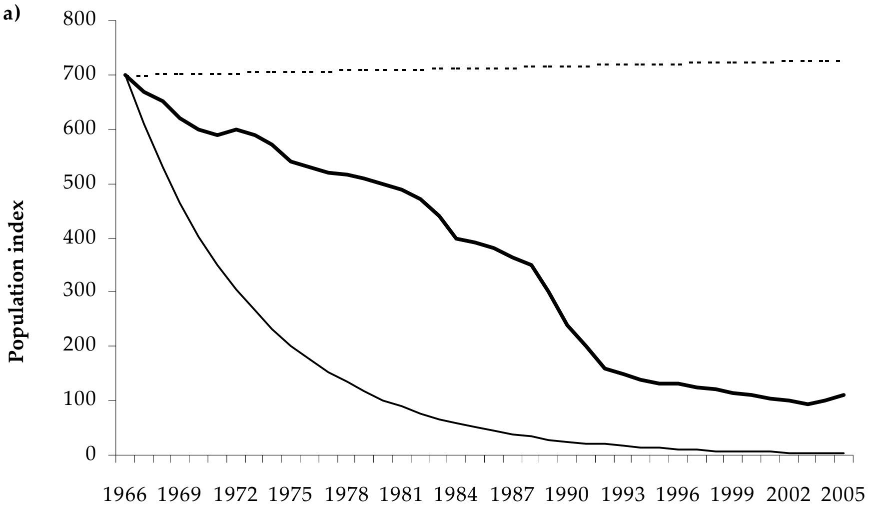


Figure 3. Predicted population indices for the period (a) 1966–2005 and for (b) 1994–2005, using mean productivity estimates (weighted by proportion of birds breeding in each habitat type and assuming there is no movement of birds between habitats) for the Devon (dotted line; asymptotic population multiplication rate λ = 0.988) and Beds/Cambs (solid line; λ = 1.049) study areas. A population index based on (a) CBC/BBS data for England (bold line) and (b) BBS data for Eastern (bold) and South West (dotted bold) England during the same period are shown for comparison (in bold).



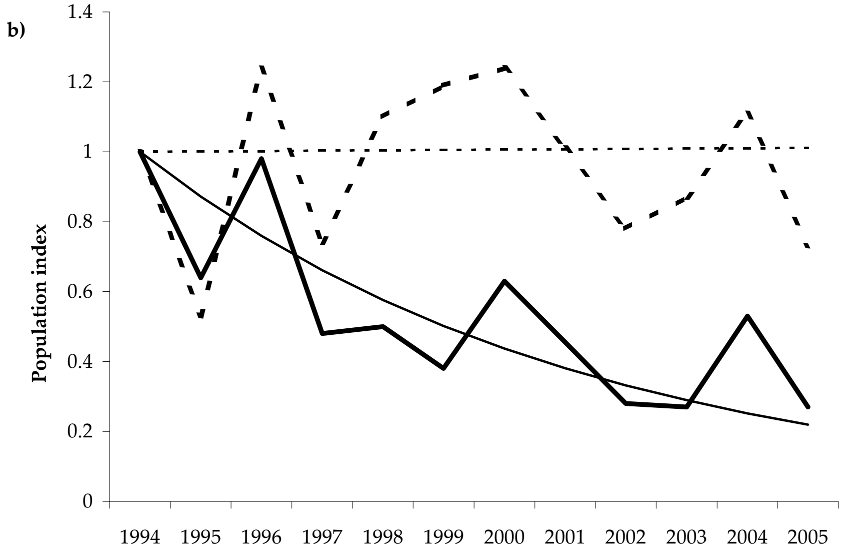


Figure 4. Predicted population indices for the period (a) 1966–2005 and for (b) 1994–2005 using habitat- and region-specific productivity estimates weighted by proportion of birds breeding in each habitat type and assuming birds settle randomly in each habitat according to the availability of the habitat within the study area. Modelled indices are shown for the Devon (dotted line; asymptotic population multiplication rate $\lambda = 1.001$) and Beds/Cambs (solid line; $\lambda = 0.871$) study areas. A population index based on observed (a) CBC/BBS data for England (bold line) and (b) BBS data for Eastern (bold) and South West (dotted bold) England during the same period is also shown for comparison.

7.4 Discussion

The population model based on observed habitat use within the two study areas, which does not take into account movement of birds between habitats, produces population trends for the two study areas that do not reflect the differences in observed regional population trends. Although the modelled trend for Devon appears to fit observed trends for south-west England, the modelled trend for the Beds/Cambs study area increases exponentially, in contrast to the observed trend for the East of England which shows a period of considerable population decline. There are two possible explanations for the apparent failure of this model to predict reality. Firstly, it is possible that some of the figures entered into the model are either incorrect, or inappropriate. Since the model for the Devon study area appears to fit the observed trends reasonably well, and since they are the best estimates available, it may be safe to assume that the values used for adult, first-year and post-fledging survival, which are constant between the two models, are probably not the issue. It is more likely that the figure that is driving the differences in the modelled trends is the derived productivity for birds breeding in the two study areas. For each study area, seasonal productivity in this model is derived by generating a weighted mean productivity based on the proportion of nests found in each habitat. Since this approach does not allow for any redistribution of birds between years, the model will consistently weight the population trend in favour of those habitats in which, in the years of this study, most nests were located. One of the problems with this approach is that this does not allow for any change in the differential use of the three habitats over time, and consequently imposes that which is observed today on the entire period of the modelled trend. However, during the last few decades, changes in the structural diversity and possibly the extent of habitats within each region make it likely that this assumption is unsound. The effects of agricultural intensification may have been more far reaching in the East of England than in the South West, and this may have had a corollary on the breeding distribution of Spotted Flycatchers. In the UK Government's Rural Development Programme for the South West Region (Ministry of Agriculture Fisheries and Food 2000b), the "variety and quality of the landscape and farmed and wooded countryside" is still listed as a particular strength of the region, with field boundaries in particular noted as important features, existing in a landscape characterised by a pattern of small deciduous woods and pasture. In consequence perhaps, the observed breeding distribution of Spotted Flycatchers appears to be well balanced, and birds are still extant in all of the three major habitat categories defined in this study. In contrast, the report for the East of England Region (Ministry of Agriculture Fisheries and Food 2000a), recognises that increasing agricultural intensification and specialisation has resulted in a loss of biodiversity in a region where the characteristic scenery is formed by centuries of agricultural management. The report highlights the loss of many natural landscape features, including hedgerows, hedgerow trees, riparian features and semi-natural habitats, and that there has been both a reduction in grazing enterprises and a general enlargement of field sizes. These major changes in the landscape would have had consequential implications for Spotted Flycatchers, in that farmland in the region is now largely unsuitable as a breeding habitat, with this being reflected in the breeding distribution recorded during this study. Although this is perhaps not the case historically, by modelling a population using productivity weighted by current breeding distribution, a bias is imposed in favour of the productivity of birds breeding in garden habitats. Since this is estimated to be high, it is not surprising that a model, which does not allow redistribution of birds, demonstrates an exponential growth. In reality, such population expansion is limited by the carrying capacity and availability of suitable garden habitat, such that surplus birds disperse either into less productive habitats within the vicinity, or leave the area entirely.

The assumption that birds do not move between habitats is therefore, very unlikely to be true, especially if each habitat contains the resources required for successful breeding. Having said that, as with many species of birds, knowledge and understanding of both natal and breeding dispersal in Spotted Flycatchers is lacking. Hence, the "open" population model reported here is based on between-year dispersal following a random settlement pattern according to the availability of each habitat within the study area, with the assumption that, at least historically, each may have been suitable for breeding Spotted Flycatchers. Using this approach, the observed CBC/BBS population trend for Spotted Flycatchers in England between 1966 and 2005 lies within the variation generated by the regional models for Devon and Beds/Cambs, with the slope of the observed trend also being midway between the two modelled trends for much of this period. However, between 1988 and 1992 the observed population trend declined more rapidly, before the same trajectory resumed for the latter part of the period covered by the index, and this is obviously not mirrored within the constraints of the parameters used for the modelled trends. Having said that, the trajectory of the observed trend for the period between 1992 and 2005 is much closer to the modelled trajectory for Beds/Cambs, perhaps providing evidence that the majority of the UK population has followed a path similar to that of the East of England, rather than that observed in the South West. This would support other studies which have suggested similar patterns of regional population decline in all regions other than the South West (Amar *et al.* 2006). Furthermore, the modelled population trends for both the Devon and Beds/Cambs study areas for the period 1994 – 2005 are consistent with the observed regional BBS trends for the same time period, thus providing evidence that demographic parameters operating at a regional level during the breeding season may be contributing to the observed UK population decline of this species. This presents reasonable support that the recent population decline is consistent with being caused primarily (but not necessarily exclusively) by factors affecting productivity, through the proximate mechanism of predation by avian predators. This, plus the observed differences in UK regional breeding population trends, provides further evidence that population limitation mechanisms have acted in the breeding season for this species. Furthermore, this study reports considerable differences in seasonal productivity between birds breeding in gardens and those in other habitats, and demonstrates how this may have related to population trends during the period of decline reported by the CBC and BBS monitoring schemes. The results presented here do not concur with previous population modelling (Freeman & Crick 2003), which suggested that changes in annual fecundity were unlikely to be important drivers. However, Freeman and Crick (2003) further suggest that declines in first year, and possibly post-fledging survival were the most likely demographic causes of population decline for this species, and though this has not been tested here, it is possible that these may be contributing factors, particularly if regionally differential trends could be detected in these two demographic parameters.

The increased survival probability of nests in gardens results in flycatchers breeding in this habitat having to make fewer nesting attempts per season. The greater productivity resulting from increased nest survival suggests that gardens may constitute a high quality breeding habitat for this species. Differences in annual productivity play a large role in determining changes in population size in short-lived species (Sæther & Bakke 2000). Indeed, population trends derived using these productivity estimates indicate that if gardens were not available as a breeding habitat, the population would have declined more rapidly, perhaps highlighting the importance of this habitat type. Since flycatchers are highly territorial, nest sites in optimal breeding habitats are likely to be vigorously defended. However, since birds are likely to select breeding habitat on visual cues related to the structure of the habitat, rather than by the definitions imposed here, they may not possess the ability to detect the predator-safe havens and hence optimality in terms of successful breeding that gardens offer. Anecdotal evidence collected as part of this study (DS pers. obs.) perhaps suggests that early returning birds settle preferentially in woodland, although this is not reflected in observed first egg dates, possibly because the timing of breeding may be linked to the timing of food supply. However, if this were true, it may indicate that decisions made by birds based on evolved cues that determine good quality breeding habitat may now be incorrect. However habitat quality is perceived, once available 'high quality' sites have been occupied, remaining birds will be forced into occupying 'suboptimal' breeding habitats, or even to remain as non-breeders. This follows the pattern of an ideal preemptive distribution (Pulliam & Danielson 1991), and gives rise to source-sink population dynamics governed by density-dependent processes. If this were to be applied to the habitats occupied by Spotted Flycatchers in the UK, we could regard farmland and woodland as the 'sink' population, serving as a buffer habitat to gardens, representing the 'source' population. This theory assumes that there is movement of birds between these habitats, a situation that is supported by anecdotal evidence from this study (DS unpublished data). Although a landscape such as found in the Devon study area, heterogeneous in both source and sink habitats, may maintain a population in both habitats for a long period of time (Pulliam 1988), large-scale changes in the availability, or relative balance of source and sink habitats may bring about population regulation. Although it seems likely that the area of suitable mature garden or mature woodland habitat may have undergone subtle change during the last 40 years, the same cannot be said for the area of suitable farmland habitat. As already described, farmland has undergone considerable change, particularly in the east of England, the outcome of which being the loss of habitat that may have been formerly suitable for breeding flycatchers. Specifically, the loss of active livestock farms, and associated farm buildings, and a reduction in the number of boundary trees and copses, will have reduced both nesting and foraging opportunities for flycatchers. When coupled with a more general degradation of farmland habitat in terms of a reduction in the abundance of invertebrate food (Woiwood & Thomas 1993, Benton *et al.* 2002, Gruar *et al.* 2003, Conrad *et al.* 2006, Lewis *et al.* 2007), farmland would now appear to be a poorer quality breeding habitat than it was formerly. Data from the BTO's Common Bird Census for the period 1962 to 1988 shows consistent declines in both farmland and woodland populations of Spotted Flycatchers, with the most notable declines being in farmland populations in western, eastern and southern England (Marchant *et al.* 1990). It is possible, therefore, that the severe population decline suggested for the East of England region is at least partly attributable to the loss of birds from this key habitat. Although the population modelling for lowland England does not vary the proportion of birds breeding in garden and non-garden habitat through time, this is likely to have been the case given changes in agricultural practices in some parts of lowland England.

Within time limits imposed by their migratory schedule, Spotted Flycatchers can compensate for nest mortality by re-nesting following nest failure, or double-brooding following successful nesting attempts. The estimated overall proportion of birds successfully double-brooding in this study (0.31, weighted mean) is higher than the figure estimated by Kirby *et al.* (0.14, 2005) or Summers-

Smith (0.20, 1952). However, being derived from re-nesting simulation models, the figure estimated here may be a truer indication of the actual figure since without being able to individually identify the majority of birds within a study population, it is very difficult to follow successive nesting attempts through a season. As there is currently no evidence available to suggest that there may have been changes to this figure over time, it is not possible to link this aspect of fecundity with population trends.

Low nest survival rates and productivity for birds breeding out-with mature garden habitats provide evidence of a problem on the breeding grounds for this species. The fact that Spotted Flycatchers still breed in relatively good numbers in habitats, which, if judged by seasonal fecundity, appear to be of poor quality, may lead to a misinterpretation of what constitutes good quality habitat for this species'. Similarly, despite the fact that flycatchers do well in gardens, it is clear that not all gardens would be suitable for breeding flycatchers. Although it seems likely that habitat heterogeneity provided by a mixture of mature trees and open spaces may be important predictors of site occupancy (Kirby *et al.* 2005), further work would be required to identify key features within gardens that fulfill the breeding requirements of the species before recommendations on effective conservation measures could be made.

Chapter 8

Synthesis and general discussion

8.1 Introduction

The aim of this thesis was to investigate the decline of the Spotted Flycatcher in the UK, principally by examination of its breeding ecology in lowland England. The study adopted a comparative approach in order to investigate the possible causes of population decline, comparing the breeding ecology of birds in a stable population with that of birds in a declining population. The study also briefly explored the possibility that factors in the non-breeding season may be affecting the two populations separately by determining whether there were any detectable differences between where the two populations over-wintered. In this chapter, I summarise the most important results from each aspect of the study and review the evidence generated. Since previous research on the species is limited, I also suggest key aspects requiring further investigation.

8.2 Key findings of the study

- **Breeding success (Chapter 3):** This chapter examined the relationship between nest success and the predominant habitat type around Spotted Flycatcher nests in two contrasting areas of England. A breeding population in eastern England, a region where numbers of Spotted Flycatchers are known to have decreased dramatically in recent decades, was compared to another in southwest England, where numbers have remained stable or even increased. Whilst there were no regional differences in nest success detected for the two study areas, there were significant differences between habitats within study areas, with garden nests more successful than those in farmland or woodland, at both egg and chick stages. However, within these habitats, the choice of the nesting substrate (tree or building) did not appear to influence survival. Estimates of productivity per nesting attempt were also lower in farmland and woodland, with nests in gardens fledging twice as many chicks as those in either woodland or farmland. The proximate cause of lower success in farmland and woodland was higher nest predation rates during both egg and chick stages. In terms of nesting success, farmland and woodland appear to be similar in quality for this species, but both appear to be sub-optimal habitats when compared to gardens, providing some evidence of a potential problem on the breeding grounds for this species, in at least these two habitats.

- **Nest predation (Chapter 4):** Purpose-built remote, digital nest cameras were deployed at 65 out of 141 Spotted Flycatcher nests monitored in two study areas. Ninety of the 141 nests monitored were successful (non-camera nests, 49 out of 76 successful, camera nests, 41 out of 65). Fate was determined for 63 of the 65 nests monitored by camera, with 20 predation events documented, all of which occurred during daylight hours. Avian predators carried out 17 of the 20 predations, with the principle nest predator identified as Eurasian Jay, predating both egg and chick stage nests in equal numbers. The only mammal recorded predating nests was the Domestic Cat, the study therefore providing no evidence that Grey Squirrels are an important predator of Spotted Flycatcher nests. There was no evidence of differences in nest survival rates at nests with and without cameras. Nest remains following predation events gave little clue as to the identity of the predator species responsible. The study showed that nest cameras can be useful tools in the identification of nest predators, and may be deployed with no subsequent effect on nest survival. Identification of specific nest predators enhances studies of breeding productivity and predation risk.

- **Temporal trends in nest survival (Chapter 5):** There are clear temporal patterns in the daily survival of Spotted Flycatcher nests, which are related to both the age of the nest and the date on which it was initiated. However, there was no evidence of differences in the pattern of daily nest survival between either region or habitats. Low egg-stage survival is likely to be a combination of high survival rates during incubation, but very low survival during the egg-laying period. After hatching, daily nest survival decreases steadily until the chicks are 6-days old, but then gradually improves through to fledging.

- **Evidence of a migratory divide (Chapter 6):** Mean stable-carbon, nitrogen and hydrogen values were comparable across regions and between sexes, although values of δ^2H and $\delta^{13}C$ (but not $\delta^{15}N$) showed significant year effects. Spotted Flycatchers from two areas of England with contrasting population trends do not winter in different areas, but rather appear to mix, suggesting that the differing population trends probably cannot be explained by factors operating on the non-breeding areas.
- **Demographic parameters and population modelling (Chapter 7):** The mean nesting period for Spotted Flycatchers in this study was 29 days, with the mean replacement period following failed clutches being 9 days, and 12 days following successful first attempts. The average dates on which incubation of the first clutch commenced and that after which no more were started were 31 May and 23 July respectively, resulting in a laying season of approximately 54 days duration. Clutch size decreased as the season progressed. The estimated proportion of birds successfully double brooding was 0.31 (weighted mean). Estimates of productivity for the two study areas, weighted by the proportion of nests in each habitat, were 3.80 chicks pair^{-1} in Devon and 4.26 chicks pair^{-1} in Beds/Cambs. Using current survival estimates, the level of productivity required to maintain population stability was 3.89 chicks pair^{-1}. A population model that did not allow for dispersal of birds between habitats did not describe the observed regional differences in population trend for this species. However, where dispersal was taken into account, the modelled population trends for both study areas were similar to the observed regional population trends. This is consistent with the observed population trends being driven by a reduction in seasonal productivity, brought about by an increased in nest failure rate in some habitats. Seasonal productivity in woodland and farmland habitat is probably too low to maintain population stability, and hence it is likely that birds breeding in garden mature gardens are sustaining the population at current levels.
- **Nestling diet (Appendix A):** Over half the diet was made up of flies, moths, butterflies, bees and wasps and a quarter of the diet was made up of beetles. About 15% of the diet was

made up of prey items that were most likely not gathered during aerial foraging sallies, including larvae, spiders, aphids, froghoppers, springtails and certain Coleopteran groups such as weevils, click beetles and ground beetles. Dietary composition did not vary significantly between regions, habitats, and time of year or brood fate and there was no significant difference in the sizes of prey items recovered in different habitats.

- **Remote digital nest cameras (Appendix B):** Remote digital nest cameras employing a video-motion detection system, which had previously been used for studies of ground-nesting waders, were successfully trialled and used at Spotted Flycatcher nests. The system was adapted to minimize intrusive maintenance and thus reduced disturbance at the nest site, whilst maximizing the reliability of image capture and quality during predation events in a range of habitats and locations. There was no evidence that the cameras altered predation risk or influenced the behavior of parent birds. Specifically, cameras could be installed at a nest site in about 15 min, minimizing disturbance at the nests. In addition, the use of long, camouflaged cables allowed changes of batteries and memory cards to take place some distance from nest sites and, in some cases, without the birds leaving their nests.
- **The use of plastic colour rings on Spotted Flycatchers (Appendix C):** The study recorded problems with the use of plastic colour-rings on Spotted Flycatchers, and additionally identified that this was not an isolated incident. Investigation revealed that researchers using either celluloid or PVC colour rings on several other flycatcher species, particularly when the colour ring was proximal to the foot, were also reporting unacceptable levels of leg injury. In light of this, recommendations are made to consider using anodized aluminium colour rings and avoid the use of plastic colour rings on all flycatchers.

8.3 Discussion and priorities for further research

The results of this study have provided valuable information on the breeding ecology of Spotted Flycatchers in lowland England, whilst at the same time highlighting other areas that would be worthy of investigation. However, further research is required to further investigate the mechanisms responsible for the habitat related differences in breeding success before recommendations on effective conservation measures can be made.

- **Investigate whether population trends of Jays are correlated with those of the Spotted Flycatcher:** This study has revealed that nest survival is particularly low in woodland and farmland habitats, and that the proximate cause of this is predation. Additionally, the primary predator responsible has been identified as the Jay. Clearly, the role that the Jay may have played in influencing the population decline of Spotted Flycatchers requires further investigation. Although numbers of Jays in England have fluctuated from year to year, the overall picture throughout the period of decline in Spotted Flycatcher numbers, is of stability, or even decline (Baillie *et al.* 2006). During a similar time period (1964-1993), the density of Jays in farmland has increased (Gregory & Marchant 1996), and interestingly, Amar *et al*. (2006) found that the population density of Jays, as well as that of Spotted Flycatchers, was higher in farm woods than in other woods. This concurs with previous work that has shown that Jays frequently occur at a higher density when woodland is fragmented and interspersed with agricultural land, thus increasing the predation risk of other birds nesting within this landscape (Andrén 1992). More recently, evidence gathered by the BBS for the 10-year period 1995-2006, has revealed that the population of Jays in England is increasing (Baillie *et al.* 2007). It has been suggested that increased predation pressure from Jays may have played at least a part in the population decline of some woodland bird species (e.g. Hawfinch, *Coccothraustes coccothraustes*; Fuller *et al.* 2005), although this has yet to be tested. Although there seems to be no apparent link, a large-scale spatial analysis would be required to test whether BBS trends in Jay numbers are in some way related to population trends in Spotted Flycatchers. The first part of this analysis would involve looking for regional correlations between broad-scale habitat parameters and abundance, population change, or presence/absence of Spotted Flycatchers in BBS squares. Secondly, the national BBS data could be interrogated to determine whether regional population trends of Spotted Flycatchers are correlated with the population trends of Jays in these regions.

- **A survey of potential predator species at sites occupied by breeding Spotted Flycatchers**: There is evidence that corvid populations have increased in both farmland and woodland in the period 1964-1993 (Gregory & Marchant 1996). Measuring the abundance of predators in landscapes occupied by Spotted Flycatchers would establish the relative abundance of different predator species in different habitats, and hence provide information that would assist with quantifying the predation risk. An issue to overcome would be how to overcome biased density estimates due to differing detectability in different habitats. Since there are many different predator species, estimates of abundance may take many forms. Avian predators may be surveyed using point counts, transects or mapping methods. Mammalian predators would probably best be monitored using indirect methods (visual surveys, hair-tubes, track plates for e.g.) that could be used in a wide variety of habitats and are not so labour intensive as direct methods such as trapping.

- **Investigate the species' ecology and survival during the post-fledging period:** Freeman & Crick (2003) hypothesised that a change in post-fledging survival was one of the most likely demographic drivers of population decline in the Spotted Flycatcher. Currently little information exists on the post-fledging ecology of young Spotted Flycatchers in the period between leaving the nest and the start of the autumn migration, and any information that does exist is largely anecdotal. Whilst Davies (1976) studied the immediate post-fledging period in some detail with respect to the transition from parental feeding to independence, this work was restricted to three broods within one garden. Further research would be required to establish whether these results were applicable between habitats, and to test whether there are habitat- or regional-specific differences in post-fledging parental care, habitat selection and dispersal. Additionally, there is no information on survival during this period when newly fledged birds are learning to forage independently and when the risk of predation may be high, and hence survival may be at its lowest (Davies 1976, Greenwood & Harvey 1982, Magrath 1991, Vega Rivera *et al.* 1998, Monros *et al.* 2002, Wheelwright & Templeton 2003). During this period young birds tend to be restricted in their mobility, and as such may be more vulnerable to either predation, or to the extremes of environmental conditions (Anders *et al.* 1997, Kershner *et al.* 2004). Radio-tracking and observational work on colour-marked fledglings during this period would allow some degree of quantitative assessment of habitat use, diet and survival, which would provide valuable information for assessing habitat preferences and food availability. Such work may also allow assessment of the causes of mortality during this period, and may reveal whether predation continues to be a significant risk.

- **Improve knowledge of adult and first-year survival:** Assessment of population scale responses to changes in demographic factors during the breeding season requires knowledge of annual survival. Although both adult and first-year survival have been quantified for Spotted Flycatchers, this information is based on a small amount of data, and more data would be required to improve the accuracy of these figures. Since they show a reasonable level of breeding site fidelity from year to year (DS pers. obs.), Spotted Flycatchers would be good subjects for a focussed ringing effort, and more studies of this nature should be considered and encouraged. With enough data, the possibility of regional differences in survival could be tested, thus improving the quality of demographic data in any further investigation of regional population trends.

- **Investigate the effects of nest location and concealment on predation risk:** Predation risk is related to the degree to which nests are concealed, by means of vegetative or other types of cover, such that nests with less cover may be more exposed to discovery by predators relying on visual cues (Potts 1986, Martin & Roper 1988, Martin 1992, Roper & Goldstein 1997, Eggers *et al.* 2005). There are several potential mechanisms whereby predation rates may differ between habitats. Habitat characteristics around the nest may influence nest concealment and/or predator access to nests, as well as influencing predator type, abundance or distribution (Evans 2004). These two mechanisms may also act in combination to alter the search efficiency of potential nest predators (Bowman & Harris 1980, Tarvin & Smith 1995), allowing predators that rely on visual cues to locate nests more easily. Data collected during this study on nest location, the level of concealment, and the structure of the habitat within the immediate vicinity of the nest may allow investigation of the overall risk of predation.

- **Investigate whether there are any differences in incubation behaviour between habitats:** If individuals have a perception of risk, it may influence reproductive strategies in some way (Ghalambor & Martin 2001, 2002). For species with open-cup nests, as opposed to cavity-nesters, this may be particularly important. Predators with visual search strategies may locate nests either by detecting the nest itself, or the eggs within it, with several studies focussing on how egg-crypsis is related to predation risk (Götmark 1992b, 1993, Weidinger 2001). During the egg-stage, by camouflaging the contents, incubating birds afford additional crypsis to the nest, whilst at the same time as being present to deter potential predators. Thus, a greater perception of predation risk should favour increased levels of nest attentiveness (Marzluff 1985, Kleindorfer & Hoi 1997). Incubation, in many temperate passerines, is carried out only by one sex, this usually being the female (White & Kinney 1974, Conway & Martin 2000b). In such circumstances, incubators must balance their own energetic requirements with the need to maintain the thermal environment of the eggs (Conway & Martin 2000a). Energetic constraints related to reduced food availability may increase the time the incubating bird spends foraging, therefore reducing the overall time available for incubation (Drent *et al.* 1985, Moreno 1989). Research is required to examine the factors that may be related to Spotted Flycatcher nest survival during the egg-stage, and specifically during incubation, focussing on those that may influence the predation risk of the nest. The hypothesis to test would be that there may be habitat-specific behavioural differences during incubation that may make a nest more vulnerable to predators with visual search strategies, taking into account factors that may relate to the level of nest concealment.

- **Investigate whether there are differences in provisioning rate and/or prey load in different habitats, and the correlations with chick condition:** Although predation risk is related to the degree to which nests are concealed, the risk is also confounded by variability in adult behaviour at the nest. Thus the possibility exists that parental activity at the nest may focus the attention of visual predators and that nest predation would increase in line with adult activity at the nest (Skutch 1949, Martin *et al.* 2000). Although this hypothesis has been tested several times (Roper & Goldstein 1997), results are often confounded as it is difficult to separate effects related to nest location (Eggers *et al.* 2005, Muchai & du Plessis 2005). One measure of habitat quality may be the abundance and/or availability of large flying insects, the favoured prey items delivered to nestling Spotted Flycatchers. Where the energetic demands of the nestlings are met, the relationship between provisioning rate and habitat quality is most likely not a linear one. Thus, in a poor quality habitat, the parent birds may respond in one of two ways; they may either make few visits to the nest, but each time may deliver a high quality prey item, or conversely, they may make many more visits, each time delivering only poor quality food items. In habitats with a good supply of high quality prey, provisioning rates may fall somewhere in between these two extremes. Thus, differential provisioning rates may exist if there were a disparity in the availability of high quality prey items between the habitats in which Spotted Flycatchers nest. If nesting in a poor quality habitat resulted in the energetic demands of the nestlings not being met, a reduced provisioning rate, coupled with lower growth rates and a poorer body condition may be expected.

- **Investigate whether the Spotted Flycatcher presence/absence and breeding success is related to invertebrate abundance:** Measuring the abundance of aerial (and possible foliage) invertebrates in a range of breeding habitats, both occupied and unoccupied, may indicate whether differences in food availability are correlated with the species persistence and/or nest success. Furthermore, establishing a continued monitoring programme could link changes in invertebrate abundance with the probability that the site would be occupied in the future. To adequately sample the full range of aerial invertebrates available to foraging flycatchers, a sampling strategy that encompassed a full range of height classes would have to be employed. A successful sampling method for aerial invertebrates that has been trialled in a range of habitats, at different heights is pan-trapping, whereby uniquely coloured dishes containing water are suspended at different heights in selected sampling locations.

8.4 Overall conclusion

This study has demonstrated that there are clear habitat specific differences in both nest survival and seasonal productivity. Although no regional differences were detected in nest survival estimates, simulation modelling that accounted for the probability of re-nesting produced productivity estimates that showed clear regional differences in woodland and farmland habitats. Subsequent population modelling has indicated that differences in the breeding distribution of birds within regions with contrasting population trends (related to habitat availability) may have driven the population decline of Spotted Flycatchers. Productivity is mediated by nest failure rates, with the proximal cause being predation, primarily by the Jay. Contrary to previous studies, this study has therefore provided new evidence that the population trend of Spotted Flycatchers in the UK may have been driven by factors relating to the breeding season.

Appendix A

Nestling diet of the Spotted Flycatcher *Muscicapa striata* in different habitats in lowland England

A.1 Introduction

In some species at least, it has been suggested that the diet of birds in different areas may in some way be correlated with differences in nest productivity (Hartley & Shepherd 1997). Although Spotted Flycatchers monitored during the course of this study do not show regional differences in productivity, they do show habitat specific differences (Stevens *et al.* 2007). Since flycatchers rarely forage far from the nest when provisioning young (Davies 1977), habitat specific differences in productivity may be related to differences in the availability of food around the nest. Although flycatchers appear to have favoured perches within nesting territories, the foraging strategy of the parent birds changes with respect to weather conditions (Davies 1977). Hence, a sit and wait strategy is adopted whilst foraging for aerial invertebrates when these species are most active during periods of warm, dry and sunny weather, whilst birds spend more time gleaning insects from foliage in periods of cool and damp weather (Davies 1977).

Although there are many invertebrate sampling methods that would allow a range of species to be monitored within the heterogeneous habitats favoured by nesting Spotted Flycatchers, without adopting a suite of these, any sampling protocol would only sample a small proportion of the prey items that were actually available within any given habitat. For example, although Malaise traps (Townes 1972) were used as the standard sampling method described by Davies (1977) as most suited to capturing the preferred prey of the spotted flycatcher, this method only samples aerial invertebrates that are active between the ground and 1.12 m height. Moreover, although Malaise traps give an reasonable unbiased estimate of the abundance of Diptera and Hymenoptera within this height range (Southwood 1968), they do not effectively sample other orders which may be taken as prey by Spotted Flycatchers. Additionally, although direct sampling of invertebrates within a nesting territory would provide information on the range of prey species available, it would not identify which species adults selected when provisioning young. Therefore, in order to identify which invertebrate species are components of the diet of nestlings, a different approach needs to be adopted.

Quantitative estimates of the dietary composition of birds are commonly made through examination of faecal matter (Moreby 1988, Green & Tyler 1989, Brickle & Harper 1999, Deloria-Sheffield *et al.* 2001, Donald *et al.* 2001, Gruar *et al.* 2003). Moreover, faecal analysis is an ethically sound method compared to the use of neck ligatures, emetics or examination of the gut contents (Orians 1966, Moore 1986, Major 1990, Kleintjes & Dahlsten 1992, Mellott & Woods 1993, Poulsen & Aebischer 1995, Moreby & Stoate 2000). A particular advantage of the technique is that a relatively large number of samples can be collected during other routine practices, as birds often defacate as a response to handling (e.g. during ringing activities).

By examining morphological features, disarticulated prey remains within faecal samples may be identified, at least to family, by reference to features seen on whole specimens. Chitinous exoskeletal remains are on the whole resistant to the avian digestive system, although some can be quite fragile, consequently disintegrating to the point where they can become almost unidentifiable. However, some of the more solid chitinous structures, such as mandibles and tarsi, may be well preserved, together with some colour patterns and hairs.

A.2 Methods

A.2.1 Collection and inspection of faecal material

In 2005, faecal samples were collected during the routine handling of spotted flycatcher nestlings aged between 3 and 11 days (day of hatching counted as 1 day). Samples, grouped according to brood and sample date, were stored in individual glass vials in 70% industrial methylated spirits until laboratory examination.

Time constraints only allowed one sample to be analysed for each brood/date sampling event, this being picked at random from those available, such that each of the samples analysed was either from a different brood, or sampled on a different date. Following methods developed by Green & Tyler (1989), each sample was decanted into a custom-made glass Petri dish for analysis, with a small amount of water being added to prevent the sample drying out. Prey remains in each sample were identified using recent literature and field guides (Ralph *et al.* 1985, Moreby 1988). Identifiable body parts were counted using a 30x magnification binocular microscope according to the methods outlined in Gruar *et al*. (2003), so that the relative abundance of each invertebrate group could be scored according to the number of key body parts counted (Moreby 1988, Sutherland 2004).

For the seven most commonly occurring invertebrate groups (Diptera, Hymenoptera, adult Lepidoptera, Coleoptera, Formicidae, Araneae and Aphrophoridae), an additional abundance scoring system was adopted. Using the 36 scored 10° intervals on the underside of the Petri dish, the presence or absence of identifiable body parts from each of these groups was recorded in every sixth interval. This gave a maximum score of six, where the invertebrate group had been recorded in each of the six intervals searched, with a minimum score of zero being where the group had not been recorded in any of the 6 intervals.

In a controlled study, Davies (1977) reported that 92.5% of wings fed to four hand-reared nestlings were recovered in the faeces two to three hours after ingestion. Since Bryant (1973) demonstrated that wing length is related to body length, in addition to the methods already described, any whole wings found in the sample were counted and measured using an eyepiece graticule, before being removed for later identification as either belonging to Dipteran or Hymenopteran prey.

A.2.2 Data analysis

Compositional analysis (Aebischer *et al.* 1993) was used to identify factors influencing variation in the relative proportions of the seven most commonly occurring prey groups: Diptera, Hymenoptera, adult Lepidoptera, Coleoptera, Zygoptera, Formicidae and Hemiptera. This involved converting the seven proportions to six log-ratios (the category 'other' was used as the denominator), which were then treated as dependent variables in a multivariate analysis of variance (MANOVA, Tabachnik & Fidell 2001). Since log-ratios cannot be calculated where the proportion equals zero, all such values were adjusted to 0.0001, following Aebsicher & Robertson

(1992). Where sample sizes were large enough (see Tabachnik & Fidell 2001), models were built to test for the effects of habitat (3-level factor; farm, garden & wood), time of year (2 level factor; June & July/Aug), region (Devon & Beds/Cambs) and brood fate (3-level factor; all fledged, partial brood reduction & total brood loss).

A.3 Results

79 samples were analysed from 49 broods (25 from the Beds/Cambs study area and 24 from Devon). 38 of the samples were collected early in the season (June) with 41 being collected later than this (July/Aug). Samples were collected from each of the three main breeding habitats, with 15 coming from nests in farmland, 54 from gardens and 10 from woodland. 53 of the samples came from nests from which all chicks subsequently fledged, 18 came from nests in which a reduction in brood size was recorded between hatching and fledging and 8 came from broods which subsequently failed to fledge.

A.3.1 Invertebrate composition of the diet

A minimum of 242 individual prey items were identified in the faecal samples analysed (summarised in Table 1). Over half the diet was made up of flies, moths, butterflies, bees and wasps (Table 1, 54.4% of all prey items), being found in 94% of samples and a quarter of the diet was made up of beetles (Table 1, 24.8% of all prey items), with this order being found in 52% of samples. About 15% of the diet was made up of prey items that were most likely not gathered during aerial foraging sallies, including larvae, spiders, aphids, froghoppers, springtails and certain Coleopteran groups such as weevils, click beetles and ground beetles (Table 1). A small piece of gastropod shell was recorded in one sample. Twenty-five intact and whole dipteran wings were recorded in the faecal samples (n=8 from farmland nests, n=12 from garden and n=5 from woodland). The mean size of these was 6.62 ±1.47 mm (range 3.3 – 9.5 mm), with no significant differences in sizes of those recovered in different habitats ($F_2 = 1.00$, $P = 0.377$) or regions ($F_1 = 0.48$, $P = 0.491$). Only 12 intact hymenopteran wings were recovered, with a mean size of 4.42 ±0.98 mm.

Table 1. Overall proportions by number (n= 242) and the mean proportions per sample (±1 s.d.) of invertebrates identified in 79 samples from 33 broods of Spotted Flycatchers. The percentage of samples that contained each invertebrate group is also shown.

Invertebrate group	*Overall proportion*	*Mean (± sd)*	*Percentage of samples*
Adult flies (Diptera)	0.186	0.280±0.329	58
Moths and butterflies (Lepidoptera)	0.182	0.203±0.263	56
Bees and wasps (Hymenoptera)	0.176	0.135±0.228	38
Unspecified beetles (Coleoptera)	0.155	0.125±0.194	42
Ants (Hymenoptera: Formicidae)	0.070	0.031±0.104	10
Weevils (Coleoptera: Curculionidae)	0.052	0.033±0.100	14
Adult damselflies (Odonata: Zygoptera	0.052	0.053±0.117	25
Froghoppers (Homoptera: Aphrophoridae)	0.030	0.048±0.146	15
Spiders (Araneae)	0.025	0.020±0.056	13
Rove beetles (Coleoptera: Staphylinidae)	0.023	0.011±0.058	5
Fly larvae (Diptera)	0.012	0.012±0.063	4
Click beetles (Coleoptera: Elateridae)	0.008	0.010±0.090	1
Aphids (Homoptera: Aphididae)	0.008	0.014±0.113	3
Ground beetles (Coleoptera: Carabidae)	0.008	0.004±0.022	5
Springtails (Collembola)	0.004	0.002±0.014	1
Crickets and grasshoppers (Orthoptera)	0.003	0.002±0.012	3
Ladybirds (Coleoptera: Coccinellidae)	0.002	0.002±0.019	1
Hymenoptera larvae	0.002	0.002±0.016	1
Bugs (Hemiptera: Homoptera)	0.002	0.001±0.006	1

A.3.2 Differences in prey composition between different regions, habitats, brood fates and time of year

Dietary composition did not vary significantly between regions, habitats, and time of year or brood fate (region, Wilk's $\lambda = 0.82$, $F_{7,66} = 2.04$, $P = 0.0635$; habitat, Wilk's $\lambda = 0.85$, $F_{14,132} = 0.78$, $P = 0.6878$; time of year, Wilk's $\lambda = 0.82$, $F_{7,66} = 2.09$, $P = 0.0572$; brood fate, Wilk's $\lambda = 0.81$, $F_{14,132} = 1.07$, $P = 0.3937$).

A.4 Discussion

Evidence from this study suggests that Spotted Flycatcher chicks are provisioned with a wide variety of invertebrate prey, with aerial invertebrates representing the largest group, thus concurring with previous studies (Cramp & Perrins 1993). However, many of the invertebrates groups identified, albeit representing a smaller proportion of the diet, were probably taken by methods other than aerial foraging, suggesting that adults used other search strategies when provisioning young. Some groups of invertebrates, particularly if small or soft-bodied and lacking robust, exoskeletal body parts, may have been overlooked or rendered unidentifiable by the digestive system. As such, it would not be possible to say whether invertebrates of this type were important as prey for Spotted Flycatchers, and even where they are recorded, the contribution they make to the diet as a whole may be underestimated.

Whilst there were many similarities in the components of the nestling diet recorded between this study and that of Davies (1977), there were also several differences. Although both studies recorded Diptera as being the primary prey item in the nestling diet, this study found that Lepidoptera were also an important element, whereas Davies (1977) stated that they were "unimportant". Similarly, whilst both studies recorded Hymenoptera, Coleoptera and Odonata, the order Homoptera was only represented by Aphididae in the Davies study, but additionally by the Aphrophoridae in this. Orders recorded by Davies (1977) but not in this study were the Trichoptera (caddisflies), Neuroptera (lacewings) and Psocoptera (barklice), whilst this study recorded dietary components from Araneae (spiders), Orthoptera (grasshoppers and crickets), Hemiptera (true bugs) and Collembola (springtails), whilst Davies did not.

On the whole, the length of the dipteran wings recovered from the samples during this study was smaller than that recorded by Davies (1977), who reported that nestlings were fed fewer small (wing length 7 – 8 mm) and more large (wing length 9 – 12 mm) Diptera. This may suggest that nestlings in this study are being fed prey of a smaller size than in the Davies study, and since flycatchers preferentially feed their nestlings larger invertebrates (Davies 1977), this may indicate that prey of this size are less available than formerly. Perhaps in support of this suggestion, Davies (1977) also reported that the proportion of Diptera in the diet of nestling flycatchers was between 0.632, during periods of cool weather and 0.808 when the activity of aerial invertebrates was higher in periods of warm weather. Similarly, Davies (1977) reported that, as a proportion Coleoptera made up 0.127 of the diet on cool days and 0.061 in warm weather, representing a switch from aerial foraging with a sit and wait strategy to a canopy feeding/gleaning strategy. In contrast, the respective proportions of Diptera and Coleoptera in this study were 0.186 and 0.248, suggesting that the proportion of Diptera in the nestling diet may have considerably reduced since the Davies study, whereas the proportion of Coleoptera has increased. There is a growing body of evidence that the abundance of invertebrates has declined on farmland (Aebischer 1991, Donald 1998, Sotherton & Self 2000, Benton *et al.* 2002), and it is possible that these trends would also be similar in adjacent habitats, particularly for more dispersive species with less restricted ranges. The scale of the short-term effects of pesticides suggest that they are an important contributory factor in invertebrate declines (Campbell *et al.* 1997, Morris *et al.* 2005). Whilst many groups of invertebrates may be affected, there is evidence that some species of Coleoptera at least, may be more resilient (Campbell *et al.* 1997), whilst populations of others may be able to recover within a few weeks of application (Brown *et al.* 1988).

Nestling diet in this study did not vary with time of year (early or late nests), this effect has been previously shown in other species (Evans *et al.* 1997, Brickle & Harper 1999). In contrast to other species however, the breeding season for Spotted Flycatchers is comparatively short: samples from flycatchers in this study were collected between mid-June and early August, over a period of spanning only 56 days, and it is possible that the range of available prey in the environment did not change to any great extent during this period. Similarly, it was not surprising differences were not detected between regions, as adult flycatchers forage preferentially for larger invertebrates when provisioning young. It is therefore probable that the nestling diet is not an accurate reflection of the entire spectrum of invertebrates available, or their relative abundance in the environment, and a simple analysis of nestling diet would therefore not be subtle enough to pick up regional differences in invertebrate diversity.

Differences in nestling diet associated with habitat may have been expected given that productivity is lower in both farmland and woodland than in garden habitats (Stevens *et al.* 2007). However, these differences may be reflected in either the size or the quantity of prey items brought to the chicks, rather than the species composition, and so would not have been picked up in this study. Further work looking at provisioning rate and prey load would be required in order to examine habitat-specific differences in quality with respect to nestling diet and productivity.

Although the dietary composition of nestlings may be related to many external factors, information on the nestling diet of Spotted Flycatchers may help in assessment of the quality of surrounding habitat, thereby informing future conservation measures aimed at this species.

Appendix B

Remote monitoring of nests using digital camera technology

This appendix is published as follows:

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Remote monitoring of nests using digital camera technology.

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B.1 Abstract

Although cameras have been used for many years to collect data at birds' nests, recent advances in digital technology have led to increased storage capacity, faster and easier review of data, and reduced power consumption. The development of sophisticated triggering mechanisms, such as video motion detection, herald a new era of portable, energy-efficient systems that require less frequent maintenance. We used a digital infrared camera system to monitor predation events at the nests of ground-nesting Lapwings (*Vanellus vanellus*; *N* = 40) and tree-nesting Spotted Flycatchers (*Muscicapa striata*; *N* = 17). Eight predator species were recorded taking eggs or chicks at Lapwing (*N* = 10) and Spotted Flycatcher (*N* = 7) nests, including red fox (*Vulpes vulpes*), badger (*Meles meles*), sheep (*Ovis aries*), and Carrion Crow (*Corvus corone*) at Lapwing nests and Eurasian Jay (*Garrulus glandarius*), European Buzzard (*Buteo buteo*), Great-spotted Woodpecker (*Dendrocopus major*), and domestic cat (*Felis catus*) at flycatcher nests. We tested three system configurations in an attempt to minimize power requirements and maximize predation-event recording capability. We found that the use of a passive-infrared sensor to awaken the system from standby mode did not compromise reliability and reduced power consumption. With this system, a 38-Ah battery operated the system for 120 h with no maintenance at a cost per unit of about $800 (US; or £400 UK Sterling). Further modifications would permit adaptation of the system for a wide range of scientific and nest surveillance operations.

B.2 Introduction

Nest predation is a primary cause of nest failure for many bird species (Ricklefs 1969). Populations of many farmland and woodland species are declining (Gregory *et al.* 2004), and additional information is needed concerning the possible role of predation and the role of specific nest predators in such declines. Several techniques have been used in an attempt to identify nest predators. For example, data-logging thermistor probes placed in nest cups provide information about the timing of predation (Flint & MacCluskie 1995, Joyce *et al.* 2001), but cannot identify individual predator species. Image-capture devices do permit identification of nest predators. Image-capture systems vary from simple setups of 35-mm cameras linked to triggers that activate the shutter (Picman & Schriml 1994, Danielson *et al.* 1996, Sawin *et al.* 2003, Anthony *et al.* 2004) to time-lapse video recorders (Pietz & Granfors 2000, Booms & Fuller 2003, Renfrew & Ribic 2003, Thompson & Burhans 2003). Because time-lapse video recorders do not rely on a triggering system, the chances of missing a predation event are small. However, they are often large, expensive, and require frequent maintenance (e.g., replacement of batteries and tapes), potentially limiting the simultaneous deployment of multiple units necessary to obtain large sample sizes. Recent advances in digital camera technology have produced relatively inexpensive, lightweight, reliable systems that require less maintenance. Here we report field tests of a new digital camera with three different activation systems. Our objective was to minimize maintenance and maximize the reliability of image capture and quality during predation events at the nests of Lapwings (*Vanellus vanellus*) and Spotted Flycatchers (*Muscicapa striata*). Both species are the focus of ongoing research to identify causes of population declines in the United Kingdom.

B.3 Methods

B.3.1 Digital device

A new digital device developed in 2004 was field-tested in 2004 and 2005. The image storage unit was based on the Memocam DVR unit (Video Domain Technologies Ltd., Petah Tikva, Israel) that weighed 250 g and was supplied with a metal enclosure unsuitable for outdoor use. This unit was designed for the security industry, but was adapted for use in the field by mounting in a weatherproof box (18 x 11 x 9 cm; IP66, Farnell, Leeds, United Kingdom). The unit stored up to 40 000 low-resolution images on a 256MB multi-media card (MMC), the maximum card capacity that the unit will accept. Images could be downloaded using a card reader that connected directly to the USB port of a PC or laptop.

The Memocam unit is configured using Windows™-based software supplied with the unit. One user-selectable function is the over-write facility, permitting either the recording of additional images when the card is full or the termination of image capture. In over-write mode, the degree of autonomy is determined by power consumption rather than image storage capacity

We used the Video Motion Detection (VMD) facility to record images when activity occurred at the nest. The VMD facility allows users to select specific parts of the image to trigger image capture and allows adjustment of trigger sensitivity. Movement of an incubating bird triggered image capture if the movement occurred in the area(s) of the image selected for VMD and was above the threshold sensitivity selected. We used the lowest sensitivity setting and selected only the area occupied by the nest cup (Fig. 1). The unit was configured to take either three (Lapwing nests) or five (Spotted Flycatcher nests) images each time the camera picture changed significantly at the nest using VMD (up to 101 images per event could be stored). The Memocam software allows capture of the pre-event frame (the image approximately 0.5 s before the trigger event occurred) and this was recorded, together with subsequent images at either 0.5 (Lapwing) or 0.3 sec (Spotted Flycatcher) intervals. The minimum time interval permissible between frame storage was 0.3 s. A delay was then initiated between recordings to reduce duplicated events. This delay feature was software selectable (0-999 sec) and, in our trials, was set to 10 sec for Lapwing nests (on the basis of previous information gained from time-lapse recording). This value was selected in an attempt to minimize image capture (by preventing repeated triggering caused for example by vegetation blowing in front of the nest) without compromising ability to record predation events. The delay was reduced to 5 sec for flycatcher nests because one objective of our study was to record prey delivery by adults to the nest and previous observations indicated that both members of a pair may feed nestlings in quick succession.

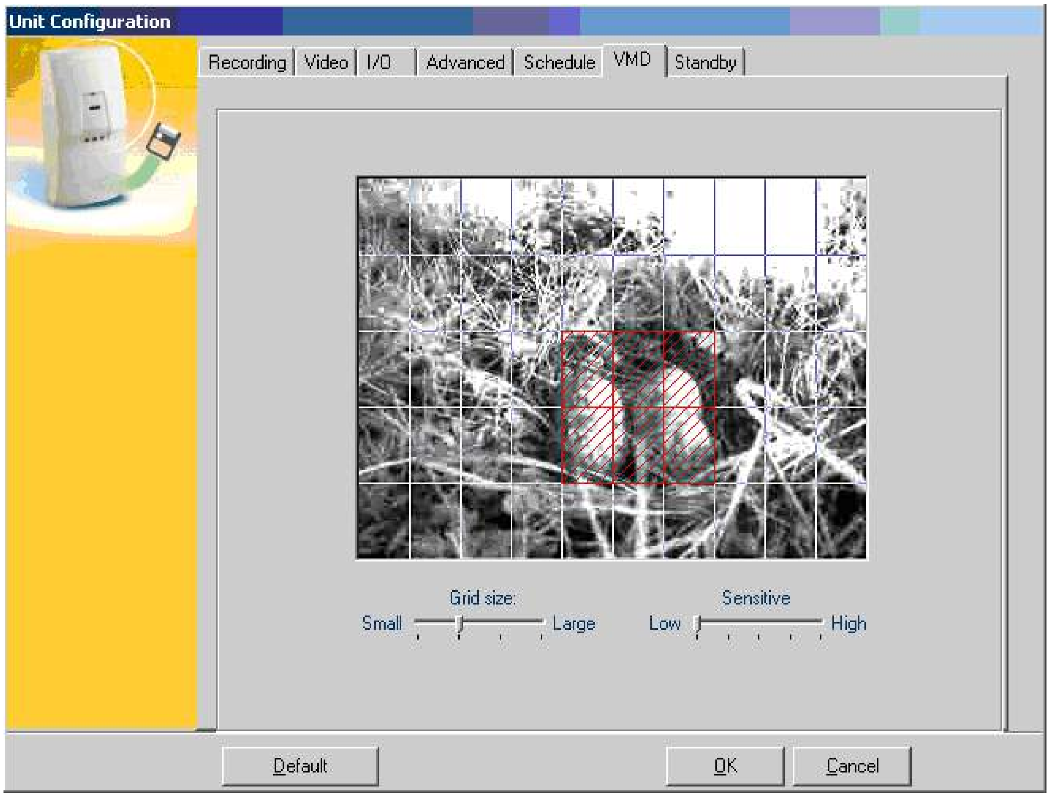

Figure 1. Selection of the nest cup as the "active area" for triggering the Video Motion Detection facility of the Memocam software.

B.3.2 Ancillary equipment

The black-and-white camera used was of low resolution (240 lines) with a 3.6-mm lens (PH86T; Maplin, Barnsley, United Kingdom) that had low current consumption (10 – 20 mA). It was 22 x 14 x 14 mm and six infrared light emitting diodes (LEDs) were attached in an array around the lens to provide illumination at night. The LEDs (TSUS5400) had a peak wavelength of 950 nm, and were connected in series emitting no visible glow. A 24-hour electronic timer (678-340; Farnell, Leeds, United Kingdom) was adapted with the addition of a relay to control the timing of night-time infrared illumination. This could also be done using either a Light Dependent Resistor (LDR) or Photodiode detecting ambient light levels. The camera assembly (3 x 2 x 2 cm) was painted in a camouflage pattern and placed near nests mounted on a suitable support to provide a clear view of the nest. The assembly was connected to the Memocam recording unit and 12V battery by cable (minimum of 5 m) and connectors (EN3 IP68; Switchcraft, Chicago, IL) so larger items could be placed further from the nest. At Lapwing nests in an open landscape, the camera was placed within 1 m of nests. The larger items (Memocam recording unit and battery) were buried underground about 5 m from nests to avoid attracting predators. At Spotted Flycatcher nests, the camera was placed as close as 30cm and as far as 4m from the nest.

B.3.3 Power considerations

The Memocam image storage unit tested in 2004 drew a current of 300 mA for a daily consumption of 7.2 Ah. The camera and infrared illumination required around 1Ah, yielding a total consumption of 8.2 Ah per day. The current consumption of newer Memocam units is as low as 100 mA, with a daily consumption of 3.4Ah if powered continuously. However, if sensors are used as triggers, the unit can be put into standby/sleep mode that reduces consumption to 10 mA in addition to the power used by the sensor circuitry. Although use of a standby facility reduces daily power consumption, rapid and reliable activation is needed to record predation events.

B.3.4 Triggering methods

Three configurations with different triggering mechanisms and using a 12V 38 Ah cyclic battery (Yuasa, Laureldale, PA) were tested at Lapwing nests in 2004. (1) Permanently active. The image capture unit was not set on stand-by mode, maximizing the likelihood of recording a predation event. However, this mode produces numerous images that take longer to review. In addition, the greater power consumption shortened battery life and required maintenance every four days. (2) Passive Infrared sensor. The Memocam was activated from standby mode by triggering of a 5-m spot passive sensor (416-0253; Farnell, Leeds, United Kingdom) mounted on the camera support pole just below the camera and pointed at the nest. Triggering (e.g., by movement of an incubating bird) switched on the Memocam for 2 min and activated the VMD facility. The card configuration was the same as for Configuration 1. A limitation of using the internal VMD with standby mode was an unavoidable 10-s delay between activation from standby and the first image capture via

VMD. From previous work, we found that adult birds generally left nests at least 1 min before arrival of a predator. The predator would then re-trigger the system if 2 min had elapsed, but, if completed within 10 s, predation events would not be recorded. This system required battery replacement about every five days. (3) Infrared beam. An infrared emitter and detector (940 nm) were located at either end of a 500 mm, U-shaped frame and positioned so the beam passed a few centimeters above the eggs. The frame, where the emitter and detector were housed, was hidden under soil with only 50 mm of the vertical frame at each end exposed. Once the beam was broken or completed, the system was activated for 3 min and the unit switched on to VMD. The Memocam was configured as in Configurations 1 and 2 and required battery replacement every seven days.

B.3.5 Field trials

For Lapwings, five camera units were field-tested at three study sites in North Wales from April-July 2004 (Beeches Farm, 52°54′N, 2°30′W; Inner Marsh Farm, 52°53′N, 2°25′W; and Sealand Ranges, 52°52′N, 2°24′W). Predation was the main cause of nest failure, with 47% of nests hatching at least one chick at Beeches Farm, 22% at Inner Marsh Farm, and 18% at Sealand Ranges. One unit was configured to be permanently active (Configuration 1), two units used passive infrared sensors (Configuration 2), and two units used infrared beams (Configuration 3). Lapwing nests were monitored every 1-2 days to determine nest fate and verify the correct functioning of the camera units.

For Spotted Flycatchers, eight camera units were field-tested at nests within a 32-km^2 study area in South Devon from May-August 2005. Five monitored nests were in farmland, three in gardens, and nine in woodland. For flexibility in placing the cameras, two different lenses were tested. In addition to the 3.6-mm (90^o) lens used for the Lapwing nest trials, a 12-mm (25^o) lens (MW69, Maplin, Barnsley, United Kingdom) was used when it was not possible to place the camera within 0.5 m of a nest with leads extended where necessary. In such cases, the night-time infrared illumination was increased to an array of 12 LEDs. These allowed the camouflaged lens unit to be placed either on the same tree as the nest or on an adjacent tree. All camera units were permanently active (Configuration 1). Nests were monitored every three days to determine nest fate and maintain the camera units.

Daily mortality rates were calculated for the period from locating the nest up to successful hatching (for Lapwings), fledging (for Spotted Flycatcher), or nest failure, with data from nests known to have failed being included up to the time of failure. Nest failure or successful hatching was assumed to have occurred midway between the last observation of the intact nest or incubating adult and the visit when the outcome was confirmed. Lapwing nests were considered successful if at least one chick hatched and three nest stages were defined: the "laying stage" when the clutch was found incomplete and further eggs were added, with the assumption that one egg was laid each consecutive day; the "hatching period" when cracks started to appear in eggshells and chicks were heard peeping or tapping inside the egg (which typically lasted two or three days until the chicks hatched), and the "pre-hatching" period between clutch completion and the onset of the hatching period. For Spotted Flycatchers, fledging was defined as when the last chick left the nest.

B.3.6 Statistical analyses

Generalized Linear Mixed Models (Littell *et al.* 1996, SAS Institute Inc. 2002-2003) were used to investigate daily predation rates of Lapwing nests (with binomial error structure and logit link), with site and field as random terms and nest identity as a random term to control for repeated measures of nests and sites. We included field as a random factor to account for variation in levels of predator activity among fields. The nest stage (laying, pre-hatching, hatching) was included as a fixed factor to account for potential differences in predation rate among stages (for example, the calling of unhatched chicks within the eggs may attract predators). In the modelling analyses, both backwards and forwards stepwise regression was undertaken to establish model robustness and terms were added to the model at $P < 0.1$ (forward regression) and omitted from the model at $P >$

0.05. Only significant terms remained in the final minimal models. Two-way interactions terms were included in the modelling procedure. Any over-dispersion in the data was automatically controlled for by SAS procedures and model fit was checked by examining plots of residuals.

B.4 Results

Cameras were placed at 40 different Lapwing nests during the incubation period. For Spotted Flycatchers, cameras were placed at 17 nests (two during nest-building, 10 during incubation, and five during the nestling period).

B.4.1 Problems encountered in the field

Cameras did not operate effectively at high light levels, e.g., at nests in open situations and exposed to full sunlight. At high light levels, images often appeared 'bleached out', preventing the VMD from working reliably. This problem was solved by attaching an infrared filter to the front of the lens at nests in exposed locations. This reduced light intensity during the day, but did not affect night-time images because infrared light was used for illumination.

If the voltage of batteries dropped too low (typically below 6V) when images were being recorded, memory cards were permanently corrupted and all saved images were lost. This problem became evident towards the end of the 2004 season as battery life deteriorated. The addition of a low battery voltage (<10.5 V) switch off circuit resolved this problem before the start of the 2005 season. This improvement has since been incorporated into the latest Memocam units.

B.4.2 System performance

In 2004, cameras activated from standby using an infrared beam (Configuration 3) had the highest failure rate (number of camera failures/nest days deployed; Table 2) of the three systems tested, with a rate of 0.26 failures/nest.day. In three cases, the reason for failure was unknown. Difficulty in correctly aligning the beam across the nest could explain why, in some cases, no images were recorded. This system also took more time to set up than the permanently active or passive infrared systems. At Lapwing nests, the passive infrared system had the lowest failure rate (0.12 failures/nest.day) and the failure rate of the permanently active system was 0.17 failure/nest.day, with 10 of 11 failures due to corrupt MMC cards. In 2005, having resolved the problems of card corruption due to low battery voltage, the daily failure rate was lower (permanently active system; 0.008 failures/nest.day, and both failures due to poor battery connections). No moisture or condensation problems were encountered in any cameras.

We recorded nest failure events at 10 Lapwing nests in 2004. Three predation events were not recorded due to a corrupted storage card (*N* = 2) and a broken LED. At Spotted Flycatcher nests, nine nest failure events were recorded. Two predation events were not recorded due to battery failure and stored images being over-written. Although the 128 MB storage cards held about 16 000 images (dependent on resolution), cards became full and images overwritten at nests where vegetation was constantly moving in front of the nest. At one Flycatcher nest, movement of vegetation caused images to be overwritten every 3 h and so the camera was removed to be deployed elsewhere.

B.4.3 Image quality

Image quality was poor at the start of the field trials (Fig. 2a), but we were still able to identify nest predators. Adjusting Memocam image quality settings and attaching infra-red filters to the cameras lens improved image quality (Fig. 2b).

a. Day-time

a. Night-time

b. Day-time

b. Night-time

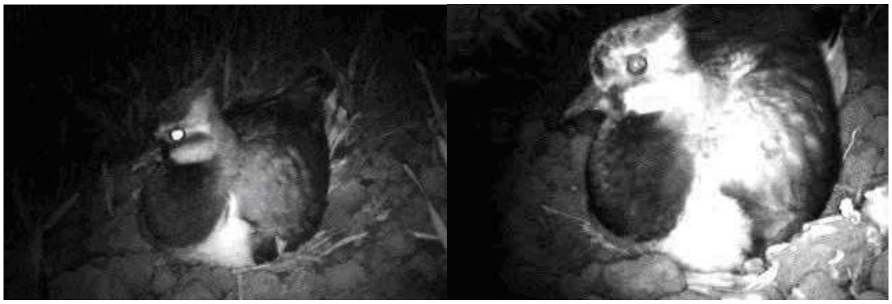

Figure 2. Comparison of day-time and night-time images recorded on cameras at the start of the field trials (a) and towards the end of the field trials (b).

At Spotted Flycatcher nests, cameras placed on the same tree as the nest provided the best quality images. Camera units placed on adjacent trees produced lower quality images, but still allowed identification of nest predators (Fig. 3).

Figure 3. Images obtained at Spotted Flycatcher nests using (a) 12-mm lens with camera placed 4 m from a nest and (b) 3.6-mm lens with camera 0.5 m from a nest.

B.4.4 Effect of cameras on nest survival

At Lapwing nests, daily predation rates were not influenced by the presence of cameras ($F_{1,1359}$ = 1.78, P = 0.18). Similarly, frequency of nest predation did not differ between nests with and without cameras (χ^2_1 = 0.14 P = 0.14). In addition, nest abandonment was infrequent at both nests with cameras (N = 1 of 40) and nests without cameras (N = 3 of 63; χ^2_1 = 0.36, P = 0.55).

At Spotted Flycatcher nests, the presence of cameras had no effect on the frequency of nest predation (χ^2_1=2.39, P = 0.12,). Similarly, we found no difference between the number of nests abandoned at nests with cameras (N = 2) and nests without cameras (N = 4; Fisher Exact Probability Test, P = 0.62).

B.4.5 Predator identification

Four predator species were recorded taking eggs at 10 Lapwing nests, including red fox (*Vulpes vulpes*, six nests, Fig. 3a), badger (*Meles meles*, two nests), sheep (*Ovis aries*, one nest), and Carrion Crow (*Corvus corone*, one nest). Limited activity at nests after predation events meant that no key images were overwritten. However, in two cases, predators took only part of the clutch and Lapwings continued to incubate the remaining eggs. Thus, with partial predation, images identifying predators could be overwritten.

Four predator species were recorded at Spotted Flycatcher nests, including Eurasian Jay (*Garrulus glandarius,* four nests), European Buzzard (*Buteo buteo,* one nest), Great-spotted Woodpecker (*Dendrocopus major*, one nest), and domestic cat (*Felis catus*, one nest). Other species also visited nests, but were not responsible for nest failure. Grey squirrels *Sciurus carolinensis* visited nests during both the building stage and in the period post fledging, but were not recorded at nests with eggs or young. A common shrew (*Sorex araneus*) visited a nest briefly on two subsequent nights, but did not take or damage the eggs. Flycatchers subsequently abandoned this nest before laying was complete.

No signs useful for determining predator identity were found at five of 10 predated Lapwing nests or at four of seven predated Spotted Flycatcher nests. At one lapwing nest where eggs were taken by a badger, the subsequent nest inspection also found evidence of visits by a hedgehog (feces) and red fox (footprints). The other two species may have been attracted to the nest by the smell of egg contents following badger predation.

B.5 Discussion

We found no evidence that the cameras altered predation risk or influenced the behavior of parent birds. Cameras could be installed at a nest site in about 15 min, minimizing disturbance at the nests. In addition, the use of long, camouflaged cables allowed us to change batteries and memory cards some distance from nest sites and, in some cases, without the birds leaving their nests. All three system configurations produced images of sufficient quality to identify nest predators.

Predation events were only missed due the early problem of memory card corruption (2 cases), battery failure (1 case), LED failure (1 case), or overwriting of images (1 case). Overwriting of images occurred only at flycatcher nests when cameras were configured to be permanently active and vegetation triggered the system when blown by the wind in front of the nest.

Advantages of the passive infra-red system included the recording of fewer images (and, therefore, longer battery life), cards had to be changed less frequently, and there was less chance of overwriting images of predation events. However, the infra-red beam system was the least reliable system. The failure of this system, in some cases, to record images was probably due to the difficulty of correctly aligning the beam across the nest. When there was a lot of vegetation around a nest or a nest was on uneven ground, it was more difficult to align the two sensors necessary for the completion of the beam. Because of the extra wires needed for the beam sensor, this system was also more fragile and prone to failure. Overall, the infra-red beam system was more time-consuming to set up, involved more disturbance around the nest than the other two systems, and could only be readily installed at nests on the ground.

B.5.1 Latest developments

Advances in the specifications of the recording system have taken place over the two years of development and deployment reported here. Power consumption of the Memocam DVR recording unit has dropped from 280mA to 150mA. A model (DV58) is now available that uses Secure Digital (SD) cards rather than MMC, which only consumes 100mA and stores images at 0.1 sec intervals. Up to 300 000 images can be recorded with this unit on cards with capacities up to 2GB, eliminating the risk of overwriting a partial predation. In addition, this model can record images within 0.3 s of activation from standby mode and at 0.1 s intervals thereafter. The timing of first image capture and activation period is now user-selectable within the Memocam software so no external timing hardware is required. With such a fast activation time, the use of an external sensor to activate the system from standby should not compromise the system's capability to record even the most rapid predation event. Although designed for monitoring predation, the system can also be utilized for many other remote monitoring applications such as incubation behavior, determining provisioning rates, and identification of prey delivered to nestlings (Fig. 3b).

B.6 Acknowledgements

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Appendix C

Plastic colour rings and the incidence of leg injury in flycatchers (Muscicapidae, Monarchidae and Dicruridae).

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Plastic colour rings and the incidence of leg injury in flycatchers (Muscicapidae, Monarchidae and Dicruridae).

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C.1 Summary

Studies of birds involving colour-ringing can provide much detailed information concerning bird movements and behaviour without the need for recapture. However, a fundamental premise of colour-ringing, and indeed all ringing studies, is that the rings applied should neither cause harm to the birds concerned, nor alter their behaviour or survival. Colour rings have been used safely for many studies on a wide range of species, and problems are rarely reported. Here, we report on problems associated with colour-ringing several species of flycatcher, and discuss the nature and extent of the issue. Unacceptable levels of leg injury were reported when flycatchers were ringed using either celluloid or PVC colour rings, particularly when the colour ring was proximal to the foot. In light of our evidence, we would urge those considering embarking upon colour ringing projects involving flycatchers to consider using anodized aluminium colour rings and avoid the use of plastic colour rings.

C.2 Introduction

Techniques involving the catching and marking of birds, and the subsequent monitoring of marked individuals have been safely and successfully used for many years to provide information on the movement, population dynamics and behavioural ecology of a wide range of species. As ringing (banding) techniques have developed they have been widely deployed to help identify causes of population decline, thus informing targeted population recovery programmes, including conservation efforts for threatened species. Colour-ringing (using plastic or metal coloured rings) is a particularly useful technique, as it allows individuals to be recognised without the need for recapture, vastly increasing the potential for monitoring bird movements and behaviour (Evans *et al.* 1997, Hole *et al.* 2002, Field & Anderson 2004, Salewski *et al.* 2007), but see Calvo & Furness (1992).

Although certain species may respond adversely to capture and handling (e.g. haemorrhaging in finches (Redfern & Clark 2001), and leg cramp in waders; (Bainbridge 1975)), ringing has fortunately been shown to carry an extremely low risk of injury (Marion & Shamis 1977, Redfern & Clark 2001), and little or no effect on subsequent return rates, even in intensively studied populations (Perkins *et al.* 2004, Cresswell *et al.* 2007). When injuries do occur, it is usually possible to identify a specific cause. For instance, in some species, injury may be caused by the specific structure (Common Tern Sterna hirundo, Nisbet 1991) and/or behaviour (North Island Robin Petroica longipes, Berggren & Low 2004) of the species under study. Alternatively, injury may be caused by the use of rings of an inappropriate size. If the ring is too large, or opens up after being fitted, it may slip over the foot, resulting in injury to the tarso-metatarsal joint or the foot. If it is too small (Gratto-Trevor 1994), or becomes constricted because of accumulated mud (Amat 1999), ice (MacDonald 1961) or faecal matter (Henckel 1976) around it, injury or even foot loss may result from the restriction of blood flow.

Most published evidence of injury resulting from leg ringing concerns metal rings. The incidence of injury caused by coloured plastic rings in passerines is less often reported. Sedgwick & Klus (1997) described injury resulting from a ringing program of Willow Flycatchers (*Empidonax traillii*), which involved problems with coloured plastic rings being used in combination with metal rings. More recently, Splittgerber and Clarke (2006) identified ring-related injuries in colour-ringed Bell Miners (*Manorina melanophrys*). Here we report on injuries to the legs of several species of flycatchers fitted with both metal and plastic colour rings. We consider possible reasons for the injuries and recommend strategies to minimise the risk.

C.3 Methods

Evidence for this paper was gathered from a number of ongoing studies involving different flycatcher species from widespread geographical locations. In all cases, the plastic colour rings used were split celluloid or Darvic (PVC) obtained from A. C. Hughes Ltd., Hampton Hill, Middlesex, UK. The size used was XF, height 4 mm, internal diameter 2.3 mm. Numbered anodised colour rings used in these studies were of the same dimensions as XF plastic rings and were also obtained from A. C. Hughes Ltd.

C.3.1 Black-naped Monarch (Hypothymis azurea), Thailand

Work was carried out as part of a long-term study monitoring bird populations and ecology on the 30 ha Mo-singto permanent forest plot, Khao Yai National Park, Nakhon Nayok Province (14° 26′ N, 101° 22′ E). The plot was situated in mature, seasonally-wet evergreen forest at 723–817 m elevation (Brockelman 1998). During 2003 – 2004 a total of 20 adults and 12 nestlings were ringed. Adults were ringed with a single aluminium ring as issued by the British Trust for Ornithology (BTO) ringing scheme (size AA, height 5.5 mm internal diameter 2.0 mm) on one leg and two plastic rings on the other. Nestlings were ringed with a single plastic ring on one leg and one or two plastic rings on the other leg. The plastic rings used were a mixture of both celluloid and Darvic, and were not sealed. During 2005 nine adults and three nestlings were ringed with only one anodized ring on each leg. Anodised aluminium rings (equivalent to BTO size AA), provided by Porzana Ltd., Icklesham, E. Sussex (but anodised locally), were also used, thus increasing the available colour combinations. Birds retrapped from 2005 onwards had their plastic rings removed and those without injuries were fitted with anodized rings. Although problems with availability of small sized plastic rings resulted in birds being fitted with plastic rings of a larger internal diameter than the BTO issued aluminium rings, they did not slip off or restrict the foot, nor could they move above the inter-tarsal joint.

C.3.2 Madagascar Paradise Flycatcher (Terpsiphone mutata), Madagascar

Work was carried out as part of an intensive research programme looking at ornamentation and symmetry. The research was based in the Bealoka Reserve, southern Madagascar (23° 75′ S, 46° 15′ E). The 120 ha reserve covers an area of dry gallery forest along the Mandraré River. Between June 1993 and June 1994, 106 birds were ringed using three rings in combination (metal above plastic on one leg, one plastic ring only on the other). The metal rings were split aluminium rings of size 01 provided by the Australasian Bird and Bat Banding Scheme (ABBBS), height 6mm, internal diameter 2.2 mm. The plastic rings were celluloid and were all sealed using acetone. In August 1996 ringing recommenced using a different method, replacing the ABBBS metal ring with anodized metal rings. This reduced the overall height of the rings on the leg carrying two rings from 10 mm to 8 mm, leaving more of the tarsus (length about 13 mm) uncovered. These rings were made from slightly thicker material and appeared less sharp at the edges than the ABBBS-issued rings. Birds captured between August and November 1996 were fitted with either a single metal ring on one leg and a single plastic ring on the other (n=21), or with a single metal ring on one leg and two plastic rings on the other leg (n=70). From July 1997 only anodised coloured metal rings were used, with a single ring fitted on each leg. However, since this would offer insufficient combinations, starting in October 1997, single-colour plastic rings were cut in half so that they were only 2 mm in height, and these were used in a combination in which a metal ring was used on one leg, and a half-plastic ring over a metal ring on the other. Since July 1997 a total of 256 adults and 860 nestlings have been ringed with this method.

C.3.3 Spotted Flycatcher (Muscicapa striata), United Kingdom

Work was carried out as part of an intensive three-year autecological study. The study area in Devon (centred on the parish of Aveton Gifford in the South Hams area, 50° 18′ N, 3° 50′ W) covered approx 3200 ha, of which c. 2670 ha was farmland, 160 ha woodland and 111 ha of villages and rural gardens. Fifty adult birds were fitted with combinations of metal rings (size A, height 5.5 mm, i.d. 2.3 mm) supplied by the BTO ringing scheme, and Darvic (PVC) colour rings in 2004 & 2005. The Darvic colour rings were not sealed, but all were checked for correct closure. Two colour rings were applied to the left leg, with the BTO metal and colour ring on the right leg, the colour ring being placed in both proximal and distal locations over the course of the study. In 2006 22 adult birds were marked with a single anodised aluminium colour ring on one leg, and a BTO metal ring on the other.

C.3.4 Pied Flycatcher (Ficedula hypoleuca) and Black-headed Paradise Flycatcher (Terpsiphone rufiventer), Ivory Coast

Work was carried out as part of a joint project of the Institute for Avian Research, Vogelwarte Helgoland in Wilhelmshaven, Germany and the Max-Planck Institute for Ornithology, Vogelwarte Radolfzell, in Radolfzell, Germany, investigating the wintering ecology of Palearctic passerine migrants in Africa. It was performed in the Comoé National Park in north-eastern Ivory Coast (8° 45′ N, 3° 49′ S). 115 Pied Flycatchers were fitted with one or two colour rings (celluloid) on one leg, with a metal (diameter 2.3 mm) and a colour ring on the other leg. Additionally, 58 Paradise Flycatchers were fitted with one or two (celluloid) colour rings, but were not ringed with a metal ring. The colour rings were not sealed. When a colour ring was used together with a metal ring the colour ring was always distal to the foot.

C.4 Results

C.4.1 Injury rates

The rate of injury in colour-ringed individuals was not straightforward to compare since not all ringed individuals were sighted with equal frequency, and many were never re-sighted. Additionally, injury may not be visible without direct, physical examination of birds in the hand, particularly in the early stages. Where the number of birds re-sighted or re-captured was known, it was therefore more appropriate to calculate rates of injury from these figures, rather than the total number of birds ringed. Overall, injury rates of birds colour-ringed before any remedial action was taken ranged from 13.2% to 35.3% (Table 1). Rates of leg injury noticed in unringed birds were much lower, ranging from 0% to approximately 2% (three out of approximately 150 unringed individuals, RM unpublished data). Of the 1295 legs bearing only a metal ring that were checked, only three showed signs of injury. All of the injured Spotted Flycatchers were female (n=4).

Table 1. Injury rates of birds colour-ringed in the four studies. For ring combinations, M = metal ring (plain or anodized), C = plastic colour ring. Where figures for resighting are available, the injury rate is calculated from on the number of birds resighted, where not recorded (-) the injury rate is the percentage of birds ringed. Species codes used: MAPFL Madagascar Paradise Flycatcher, BLAMO Black-naped Monarch, SPOFL Spotted Flycatcher, PIEFL Pied Flycatcher, BLPFL Black-headed Paradise Flycatcher.

Species	Year	Ring combination		Number of birds		Total no. of injuries observed for ring combination		Rate (%)
		Leg 1	Leg 2	Ringed	Resighted	Leg 1	Leg 2	
MAPFL	93-94	C	M/C	106	-	3	11	13.2
MAPFL	96	C	M	21	-	3	0	14.3
MAPFL	96	C/C	M	70	-	19	0	27.1
MAPFL	97-04	M	C/M	1116	-	3	10	1.2
BLAMO	03-04	C/C	M	20	17	6	0	35.3
BLAMO	05	M	M	12	6	0	0	0
SPOFL	04-05	C/C	M/C	50	24	3	1	16.7
SPOFL	06	M	M	22	-	0	0	0
PIEFL	94-98	C/C	C/M	115	21	2	0	9.5
BLPFL	94-98	C/C	-	58	6	1	-	16.7

C.4.2 Systematic patterns in injury associated with colour rings

In most cases the injury seemed to occur on a leg on which a plastic ring had direct contact with the foot, particularly when there were two rings on the leg (a plastic ring in combination with either another plastic ring or a metal ring). However, it was not possible to test this data statistically since during the course of the four studies, different combinations of rings were utilised, some birds were ringed and not resighted and others were seen repeatedly for many years. Additionally, most observations were made coincidentally and were not planned within the framework of the respective research projects. A small number of injuries were recorded on legs with only metal rings (Table 1). Injuries occurred in birds with either sealed or unsealed plastic rings.

C.4.3 Onset of injury

For all the species, most individuals developed the injury between six months and two years after ringing. Indeed, many of the individuals later found with injury had been recaptured in the interim period and had shown no signs of injury, confirming our belief that injuries were not immediate. Based on census and capture data, onset of injuries in Madagascar Paradise Flycatchers took between seven weeks and six years to occur. When birds were observed in the field with leg injuries, and could be recaptured, rings were removed. These birds recovered well from their injuries, some making a complete recovery and being observed injury-free for at least six months after the injury disappeared, with no apparent ill effects.

C.4.4 Description of injuries

Leg damage ranged from an accumulation of shed scales on the tarso-metatarsus (n=2, 3.2% of all injuries), and signs of necrotic skin, through to swellings above and/or below the rings (n=53, 85.5%), and finally to complete amputation of the foot (n=7, 11.3%; Fig. 1). All birds were in an otherwise healthy condition, with no apparent loss of body condition. In most individuals, a large swelling formed over the foot, underneath and inside the ring, similar in appearance to avian pox swellings (RM, pers obs.). The ring constrained the growth of the swelling, which led to deformation and subsequent loss of the foot. The usual site for the swelling was around the 'ankle' (tarso-metatarsal joint), below the lower colour ring and proximal to the foot, although there was also some lesser swelling between the rings and above distal rings. It seems likely that all early stages of leg injury would have developed into the more serious injuries had the rings not been removed.

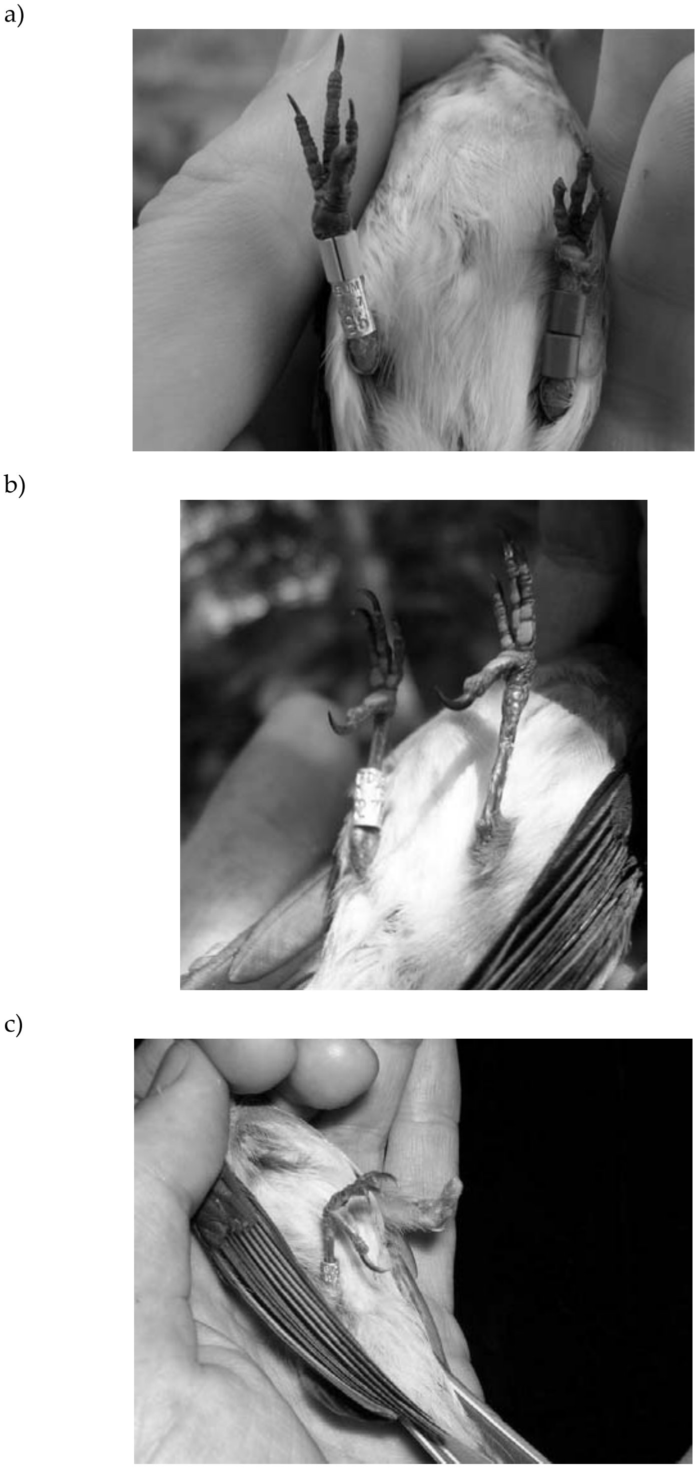

Figure 1. Photographs showing the types and various stages of injuries encountered, from a) injury visible in field on left leg below the white plastic ring, b) early stages of leg injury (colour rings removed from left leg) through to c) extreme injury results in amputation of the foot.

The injuries mainly hampered the bird's ability to perch comfortably, and individuals with injuries characteristically fluttered for balance when descending on a perch. Several birds nevertheless managed to breed successfully despite having damaged or amputated legs. It is not believed that injured birds had higher resighting probabilities since data reported here were collected during the course of intensive research projects involving the location of all birds within a specific area.

C.5 Discussion

Data presented here on colour-marked flycatchers suggests that plastic colour rings were more likely to cause infection/injury than metal rings, particularly when proximal to the foot or when two rings are fitted to the same leg. Although injuries were recorded in birds ringed only with metal rings, we believe that this was comparable to the incidence of injury recorded in unringed birds (RM unpublished data) and we thus remain convinced that it was the colour rings which were problematic, not the metal rings. Similar conclusions have been reached by others reporting comparable injuries (Sedgwick & Klus 1997, Splittgerber & Clarke 2006). Sedgwick and Klus (1997) proposed that leg injuries in ringed Willow Flycatchers were caused by irritation of the tarsus, due to friction between the leg and sharp edges on the plastic colour rings. Continued irritation may lead to infection, swelling and ultimately, amputation. Splittgerber and Clarke (2006) suggested that the main factors influencing the chance of injury were the smoothness of the internal surface of the ring (plastic rings being more pitted and generally rougher than metal rings) and the material from which it was made (plastic generating more static electricity than metal). They went on to suggest that both factors affected the likelihood that tarsal scales shed from the leg would accumulate inside the band and that smooth surfaces decreased the probability of scales adhering to the band, while materials such as plastic increased the probability of adherence. Therefore, Splittgerber and Clarke (2006) concluded that injuries were more likely to develop in rings that were a closer fit. The close fitting of rings is unlikely, however, to be a factor with flycatchers. In the species studied and reported on here, the tarsus is relatively narrow in proportion to the internal diameter of the colour ring, and the 'ankle' is very thin compared to most passerines.

During the course of the Black-naped Monarch research, birds were fitted with plastic rings of a larger size than the metal rings and were a looser fit, yet they still suffered a high rate of injuries. Significantly, this is contrary to the findings of Splittgerber and Clarke (2006) who found leg injuries in Bell Miners which had colour rings that were of a tighter fit than the metal rings. This therefore suggests that the injuries are more likely caused by the material than the size of the ring. During 2003 – 2005 a total of 123 individuals of five other species were fitted with same size and combination of rings as Black-naped Monarchs. Forty-three of these, including five returning Palearctic migrants, were recaptured and examined in the hand but none showed any sign of leg injury.

Birds moult tarsal scales on a regular basis (Storer 1952), but whether this occurs as a continual process or annually under the influence of endocrine cycles is unknown. Whitaker (1957) reported that Lark Sparrows (*Chondestes grammacus*) use the secretions from the uropygial gland to oil their tarsal scales, and Elder (1954) reported that when the uropygial gland on ducks was experimentally removed, skin on the legs became cracked and dry. Because rings hamper access to the scales, it is possible that they make regular maintenance and oiling of tarsal scales more difficult, which may increase the rate at which scales are shed. Furthermore, *in vitro* experiments have reported that secretions from the uropygial gland inhibit bacterial growth (Bandyopadhyay & Bhattacharyya 1996, Jacob *et al.* 1997, Law-Brown 2001). If this is the case *in vivo*, reduced opportunities for preening and oiling of metatarsal scales due to the presence of rings may mean that the scales are less often exposed to both the moisturising and anti-bacterial properties of preen oil. This might compound any problem of scale build-up inside the rings and increase the chances of leg injury through subsequent infection. In the case of flycatchers, the addition of more than one ring to what is a relatively short tarsus will leave little room for the rings to slide up and down the leg. However, it is interesting that we also observed leg injuries in unringed birds (albeit at much lower frequency), which may also suggest that colour rings may have increased the occurrence of a naturally occurring infection.

Although the mechanical causes of injury described above are entirely plausible, they do not help to explain why certain species should be more susceptible to infection and injury. In two of the studies reported here (AP, Thailand and VS, Ivory Coast), over 1,500 birds of more than 85 species were colour-ringed and observed over the same time periods without similar incidence of associated leg injuries. Indeed, despite the widespread use of colour marking, leg injuries have been reported only in a handful of species (Sedgwick & Klus 1997, Dettmann 1999, Splittgerber & Clarke 2006). Splittgerber and Clarke (2006) also highlighted several other (unpublished) cases involving intensive studies on particular species (Helmeted Honeyeater *Lichenostomus melanops*, Leaden Flycatcher *Myiagra rubecula* and thornbills *Acanthiza* spp) where leg injury associated with colour ringing has been reported. Colour rings are widely used by both amateur and professional ornithologists for the study of birds without the need for recapture. Apart from extreme cases of amputation, many of the instances of leg injury reported here were only visible upon direct physical examination of the bird in the hand. It is possible that other instances go unrecorded because the deployment of colour rings negates the need for birds to be recaptured. That some species appear to be more susceptible to injury than others, and that injury does not manifest itself immediately, highlights the requirement for regular monitoring of colour-ringed birds for signs of injury. It may be that there is something in the morphology or behaviour of birds in the Muscicapidae and closely related Dicruridae families (and perhaps even the Tyrannidae flycatchers of the Americas), that causes them to be particularly susceptible to damage by plastic rings. This could explain the largely anecdotal evidence that a great many other species of birds are colour ringed apparently with no adverse effects (and see also for e.g. Perkins *et al.* 2004, Cresswell *et al.* 2007). At present, we have no compelling morphological, ecological or behavioural explanation for the prevalence of such injuries in flycatchers.

Sedgwick & Klus (1997) reported that the incidence of leg injury was greater in female Willow Flycatchers than males, and we observed the same pattern in at least one species in this study (Spotted Flycatcher), albeit anecdotally. This apparent sex bias is similarly difficult to explain. Both Willow and Spotted Flycatchers have similar behavioural traits during breeding, with the females taking a more active role during the breeding season, nest building and incubating, but this offers no obvious explanation as to why leg injury rates should be different from that observed in males. Interestingly, there was no observed sex bias to the incidence of injuries in Black-naped Monarchs, a species where males and females tend to take equal roles in the breeding season. Although these observations are supported by only anecdotal evidence, they are perhaps worthy of further study.

C.6 Conclusions & recommendations

Since substituting anodized metal rings for plastic rings we recorded no further injuries in both Black-naped Monarchs and Spotted Flycatchers (Table 1), and the incidence of injury in Madagascar Paradise Flycatchers was reduced to a level comparable with that observed in unringed individuals (in the order of two individuals a year in a population of around 200 adults). Clearly, any researcher wishing to commence a colour-ringing study on flycatchers should avoid using plastic colour bands. We recommend the use of single anodised aluminium colour rings in place of either celluloid or PVC (Darvic) plastic rings. Because of the use of a single ring, this does reduce the number of colour combinations available, but Koronkiewicz (2005) reported on a method to overcome this by making striped anodized colour rings. If plastic rings are to be used, we recommend placing them above metal rings (i.e. distal to the foot) and not placing two colour rings together.

It is important to stress again that plastic colour rings have been used in many studies worldwide without incidence of injury, and they remain a useful tool in ecological studies of birds. Occasional accidents and injuries due to handling and ringing may be inevitable but should be kept to a minimum for ethical reasons, to avoid errors and bias in data collection, and to avoid affecting populations of rare species. Where an adverse number of injuries occur, changes to the methods should be implemented immediately and the problem reported promptly to the relevant ringing regulatory authority and/or the ring supplier. Potential effects of injury may be minimised by detecting injuries at an early stage, recapturing affected individuals and removing rings from the injured leg. Any project targeting a rare species would be wise to undertake preliminary studies on a more common, taxonomically and physically similar species beforehand, to avoid potential problems.

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