Investigating the causes of the decline of the urban House Sparrow *Passer domesticus* population in Britain

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ABSTRACT

In Britain and parts of northwest Europe, House Sparrow *Passer domesticus* populations have declined markedly in urban-suburban landscapes since the mid-1980s. Little is known about the demographic mechanisms or environmental causes of these population declines, although lack of winter seed has been implicated as a cause of the decline in House Sparrow numbers on English farmland (Hole, 2001). This study focused on factors affecting nesting success and annual productivity of nesting House Sparrows along an urban-suburban-rural gradient centred on the city of Leicester, England. Chick diet (inferred from faecal remains), habitat selection by foraging adults and over-winter survival were also studied.

Data were collected during 2001-2003 from 9 study areas spread along the urbanisation gradient. Most sparrows in most study areas nested in or close to domestic gardens. Counts of territorial males declined by 28% between 2001 and 2003, with the largest declines in rural villages (25%) and suburban fringe (16%) and a small increase (4%) in the urban centre.

Annual productivity (the estimated number of fledged young/pair/year) was 25% lower in suburban areas and 18% lower in rural areas than that measured during a recent study of farmland House Sparrows in Oxfordshire. The main cause of this lower productivity was starvation of chicks, (usually the first 5-6 days after hatching) during June and July.

Chicks were more likely to starve if their diet contained a high proportion of vegetable material (mainly supplementary food) or ants, and less likely to starve if their diet contained a high proportion of spiders. The number of young sparrows successfully fledging, and the aggregate chick biomass, per nesting attempt were greater in home ranges containing relatively high proportions of deciduous shrub, trees and grass, and relatively little concrete. During June and July 2003, more young fledged from home ranges containing a higher density of aphids. Dipteran prey (Tipulids and other flies) constituted a higher proportion of the chick diet in rural localities than in urban-suburban localities, while Homopteran prey (mainly aphids) constituted a higher proportion of chick diet in urban-suburban localities.

After allowing for effects of weather, nestling body mass and condition were negatively correlated to local levels of nitrogen dioxide air pollution. Since body mass at fledging is known to be a good predictor of immediate post-fledging survival, I predicted that the lower average body mass at fledging among suburban broods (compared to rural broods) would result in lower survival during the first 10 days after fledging (57% for suburban fledglings, compared to 70% for rural fledglings). The combined effects of lower annual productivity and lower predicted post-fledging survival in suburban localities were large enough to result in rapid predicted population decline, given plausible annual survival rates of adults and first-year sparrows and no net immigration. Under the same set of assumptions, productivity and predicted post-fledging survival were high enough in rural localities to maintain and even increase adult population size.

Deciduous shrubbery, grassy areas and concrete were the main summer foraging habitats of suburban and rural House Sparrows, with trees being heavily utilised in 2003. Ornamental and evergreen shrubs were strongly avoided by foraging sparrows.

Stable isotope ratios of nitrogen ($\delta^{15}N$ scores) in chick feathers are proposed to constitute a useful integrated measure of the quality of the chick diet. $\delta^{15}N$ scores differed markedly between the vegetable (2.7), herbivorous invertebrate (4.7-6.4) and carnivorous invertebrate (7.1-7.7) components of chick diet. $\delta^{15}N$ scores in sparrow chick feathers averaged 7.7

suggesting that the average $\delta^{15}N$ score of ingested diet was approximately 4.7 (i.e. was probably dominated by vegetable material and herbivorous invertebrates). Feather $\delta^{15}N$ scores were lower in home ranges containing relatively large areas of concrete and evergreen vegetation, and were a positive predictor of chick growth rate and body condition.

The data presented in this thesis suggest that the abundance of invertebrate prey within home ranges of House Sparrows breeding within suburban and rural garden habitats limits the quantity and quality of chicks raised to fledging. The combined effects of relatively high rates of chick starvation and low body masses at fledging (and consequently low post-fledging survival) observed in suburban localities are large enough to result in rapid population declines. Invertebrate abundance in suburban areas is probably determined, at least in part, by the availability of suitable habitat including native deciduous shrubbery, tress and grassland. Although there is no evidence that the abundance of key invertebrate prey have declined in urban-suburban landscapes, such declines do provide a plausible mechanism for the observed declines in urban-suburban House Sparrow populations. Management techniques, which increase densities of key invertebrate prey during summer, have the potential to increase the annual productivity and possibly the breeding densities of House Sparrows in urban-suburban landscapes.

DEDICATION

Janet Linda Vincent

1949 - 2005

This thesis is dedicated with love to the memory of my Mum, who instilled in me the drive and determination to follow my dreams and pursue my goals and realise my full potential. Thank you for your enduring encouragement throughout my life. I hope I have made you proud.

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‘The spirited horse which will try to win the race of its own accord, will run even faster if encouraged’ - Publius Ovidius Naso

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CONTENTS

CHAPTER 1

General Introduction

1.1 Thesis aim and objectives

The House Sparrow *Passer domesticus* is one of the most widespread and abundant birds in the world (Summers-Smith, 1988). This thesis aims to establish why a species that historically has been so common is now dramatically declining in some suburban areas of the UK. It aims to quantify important demographic parameters such as productivity and survival across urban, suburban and rural habitats.

The status of House Sparrow *Passer domesticus* populations across a number of study areas within Leicester was investigated (Chapter 3), as there is little quantitative information documenting changes in numbers in urban-suburban habitats. Chapter 4 highlights the factors affecting the diet of House Sparrow nestlings in rural and suburban habitats, as detailed knowledge of diet is critical to the study of avian biology.

The factors affecting the breeding performance and productivity in rural and suburban habitats was also examined (Chapter 5), as the estimation of reproductive success is fundamental to the understanding of the causes of animal population declines. Using the biometric data collected when handling the chicks, the factors affecting body condition of nestlings were assessed to examine their relationship to the suburban and urban environment (Chapter 6). To gain an even deeper understanding of nestling diet and its relationship to chick condition, the analysis of stable isotopes in chick feathers was used to establish an indirect measure of the quality of nestling diet (Chapter 7).

In Chapter 8, the availability of suitable foraging habitat and the habitat composition within urban and suburban areas was investigated, with reference to utilisation and selection by foraging fully-grown House Sparrows. To gain a comprehensive insight into why this species might be declining all aspects of its life-cycle and not just its breeding biology was investigated. Therefore in Chapter 9, over-winter survival of fully-grown birds was investigated using mark-resighting methodology at two study areas (one rural and one suburban).

This introduction provides a broad overview of the general themes that are present through this thesis and is arranged in three main parts: i) the urban environment; ii) an introduction to the House Sparrow and details of its decline in urban areas; iii) a discussion of potential factors that could be contributing to the decline;

1.2 The urban environment

Mankind is a rapidly increasing, social species whose industrial abilities allows the colonisation of virtual wilderness and the building of sprawling metropolises. We live virtually everywhere on Earth and wherever we settle we significantly transform the natural habitat. Human populations are becoming increasingly urban. In 1700, only 14 cities with populations of more than 200,000 people existed (Marzluff, 2001). By 1900, 42 cities on four continents had such populations, and by 2000, 171 cities on five continents had populations greater than 200,000. In 1900, only 10% of humans lived in cities; by 2000 nearly 50% did and nearly 70% are expected to do so by 2050. Thus by 2050 nearly as many humans are expected to live in cities (6.5 billion) as occupy all of Earth today (Marzluff, 2001).

Urban areas often appear as a dense, highly developed core, surrounded by irregular rings of diminishing development. Therefore the gradient paradigm is a powerful organising tool for ecological research on urban influences on ecosystems. Like natural environmental gradients, urbanisation presents ecologists with a rich spatial array to explain or predict environmental and ecological effects. The study of bird ecology and urbanisation is an under-utilised area of ecological research, but one of increasing importance given the extension and magnitude of anthropogenic effects today (McDonnell and Pickett, 1990).

Urbanisation has complex direct and indirect effects on native flora and fauna. With respect to birds, Marzluff (1997) suggested that settlement can change ecosystem processes, habitat, food, predators and competitors, and disease. These effects lead to significant changes in the population biology of birds in urban areas with resulting effects on the structure and composition of bird communities (Marzluff, 2001).

Urban gardens are likely to become increasingly important to conservation as the urban landscape deteriorates, as they are arguably the main contributor to urban biodiversity in many developed countries (Cannon, 1999). Chamberlain *et al*. (2004) have shown that the likelihood of many bird species occurring in gardens is dependent on the surrounding local habitat rather than the garden habitat. This implies that if there is a continuing degradation of the urban environment then further declines in urban bird populations will increase.

Research in southern California has focused on the effects of urbanisation on bird populations residing in natural habitat adjacent to or embedded in the urban matrix. Bolger (2001) found that the distribution and abundance of a number of bird species in this region suggested sensitivity to patterns of urban-induced fragmentation and edge. In this study Bolger (2001) found that arthropod communities change substantially with urban exposure, but an understanding of the trophic effects of fragmentation is hindered by the lack of basic autecological data on bird foraging and diet, including adult and nestling food. Urbanisation is likely to directly affect arthropods, the primary food for many birds, especially during reproduction, yet studies of the effects of urbanisation on arthropods are few (McIntyre, 2000).

To gain a fuller understanding of the effects of urbanisation on avifauna, Bolger (2001) recommends considering avian population, community and landscape ecology across a gradient of urbanisation. The design of ecological studies along urban-rural gradients is important in addressing basic ecological questions (McDonnell and Pickett, 1990). Urbanisation can create a complex environmental gradient, from undisturbed natural areas to highly-modified urban landscapes, that can be useful in exploring relationships between environmental heterogeneity and the diversity and abundance of species (McDonnell and Pickett, 1990). Local bird abundance, demographic rates, and ecological processes may be a function of the larger urban landscape (Bolger, 2001). Therefore studies of foraging, breeding, competition and predation of avian species need to be carried out along this gradient, in order to compile the complete picture and reveal the key functional elements of an urban landscape and the bird communities within it (Bolger, 2001).

Urban landscapes have a large impact on avian communities. It is characteristic of urban bird communities that from three to five species are dominant such as the House Sparrow, the Feral Pigeon *Columba livia*, the Blackbird *Turdus merula* and the Starling *Sturnus vulgaris*. Researchers have reported higher bird densities in urban areas than in natural areas, with bird diversity decreasing and avian communities being dominated by a few species (Huhtalo and Jarvinen, 1977; Bland, 1979). Huhtalo *et al.*, (1977) found that in the cities of Tornio and Helsinki in Finland, there were eight species and three species respectively that were dominant. Whereas Bland (1979), found that the city of Bristol had seven species that were dominant, of which the House Sparrow was the most abundant.

Of the studies that have been conducted on birds in urban areas many have concentrated on how habitat structure affects avian abundance, composition and richness. In most cases, these studies measured habitat structure at one scale. However different species probably respond to habitat at different scales, and single-scale studies may not adequately reflect what many species are responding to in a landscape (Hostetler, 2001).

We are beginning to understand how habitat features relate to bird abundance and diversity in urban landscapes. Research has been undertaken on the population dynamics of suburban Blackbirds in southern England to understand what determines the level of a population in this habitat. Batten (1973) found that Blackbirds had better breeding success in suburban than rural areas, but this difference was compensated by differential survival, so that both populations were balanced in the longer term. Studies at various locations in Europe have shown that nest-box populations of tits in urban habitats produce fewer eggs and fledglings than do birds in rural (Cowie and Hinsley, 1987; Solonen, 2001). Cowie *et al.* (1987) found that suburban tits suffered a reduction in breeding success, rearing half as many young as populations in woodland. Despite the additional supply of supplementary food in surburban gardens, nestling mortality through starvation was very high, perhaps due to the unsuitability of the foods provided (Cowie and Hinsley, 1987). Solonen (2001) found that urban tit populations laid fewer eggs and had lower fledgling production than their rural counterparts. This suggests that breeding conditions for tits were less good in urban areas (Horak, 1993; Solonen, 2001).

This type of research is essential to understanding the external limiting factors that have an impact on reproductive and mortality rates on species in this distinctive habitat. Advances in these areas are required if we are to foster self-sustaining bird communities with a greater proportion of native species and contribute to the quality of urban life for humans (Savard and Falls, 2001).

1.3 The House Sparrow

The House Sparrow is a member of the family Passeridae and it is one of the larger sparrows, with a length typically of 160-165mm and a wingspan of 210-255mm (Summers-Smith, 1988). It is a rather large headed, heavy billed, robust passerine. The sexes are dimorphic with the male being boldly patterned. The male is warm brown above, with a grey crown and nape. It has grey cheeks and grey underparts with black round the eyes. The mantle and scapulars are boldly streaked black, chestnut and buff and the tail is dark brown. The bib has black feathers with white tips that are gradually abraded so that by the beginning of the breeding season the bib becomes uniformly black (Summers-Smith, 1988). The female is rather featureless with a grey-brown crown, a pale-buff supercilium, two wing bars and an unmarked throat and breast. The bill becomes darker during the breeding season and a few birds have a completely black bill (Lowther and Cink, 1992).

The House Sparrow has a historical commensal relationship with man and has followed his colonisation of the majority of the earth. Through the introduction to islands and continents it would otherwise not have reached, it has become one of the most widely distributed land birds in the world (Summers-Smith, 1988). It is only absent from areas such as China, Indochina, Japan and areas of Siberia and Australia to the east and tropical Africa and northern areas of South America to the west (Summers-Smith, 1988).

Two subgroups are currently recognised; the *domesticus* subgroup which contains five subspecies with a natural range covering Siberia, Europe, North Africa and the Middle East; and the *indicus* subgroup containing six subspecies confined to Asia (Summers-Smith, 1988). The *domesticus* group are typically larger, with grey cheeks and underparts and the *indicus* group are generally smaller, with a smaller bill, white cheeks and underparts and a richer colour on the upperparts (Summers-Smith, 1988).

This thesis considers only the ecology of *Passer domesticus domesticus*, the subspecies found in Britain and throughout Europe and the species found to be at the heart of the majority of accidental and deliberate introductions around the world.

1.3.1 Habitat

The House Sparrow is primarily associated with human habitations e.g., agricultural land, villages and urban areas (Lowther and Cink, 1992). The optimum habitat for House Sparrows in temperate regions is a combination of buildings with holes under tiles or eaves to provide suitable nesting sites and sufficient green areas to provide insect food for the young (Summers-Smith, 1988). Although demographic data for urban-suburban areas are few, its optimum habitat in terms of rates of annual productivity and survival appears to be in the suburbs of towns and cities, where breeding densities can reach 100 – 400 breeding pairs per km^2 (Heij and Moeliker, 1990).

1.3.2 Behaviour

In large areas of apparently suitable habitat House Sparrows tend to breed in small colonies, usually of 10 – 20 pairs rather than spreading uniformly and is probably better described as clumped rather than a colonial breeder (Summers-Smith, 1988). Outside the breeding season House Sparrows are normally found in flocks that associate in many activities, ranging from communal roosting to feeding, dust and water bathing, and ‘social singing’ when the birds collect in bushes and call together. This can occur when they emerge from their roosting sites prior to searching for food and regularly on dull winter afternoons (Summers-Smith, 1988).

Once independent, young House Sparrows form small foraging flocks, which later coalesce at suitable feeding places into larger aggregations of young from several neighbouring colonies. These aggregations grow as more young fledge and are joined by adults that have finished breeding (Summers-Smith, 1963). In the UK members of late summer and autumn feeding associations roost close to the feeding area and, for a brief period, the breeding colony area may be deserted. Once adults have completed annual moult they return to breeding colonies to repossess their old nest sites (Summers-Smith, 1988). Young birds remain longer in these feeding associations, still roosting close to the feeding area, but gradually dispersing locally, attaching themselves to colonies that make up autumn feeding associations. Some return back to the natal colony and most are back in colony areas by October. Once birds have joined a colony the majority remain faithful to it for life, though there may be a second local dispersal at the beginning of the breeding season by birds that have failed to obtain nest sites and mates (Cramp *et al.*, 1993).

1.3.3 Diet

The House Sparrow is primarily a seedeater, in rural areas specialising on the seeds of cultivated grain crops such as oats, wheat, barley, corn, and maize. The other major food source is the seeds of annual herbs such as grasses (Graminae), rushes (Juncidae), goosefoot (*Chenopodium*), docks (Polygonacaea) and chickweed (*Stellaria* spp.) (Keil, 1972; Gavett and Wakely, 1986; Wilson *et al.*, 1999). Birds living in built up areas, supplement their diet of natural vegetable matter with a variety of household scraps, such as bread and peanuts deliberately put out by humans (Summers-Smith, 1988). The use of feeders in gardens by House Sparrows is well known and (Cowie and Hinsley, 1988) found that the House Sparrow was by far the commonest species at feeders using them throughout the year, though most commonly in autumn.

In contrast, nestlings are fed almost exclusively on insects and other invertebrates (both in the larval and adult form), with the prey species varying with season. The most important taxa being aphids (Aphidoidea), spiders (Arachnida), beetles (Coleoptera), weevils (Curculionidae), grasshoppers (Orthoptera) and caterpillars (Lepidoptera) (Seel, 1969; Gavett and Wakely, 1986; Wilson *et al.*, 1999). The work undertaken by Anderson (1984) showed that Coleoptera, Diptera and Lepidoptera were most commonly represented in the diet of village House Sparrows in Poland. The Coleoptera group was found to be the most important prey during May for sparrows in Bulgaria (Ivanov, 1990). As the young develop, vegetable matter is increasingly supplemented to the insect diet and by the time they fledge this forms the most important part (Wieloch, 1975; Summers-Smith, 1988).

1.3.4 Breeding ecology

The formation of pairs can start as early as September to October in the UK and House Sparrows are a species that are generally regarded as monogamous although extra pair paternity can vary from population to population (Summers-Smith, 1988; Griffith *et al.*, 1999). Males may begin nest site sitting displays in winter. The male proclaims his ownership of a nest site by regular chirrup calling beside it (Summers-Smith, 1988). Nest building is most intense between February and May with a wide variety of nest sites being used, ranging from holes and crevices in man made structures, trees, in earth banks, nest-boxes and even on the top of telegraph poles (Summers-Smith, 1988; Lowther and Cink, 1992). However, Cink (1976) showed that unmated females chose males calling at enclosed nest sites in preference to those at open sites. This would tend to favour the use of hole sites, except in colonies where the number of holes are limiting (Summers-Smith, 1988).

House Sparrows use a broad range of materials for nest building including feathers, grass inflorescences, stalks and roots of plants, bark, threads, string and even pieces of paper and wool (Indykiewicz, 1991). Within nest-boxes, the nest may be merely a cup of vegetation at the bottom of the box or built up so that the nest material covers the sides as well as the top of the chamber (Lowther and Cink, 1992). Indykiewicz (1990) found that the most common height when analysing the location of urban sparrow nests was between three and four metres high. House Sparrows nesting in protected sites such as nest-boxes and holes in buildings tend to start breeding earlier and are more successful, than those nesting among tree branches (McGillivray, 1981).

The breeding season starts in April and runs through to August, allowing pairs to produce up to four clutches over the summer (Summers-Smith, 1988). The clutch size normally ranges from two to five eggs with four being the modal number in the UK. The eggs are white to greenish or bluish white with markings usually around the larger end with dots or spots of brown, with the last laid egg usually having less dense markings (Novotny, 1970; Lowther and Cink, 1992). The interval between the laying of each egg is approximately 24 hours and both sexes take part in incubation (Seel, 1968). The incubation period is defined as the interval between the laying of the last egg of the clutch and the hatching of the first young (Seel, 1968). Incubation lasts between 10 – 17 days (Summers-Smith, 1988) with an average of about 11 days if measured from the last egg to the first hatch (Lowther and Cink, 1992).

The adults feed the nestlings, with most studies showing that the sexes play an equal role in provisioning (Summers-Smith, 1988). Some brooding takes place during the first eight days of life of the chicks until they develop sufficient feather coverage to become homoiothermic (Seel, 1969; Summers-Smith, 1988). The nestlings remain in the nest for between 12 – 18 days and typically averaging 14 – 16 days. Once fledged the adults continue to feed their young for a further 10 – 14 days before they become nutritionally independent (Summers-Smith, 1988). The complete cycle of nest occupancy from the beginning of egg laying to fledging of the young takes 28-31 days with an interval between successive clutches typically 36 – 40 days (Seel, 1968; Summers-Smith, 1988).

1.3.5 Dispersal

Observations of colour-ringed birds highlight the extremely sedentary nature of the House Sparrow (Summers-Smith, 1988). Once a House Sparrow has bred, it usually remains faithful to the breeding area and rarely moves more than two kilometres to find food. Those movements that do occur tend to involve either adults that have been unsuccessful in establishing a breeding site or juveniles after the post-breeding flocks have broken up in the autumn (Summers-Smith, 1988). However, research undertaken on the population of House Sparrows on the island of Lundy, off the north coast of Devon, has shown there is occasional dispersal between the island and mainland population, a distance which is approximately 20 kilometres (Griffith *et al.*, 1999).

Paradis *et al*. (1998) analysed ringing recoveries of House Sparrows in the UK and found that the mean breeding dispersal was 1.9 kilometres whereas the mean natal dispersal was slightly less at 1.7 kilometres. Cheke (1972) also studied natal dispersal and found that juveniles settled within a kilometre of their place of birth and Fleischer (1984) suggests that recruitment estimates of surviving young returning to their natal colony is between 25-50% .

1.3.6 Population trends

By the first few decades of the 20th Century the House Sparrow population had increased so much that it was considered an agricultural pest. The arrival of the automobile in the 1920s heralded the disappearance of the horse as a means of transport in urban centres. The loss of horses from towns probably resulted in a serious loss of food for House Sparrows, both through the loss of food and bedding in stables and indirectly, through the loss of dung dwelling invertebrates. However the continuing urbanisation and emphasis on agrarian production provided huge opportunities for further colonisation and an increase in its overall countrywide population (Holloway, 1996).

There seems however, to have been a long term decline in UK House Sparrow numbers since the end of the First World War, as evidenced by the well-documented long decline in numbers in London's Kensington Park (Sanderson, 1996; Moss, 2001). This long term study found that House Sparrow numbers decreased from a peak of 2,603 birds in 1925 to 885 in 1948, 544 in 1975 to just eight in 2000. More recently Easterbrook (1999) recorded a more or less continuous decline in winter House Sparrow numbers during the period 1975-1999 in the largely mixed farming landscape of Oxfordshire.

The House Sparrow was formerly ubiquitous across the UK but between 1977 and 2000, the UK House Sparrow population has declined by 65 percent (Crick *et al.*, 2004). As the decline has been more than 50% in the last 25 years, this qualifies it to be categorised as a red data listed species, a bird of conservation concern (Gregory *et al.*, 2002).

Until the inception of the Breeding Bird Survey (BBS) in 1994, the Common Bird Census (CBC) was the mainstay of terrestrial bird monitoring in Britain, however House Sparrows were only included in the count from 1976. Since this time the CBC data has shown that the sparrow population has declined by 53 percent across all habitats (Siriwardena *et al.*, 2002). However the CBC is not representative of bird populations and habitats across the country and therefore the BBS was introduced to improve on the CBC by providing a much wider geographical coverage.

By looking at the trends in numbers on BBS plots, the current status of sparrow populations in different habitats can be assessed. The BBS, through the surveying of a much wider and broader spatial area, confirms that between 1994 and 2000, populations have declined in the South East, especially in suburban and urban habitats (Crick *et al.*, 2002). Although the data is over a short period, it can be seen from Table 1.1 that there are regional differences in the decline of sparrows across Britain. This data is for all habitats within each region and the first column gives the percentage of the British population supported in that region and the second column gives the mean annual percentage change during the period 1994 to 2000. The steepest declines were observed in the North East of England, East Anglia and South East of England, where the population is the largest. In contrast, populations appear to be increasing in Scotland and Wales.

Table 1.1. The mean annual percentage change in House Sparrow numbers between 1994-2000 by region as measured by Breeding Bird Survey data

Region	All habitats	
	% of British population supported	Mean annual % change 1994-2000
Scotland	13.08	+27
Northern England	6.14	-4.4
North East England	7.38	-22.5
North West England	5.56	-14.6
Wales	7.04	+64
Central West England	9.30	+1.76
South West England	12.12	-6.5
Central East England	9.89	+37
East Anglia	5.34	-14.1
South East England	24.15	-31.2

Since 1970 the Garden Bird Feeding Survey (GBFS) has provided annual information on the numbers of birds using artificial food and water sources during winter in a number of rural and suburban gardens in Britain (Siriwardena *et al.*, 2002). Observers record the maximum number of each species using bird feeding stations in their gardens in each week of winter, of these gardens around 60 percent are classed as suburban. The GBFS data has shown that the sparrow population has declined by some 58 percent since 1970 in gardens during winter, of which suburban gardens have shown a greater decline (60 %) than rural gardens (48 %) (Siriwardena *et al.*, 2002; Robinson *et al.*, 2005).

As well as Kensington Park, House Sparrows in Buckingham Palace Gardens in London have shown a population decrease of 85% (Summers-Smith, 2000b). House Sparrows in Edinburgh and Dublin have also shown declines. In the centre of Edinburgh, House Sparrows have shown a 90% decline over the last 15 years, while other bird species in the same area have shown no change (Dott and Brown, 2000). Local surveys in cities such as Manchester and Glasgow have documented House Sparrow declines on the scale of 80-95% (Summers-Smith, 1999). However House Sparrow declines are not just confined to the UK. In the city of Hamburg, Germany, the House Sparrow population is thought to have declined by more than 50% in the last 30 years (Mitschke *et al.*, 1999). In Paris (France), a city once thought to have a high density of House Sparrows, now appears to have a declining population with a 36% decline in the last forty years (Galinet, 2003).

Although there is evidence that House Sparrow numbers have declined markedly especially in South and East Britain, and in several towns and cities, a detailed nation-wide picture is unavailable. This thesis aims to identify demographic parameters and environmental factors that are limiting House Sparrow densities in urban-suburban landscapes. In the rest of this chapter, I briefly review some proposed causes (i.e. environmental factors) that might have contributed to the population decline of House Sparrows in urban-suburban habitats.

1.4 Suggested causes of decline

A number of hypotheses have been put forward as possible causes of the decline of House Sparrows in urban-suburban habitats: predation, competition, lack of nest sites, disease, food availability and pollution (Summers-Smith, 1999).

1.4.1 Predation

In some bird species, predation might remove so few individuals that it has no discernible effects on breeding numbers. However in other species, where total mortality is density-dependent by the extent to which numbers exceed available resources, predators may take only the number that would die anyway, underlying Errington's (1946) view of a 'doomed surplus' (Newton, 1998). Errington (1946) suggested that each habitat had a limited carrying capacity and that it was only when the numbers rose above this level that predation became limiting. He believed that the effects of predation cannot be studied by counting the numbers of prey killed and that the factors that predispose predation have to determined, as well as what makes some individuals more vulnerable than others (Errington, 1946).

Errington (1946) postulated that numbers were trimmed to a sustainable level and that the excess succumbed to mortality agents such as disease, starvation or predation. This is an important point, as even though predation could be substantial, it might have no effect on breeding density (Newton, 1998). For predators to reduce breeding numbers below the level that would otherwise occur, at least part of the mortality they inflict must be additional to other forms of mortality such as disease and starvation (Newton, 1998).

There are three major candidate predators that could conceivably affect House Sparrow numbers: the Tawny Owl *Strix aluco*, the domestic or feral cat *Felix catus* and the Sparrowhawk *Accipiter nisus*. Most predators of birds are generalists, and take a wide variety of prey, switching from one prey species to another as opportunities and needs arise. Therefore because the population levels of such predators can be influenced by the sum total of prey, they are often not greatly affected by shortage of any one type.

Generalist predators such as Sparrowhawks do not usually take their various prey in strict relation to the numbers of those prey in the area but take some species more than expected from their numbers and others less so (Tinbergen, 1946; Opdam, 1978; Newton, 1998). Therefore certain prey species may experience heavy predation not because of their own numbers but because other prey species are sufficiently plentiful to attract many predators to the area, or because alternative prey become scarce (Tinbergen, 1946).

The major increase in the numbers of Sparrowhawks that are seen regularly on the outskirts of towns and villages, could be a contributory factor. The Sparrowhawk can remove a large proportion of prey individuals each year, yet it seems to cause no obvious depression of breeding densities in most species (Tinbergen, 1946; Perrins and Geer, 1980; Newton, 1986). Over much of Europe around 1960, Sparrowhawks were eliminated from large areas through the use of organochlorine pesticides, recovering and recolonising years later when organochlorine use was reduced (Newton, 1986). However when Sparrowhawks declined there was no great upsurge in songbird populations. This can be seen when thirteen woodland bird species were counted every year between 1949 to 1979 in an oakwood in southeast England (Newton and Perrins, 1997). This duration covered the decline and the recovery period of the Sparrowhawk, which bred in the wood. It was found that no species were present in significantly greater numbers when Sparrowhawks were absent and therefore the Sparrowhawk did not have a negative impact on the breeding densities of these species (Newton and Perrins, 1997).

This finding was paralleled by a more detailed study of Sparrowhawk predation on tits nesting in Wytham Wood near Oxford. It was found that the Sparrowhawks removed an estimated 18-34% of young Great Tits *Parus major* and 18-27% of young Blue Tits *Parus caeruleus* during the period of 1976 to 1979 (Perrins and Geer, 1980). However an average of more than six young tits per pair were raised in these years and only one chick per pair was needed to maintain the population at a constant level. Therefore many young tits must have died from other mortality causes at other times of the year (Perrins and Geer, 1980). Also the number of nest-boxes occupied each year were not conspicuously higher in the period when Sparrowhawks were absent than when they were present. These results gave no evidence that Sparrowhawks despite their predation, depressed the tit breeding densities and in fact Blue Tits showed a long term increase over the study period (Perrins and Geer, 1980; McCleery and Perrins, 1991).

Through the experimental manipulation of the distance between artificial bird feeders to cover, Cowie *et al.*, (1991) showed that House Sparrows are amongst the most cautious of foragers, as they would not fly to feeders even as close as 2.5m from cover. This response is likely to be to avoid predation by aerial predators (Cowie and Simons, 1991), as it has been observed that sparrows retreat deep into the hedge to avoid being caught when attacked by Sparrowhawks (Barnard, 1979). It has been shown by many studies on Sparrowhawks during the breeding season that House Sparrow is an important component of their diet (more than 5%) (Newton, 1986). However, Newton (1986) suggests that the Sparrowhawk acts mainly to change the seasonal pattern of mortality and reduce the post-breeding peak, without effecting a decline in breeding numbers of its prey. This can be seen from a study in the Netherlands showing Sparrowhawks taking about 8% of the House Sparrow population in May, about 80% of the House Sparrows that died in this period, due to the high numbers of fledglings added to the total population (Tinbergen, 1946). Opdam (1978) also found that recently fledged individuals constitute a very considerable part of the Sparrowhawks' diet during the months of May to June and therefore the adult population, suffer fewer losses due to predation.

Thomson *et al.*, (1998) used large scale, long term data from a national bird census scheme (Common Birds Census) to examine whether Magpies and Sparrowhawks could have depressed the rates of year to year population change in 23 songbird species. All the species studied are known prey of Sparrowhawks (Newton, 1986) and the nests are vulnerable to Magpies, which eat eggs and nestlings (Thomson *et al.*, 1998). The results indicate that Magpies and Sparrowhawks are unlikely to have caused the songbird declines because patterns of year to year population change did not differ between sites with and without these predators (Thomson *et al.*, 1998).

Thomson *et al.,* (1998) also investigated the presence of Collared Doves *Streptopelia decaocto* at these sites and correlations were found with declining songbird species. This demonstrates that these patterns could reflect independent but coincident population changes rather than causal effects of depredation. Thomson *et al.,* (1998) have shown that Magpies and Sparrowhawks could have effects on populations of breeding songbirds in a few species or in some specific localities but their work did not support the idea that these predators could have depressed the national populations of the species studied. Therefore the precise causes of songbird declines remain unclear but there are increasing evidence that the declines are a consequence of agricultural intensification (Thomson *et al.*, 1998).

Domestic cats are the most abundant carnivores in Great Britain. The cat is the UK's most popular pet with 4.5 million households owning approximately 7.5 million cats in 2004 (Cats Protection League, 2004). The number of feral cats in the UK is believed to be approximately 1 million, bringing the total number of felines in Great Britain to nearer 9 million (Cats Protection

League, 2004). This is believed to be over double that of 30 years ago (Cats Protection League, 2004).

A survey conducted by the Mammal Society asked a number of cat owners to record in as much detail the prey items brought home by each cat in their ownership (Woods *et al.*, 2003). Of the 696 individual cats that were studied in this survey, 91 percent brought home at least one item of prey, however approximately 25 percent of cats studied brought home no birds or mammals (Woods *et al.*, 2003). Woods *et al.*, (2003) found that cats living in households that provided food for birds, brought home fewer birds, suggesting that a greater number of birds may enhance group vigilance behaviour and warn against predator presence (Popp, 1988). Alternatively an extra food supply may reduce foraging time and therefore subsequently reducing the time at which the birds are at risk of being captured by cats (Jansson *et al.*, 1981).

The capture rates of birds were not affected by equipping cats with bells, possibly because birds rely largely on visual cues in predator avoidance behaviour or because the acoustic qualities of cat bells may not lend themselves to warning birds (Woods *et al.*, 2003). The total number of prey items caught was over 14,000 of which over 3000 were birds, 28 percent of these were House Sparrows, the highest number of any bird species caught (Woods *et al.*, 2003).

However a major caveat in this research is the likely bias of the survey towards cat owners who have a particular interest in wildlife biology and conservation. Equally there is a potential bias towards cats that have predilections for killing wild animals and for bringing home their prey (Woods *et al.*, 2003). The results of this study show that cats are a major predator of wildlife in Great Britain, however Fitzgerald *et al.*, (2000) asserts that on continental landmasses, wildlife has co-evolved with cats for hundreds of generations and that any species that were susceptible to depredation would be long extinct.

Churcher and Lawton (1987) calculated that in a single English village, cats were responsible for up to 30% of mortality in a House Sparrow population. They concluded that domestic cats were a major predator in a typical English village. Further analysis of depredation by cats such as that undertaken by Mead (1982), ascribed 31% of recoveries of ringed Robins (*Erithacus rubecula*) and Dunnocks (*Prunella modularis*) to cat predation but believed that there was no evidence that cats affected the overall populations of these species.

Although the data in all these studies should be treated with requisite caution, there could be a potential link between the frequent occurrence of sparrow depredation by cats and the national decline in the species, warranting further experimental research (Crick *et al.*, 2002).

There is little information on predation of House Sparrows in natural nesting sites. However most House Sparrow nests in natural cavities in roof spaces and nest-boxes will be inaccessible to predators such as Magpies *Pica pica*, Grey Squirrels *Sciurus carolinensis* and cats. Observations suggest that the fluctuating and unpredictable nature of predation on House Sparrow nests depends on the characteristics of the microhabitat in which the bird has chosen to nest (Cordero, 1991). In contrast with open nesting species there is relatively little predation pressure and therefore the nesting stage is more likely to be governed by mortality causes such as uncertain food supplies available to the parents (Dyer *et al.*, 1977).

The role of predation in influencing prey numbers depends on the way in which predators operate. Only if the combination of functional and numerical responses provides an appropriate total response to changes in prey density can predators regulate prey numbers. Also because predation is only one of several factors affecting prey populations, any regulatory effect it might have may be supported or counteracted by other factors (Newton, 1998).

1.4.2 Competition

Acting mainly through resources such as food, inter-specific competition is yet another factor that could limit House Sparrow numbers. An overlap in food and other resources provides the potential for competition because some of the resources removed by one species might otherwise have been available for a second (Newton, 1998). If either of such species is limited by resources then it follows that the numbers of the one could influence the numbers of the other (Newton, 1998). In exploitation competition, individuals have free access to a resource, but its use by one species reduces the amount for another. In interference competition, individuals of one species are denied access to a resource by the aggressive behaviour of another. In an extreme case, one species kept from a food source by a dominant other species could starve in the midst of plenty (Newton, 1998).

When different species feed together on the same food, individuals of a dominant species can greatly reduce the feeding rates of individuals of subordinate species. For example, many seabirds feed on discards from fishing boats and in the north Atlantic, Gannets *Morus bassanus* are dominant to all other species (Furness *et al.*, 1992). Furness (1992) found that the feeding success of Herring Gulls *Larus argentatus* was found to decline in direct proportion to the number of Gannets present. However such interactions are often construed as competition but they are not necessarily translated into reduced survival or reproduction, let alone reduced population level (Newton, 1998).

Experiments on niche shifts have been conducted with mixed flocks of tits, in conifer forests of northern Europe. Dominant Willow Tits *Parus montanus* and Crested Tits *Parus cristatus* fed mainly at favoured sites within trees, while the smaller Coal Tits *Parus ater* and Goldcrests *Regulus regulus* were relegated mainly to the outer twigs, where the risk of predation was greater (Alatalo *et al.*, 1987). This segregation was presumed to be due largely to interference, for the larger species often chased the smaller ones. However, when subordinate species were experimentally removed so that the food source in the outer parts of trees were less depleted, the dominant species spent significantly more time feeding there (Alatalo *et al.*, 1987). Therefore a combination of interference and depletion competition, caused the range of foraging sites used by each species to be reduced by the presence of other species (Alatalo *et al.*, 1987).

The invasion of an area by a new species is sometimes followed by population declines among those species already there that use the same resources. The most striking example of a species becoming common were they were formerly absent is the Collared Dove (*Streptopelia decaocto*). Until 1930, the Collared Dove extended no further west than the Balkans, but then spread rapidly across Europe, reaching Britain about 1955. For many years in newly colonised regions, its numbers increased exponentially, until habitats became filled and numbers levelled off (Hengeveld, 1988).

The Collared Dove and Wood Pigeon *Columba palumbus* are both granivorous species and would be the two most likely species to compete with House Sparrows for food (Snow and Perrins, 1998). During the summer months the House Sparrow takes invertebrate food as well as seed whereas the Collared Dove and Wood Pigeon have a much more granivorous based diet all year round (Snow and Perrins, 1998). Therefore there would only be depletion competition for food between these species at certain times of the year. There are now thought to be five million Wood Pigeons in Britain, a doubling of numbers since 1970 and the Collared Dove population is now thought to stand at half a million birds, an eight fold increase since 1970 (Crick *et al.*, 2004). Their increase has been linked to the sparrow’s decline through competition for food such as grain (McCarthy, 2003).

However, depletion competition does not always reduce numbers, as Sutherland *et al.*, (1994) showed through monitoring Wigeon *Anas penelope* and Bean Geese *Anser fabalis* numbers on a southeast England nature reserve. Both species fed on the same area of grass and over a period of years, Wigeon increased in numbers and ate more grass leaving less for the late arriving geese. Therefore the geese fed less on the reserve as the years went by. However the geese found alternative feeding areas nearby, so while depletion competition limited their use of the reserve, it did not reduce their overall numbers (Sutherland and Allport, 1994).

1.4.3 Lack of nest sites

A lack of holes suitable for nest sites on modern or renovated buildings has been proposed as a possible cause of the House Sparrow population decline. There has been an increase in the use of plastic fascia boards and the use of contoured tiles or roofing sheets to prevent the entry of birds on modern housing. House Sparrows predominantly nest in holes and gaps in soffit boards and under tiles, therefore this tendency may have an impact of the availability of nest sites.

Work undertaken in Bristol found a negative correlation with the extent to which loft insulation had been installed in houses (Tully and Bland, pers. comm.) This may result in fewer nesting opportunities and there may also be a possibility of adverse respiratory effects from airborne fibreglass on breeding birds and chicks (Crick *et al.*, 2002).

A survey undertaken by the RSPB and BBC Radio 4 ‘Today’ programme investigated the use of houses for nesting by four bird species including the House Sparrow (Wotton *et al.*, 2002). The survey revealed that houses built before 1919 are important as a source of nesting sites for House Sparrows. Wotton *et al.*, (2002) showed that houses built between 1945 and 1984 are more suitable for House Sparrows if no recent roof repairs had been undertaken. It was also shown that post 1984 homes are less attractive for nesting sparrows, irrespective of whether repairs have been carried out or not.

This work has shown that newer buildings, incorporating modern materials and constructed to conform to current building regulations seem to be generally less suitable because there is no access to the roof space (Wotton *et al.*, 2002). However, this did not deter the colonisation of the new housing estate at Pine Hills, Guisborough, where in the absence of suitable holes in the new buildings, the birds nested in the hedges of rapidly growing conifers (Summers-Smith, 1999).

Coleman (1974) added artificial nest sites to the habitat of House Sparrows and compared the breeding density before and after the addition of nestsites to the area and found that the breeding density increased with the addition of nest sites. However species of birds, not limited by shortage of nest-sites, will readily accept well-designed artificial sites in preference to inferior natural sites (Newton, 1998). Petty *et al.*, (1994) found that after nest-boxes were erected in a spruce plantation for Tawny Owls (*Strix aluco*), 83% of the population switched to using boxes in the first year and all pairs had switched to using artificial nest-boxes by the fourth year. Yet no indication was found that the observed changes in Tawny Owl breeding numbers had anything to do with box provision (Petty *et al.*, 1994). Therefore one must check whether increased box use is due to an increase in the density of territorial pairs, existing territorial pairs lacking sites being provided with an opportunity to nest, or existing territorial pairs shifting from natural sites (Newton, 1998). Consequently, care is needed in interpreting the findings of such studies involving the provision of nest-boxes (Newton, 1998).

Anderson (1990) removed female House Sparrows and eggs from nest-boxes in a colony in Missouri, U.S.A. The replacement of removed birds occurred quite rapidly, with replacement females beginning to lay on average 5 to 8 days after the removal of the previous occupant. This demonstrates that there was a surplus of female House Sparrows which were not occupying nestsites but which were nevertheless fully capable of breeding. This could be due to an inadequate number of nestsites or an inadequate number of optimal sites in good colonies, indicating nestsites may be a limiting factor in House Sparrow colonies (Anderson, 1990; Newton, 1992). The fact that nesting success is often better in purpose built boxes than in natural sites (Nilsson, 1975; Moller, 1989) could help local numbers to build up rapidly after box provision.

1.4.4 Disease

House Sparrows may serve as a reservoir of disease in urban and suburban areas (Juricova *et al.*, 1998). The infectious disease salmonella is common during winter and spring in free-living wild House Sparrows (Macdonald, 1978). In cases of fatality the birds show enlargement and congestion of the liver and spleen with liver, lung, muscle and skin abscesses. The spread of disease may be promoted by the close proximity of birds in gardens where there is communal feeding on bird table and feeders (Macdonald, 1978).

One well known strain of bacteria, *Salmonella typhimurium*, can cause outbreaks of mortality in garden birds visiting bird tables and other feeding stations (Pennycott *et al.*, 2002). Pennycott *et al.*, (2002) monitored two sites in south-west Scotland for 12 months to test for the presence of the disease. At one site *Salmonella typhimurium* was found to be endemic and was found on bird tables, underneath hanging feeders and even below a roost used by House Sparrows. The organism was also isolated from the carcases of six wild birds found dead at the site (Pennycott *et al.*, 2002). Infection with *Salmonella typhimurium* has shown to be a cause of death in House Sparrows found dead in urban or suburban habitats (Pennycott, 2004). Between 1998 and 2002, salmonellosis was diagnosed in 22 of 24 House Sparrows (from nine different sites) submitted during the months of November to March (Pennycott, 2004).

Deaths from salmonellosis have not been confined to sparrows at bird tables in the U.K. Since 1998, many sparrows have been found dead around garden feeders in the New Zealand and

Canada (Pennycott, 2004). In one incident in New Zealand in 2000, more than 400 dead birds were found at one location on one day (Pennycott, 2004). This same strain of salmonella was also found in 15% of wild Sparrows trapped in 1979 in Guelph, Canada, and caused a small outbreak of mortality in House Sparrows in Central Newfoundland, Canada in February and March 1999 (Pennycott, 2004). In Poland, Pinowska *et al.*, (1976) found that sparrows were carriers of salmonella and the transmission of the disease increased during the winter months when large flocks gathered in farm animal buildings due to the low temperatures. The spread of the disease is then increased further when the birds disperse to new areas in the spring (Pinowska *et al.*, 1976).

In the US, a disease called *Mycoplasmal conjuctivitis* is causing declines in House Finch *Carpodacus mexicanus* populations (Altizer *et al.*, 2004). This disease is caused by a novel strain of bacterium, *Mycoplasma gallisepticum*, which is a common pathogen of domestic poultry. Following exposure, infected finches develop eye infections characterized by conjuctival swelling and discharge (Altizer *et al.*, 2004). Altizer *et al.*, (2004) found that some birds persist in an infectious state and subsequently die and others recover. This newly emerged pathogen has resulted in a decline in House Finch abundance, with some areas showing a 60% decline in numbers (Altizer *et al.*, 2004).

Faustino *et al.*, (2004) believes that this disease spreads rapidly due to the aggregation of finches in large feeding flocks during the autumn and winter. House Finches are also often seen on feeders in suburban and urban gardens and it is possible that infected birds may contaminate feeders and pass the disease horizontally though indirect contact to other susceptible individuals (Faustino *et al.*, 2004). House Sparrows, like House Finches depend on feeders in some areas, therefore the possibility of transmission of disease via feeders could be translated to sparrows in the UK, transmitting disease via feeders to other sparrows.

Research undertaken in Poland on the occurrence of microorgansisms in unhatched eggs of House Sparrows, found that 67% of eggs analysed were infected with microorganisms (Kozlowski *et al.*, 1991b). The most frequently infected were day old embryos and unfertilised eggs, containing microorganisms such as *Enterobacteriaceae*, *Micrococcaceae*, *Streptococcaceae*, *Bacillaceae* and *Cryptococcaceae*. Kozlowski *et al.*, (1991b) found that embryos which died in the first days of incubation were infected most frequently and that *Escherichia coli* was the predominate microorganism present in dead embryos. This study shows that microorganisms in free-living birds could be a possible important factor influencing egg mortality in the wild (Pinowski *et al.*, 1994).

Studies on the intestinal flora and fauna of urban sparrow nestlings have indicated a significant containment of microorganisms that, under specific conditions such as reduced host immunity due to lack of food, are able to cause disease in birds (Malyszko *et al.*, 1991). Infections with *Escherichia coli* pathogenic strains were found in the early development of nestlings (1-5 days), where they were implicated in the death of those nestlings (Malyszko *et al.*, 1991). Malyszko *et al.*, (1991) found that the *Escherichia* genus was the most abundant group present, but 9 other genera were found from the *Enterobacteriaceae* family, as well as strains from the *Candida, Coccidia* and *Entamoeba* genera. All of these strains are opportunistic and under certain conditions such as a decrease in host immunity, become pathogenic and fatal, causing the possible death of the sparrow nestling (Pinowski *et al.*, 1988; Malyszko *et al.*, 1991).

An analysis was carried out on over 360 nestlings of House Sparrows of which approximately 80 were postmortem and 280 were controls, to ascertain the frequency of *E. coli* present in nestlings of sparrows (Pawiak *et al.*, 1991). Pawiak *et al.*, (1991) found that there was a higher occurrence of *E.coli* in nestlings from urban areas and in dead birds. The frequency of *E. coli* isolated from the liver of dead nestlings was four times higher than in the control group suggesting a possible cause and effect relationship in the death of sparrow nestlings (Pawiak *et* *al.*, 1991). In addition work undertaken by Kruszewicz (1995) found that *E.Coli* and *Streptococcus* spp. was more frequent in nestlings with lower body mass which compounds the theory that if a nestling becomes weak due to lack of food, it is more likely to die through disease.

Further research on sparrow nestling deaths has shown that *E. coli* pathogenic strains are likely to be the main cause of nestling mortality in certain sparrow populations (Kozlowski *et al.*, 1991a). It is possible that the pathogenic serotypes of *E. coli* and protozoans of *Coccidia* play an important role in the inhibition of the development of House Sparrow nestlings in the Warsaw area. This is because the clinical and anatomo-pathological signs of these microorganisms were found in ill and dead birds (Pinowski *et al.*, 1988; Kozlowski *et al.*, 1991a; Pinowski *et al.*, 1994).

Work by Berger *et al.*, (2003) investigating the bacterial infestation of nests for other hole nesting breeders such as the European Starling (*Sturnus vulgaris*), found a higher load of bacteria in late nests. Berger *et al.*, (2003) believed that it may be possible under certain conditions for this to be one of the factors responsible for lower quality second brood nestlings.

The prevalence of arboviruses in birds is linked to the presence of specific vectors, namely the ornithophilic mosquitoes *Culex modesti* and *Culex pipiens* and possibly ticks such as *Ixodes ricinus*. The presence of these vectors has been documented in suburban areas of Warsaw in House Sparrows where it can be fatal (Juricova *et al.*, 1998), however no study has shown long term effects on local populations.

High parasitism is the price that many hole nesters and colonial breeders pay for safety from nest predators. The effects of parasites on breeding success has been assessed in the rainforests of Puerto Rico, the hole nesting Pearly-eyed Thrasher *Margarops fuscatus* suffers from heavy infestations of the bot-fly *Philinus deceptivus* whose maggots feed from live nestlings. Arendt (1985) found that in nests where bot-flies were removed from chicks, 99% of the nestlings survived, compared with 53% of nestlings in nests containing natural levels of bot-flies. Among nestlings that died, 97% of mortality was due to bot-flies. However similar research on a species of blow-fly and the Tree Swallow *Tachycineta bicolor*, found there was no reduction in chick survival despite heavy infestation (Rogers *et al.*, 1990).

Research undertaken by Weddle (2000), on the effects of haemotophagous mites on nestling body mass in House Sparrows, showed that chicks from nests with relatively high ectoparasite loads had lower overall body masses than chicks from nests with relatively low mite loads. Therefore these findings indicate that blood-sucking mites can have a negative effect on sparrow nestling body mass prior to fledging, ultimately reducing the quality of host offspring (Weddle, 2000). Fleas are another problematic parasite of hole nesting species especially those that use nest-boxes. Fleas will jump on to almost any bird approaching an infested box, and Du Feu (1992) found that the presence of simulated fleas at the entrance of a nest-box reduced the frequency of prospecting visits by birds.

Food supply has an affect on the ability of nestlings to withstand parasitism, the effect of which may be greater in years of poor food supply than in years of good supply (Moss and Camin, 1970). Such effects were shown experimentally by Pinowski (1977) through the study of the Bluebird *Sialia sialis*. Pinowski (1977) restricted the food intake of nestlings by use of neck collars for a set time every other day. These broods accumulated significantly more blood-sucking blow fly larvae *Apaulina* sp. than other broods that were not deprived of food (Pinowski, 1977).

Lower production of young may have no impact on subsequent breeding numbers if it was offset by improved survival of remaining young. Added to this is another complication, in that if predators are present they may remove heavily parasitised individuals before they die, further reducing the importance of parasites (Temple, 1987; Moller, 1989). In assessing the impacts of parasitism on a population, the same question arises, as with predation, whether the resulting deaths are additive to mortality or compensatory (Newton, 1998).

With disease, contributing causes are often apparent for example individuals weakened by starvation might become vulnerable to disease (Newton, 1998). Disease is increasingly seen as a response not only to parasite infection but also to the overall condition of the host. This makes it hard to separate the effects of disease from the food shortage or other environmental conditions that might favour it and therefore deaths from disease are often unlikely to be additive to other mortality (Newton, 1998).

1.4.5 Food availability

David Lack's 'The natural regulation of animal numbers' (1954) argued that populations must be regulated by density-dependent mortality factors such as food shortage, predation, parasitism or disease. However Lack (1954) believed that food shortage was the chief natural factor limiting the numbers of many birds and in particular, reproductive rate.

Food shortage can affect individuals directly, through causing breeding failure or starvation (Newton, 1998). Most information on the effects of food on bird breeding comes from correlation between productivity (young raised per pair) and food supply, either year to year or place to place (Martin, 1987). Depending on the stage at which they occur, effects of food shortages can be seen through non-laying of eggs, small clutches, egg desertion, poor chick growth and survival and in multi-brooded species a reduction in the number of nesting attempts (Newton, 1998).

Anderson (1977) reported that the effects of a superabundant food supply caused increased fledging success and shortened intervals between breeding attempts in House Sparrows subsequently increasing productivity. Therefore the amount of food available to a species can be seen as a controlling factor on the birds reproductive rate (Anderson, 1977).

One way to identify a causal relationship is by experimental alteration of the food supply, monitoring the response of the population against an appropriate control. The ideal experimental species eats food that can be easily provided, lives at high density and remains in the same locality all year round, so that the effects of food manipulation on its subsequent numbers can be readily assessed (Newton, 1998).

Research on the manipulation of food supplies has shown that the provision of extra food throughout the breeding season encourages increased productivity (Arcese and Smith, 1988). Arcese *et al.*,(1988) supplemented food to Song Sparrows *Melospiza melodia* and found these birds produced larger clutches, had higher hatching success and chick survival was higher, as well as an increase in the number of breeding attempts and the number of young fledged per pair compared to birds that received no extra food (Arcese and Smith, 1988).

A major pressure on House Sparrows could be a decrease in the invertebrate prey that is necessary for rearing nestlings during the first few days of life. The changes in farming practices through the reduction in the diversity of plants in fields with weed free crops; the ploughing up of headlands to increase the amount of land under cultivation and the increase use of pesticides and herbicides have reduced the availability of arthropods in rural areas (Donald, 1998). This is through both direct toxic effects of pesticides on invertebrates and loss of food plants (Donald, 1998). It seems possible that there has also been a decrease in arthropods in urban areas as a consequence of improved hygiene in gardens and the trend for ‘tidier’ landscaping of garden areas.

In urban areas, brown field sites or wasteland are likely to be fewer as city development plans infill, rather than expand out into greenbelt. The loss of such sites might be important as these weedy areas act as a source of both invertebrate and seed food to urban sparrows. Waste ground as a source of weed seeds may provide a higher quality food source than the household and other scraps that are otherwise available to urban sparrows and therefore the potential importance of this habitat needs to be studied further (Crick *et al.*, 2002).

However a general decrease in the availability of suitable vegetable food could also be causing starvation among House Sparrows. This decrease has taken place in rural areas with the disappearance of free-living chickens around farms and the seed put out for them. The cutting of silage before it has seeded and the ploughing in of seed-rich stubbles after the harvest before winter have also contributed. Research undertaken in Oxfordshire provides evidence that a reduction in annual survival rate is likely to be the principal demographic mechanism driving the population trend in farmland areas, with suggestions that winter food supply is the limiting factor (Hole, 2001; Hole *et al.*, 2002).

In urban areas the homogeneous landscaping of mown lawns and tidy ornamental shrub flowerbeds in suburban gardens as well as the decline in the cultivation of allotments to grow vegetables have possibly contributed to a lack of provision of food for the urban sparrow all year round (Summers-Smith, 1999).

Over the last twenty years there has been a marked increase in both the prevalence of garden bird feeding and in the quantity and range of foodstuffs provided (Cannon, 2000). However the GBFS data have shown that the number of House Sparrows using gardens has not increased in response to this (Crick *et al.*, 2002; Chamberlain *et al.*, 2004). Therefore it is possible that a greater decline would have been seen had these extra resources not been available. Long term changes in abundance as measured by the Garden Bird Feeding Survey (GBFS) show that sparrow populations in rural areas have declined by 47% since the mid 1970s, whereas those in urban and suburban gardens have declined by about 60% (Siriwardena *et al.*, 2002; Robinson *et al.*, 2005). Further studies on the relative use of different artificial foodstuffs by House Sparrows and any relationship with breeding success could shed more light on House Sparrow decline (Crick *et al.*, 2002).

1.4.6 Environmental Pollutants

Many toxic chemicals are now added continuously to the natural environment, either as pesticides, industrial effluents or combustion emissions (Newton, 1998). Some of these chemicals are now regarded as important agents of bird population declines, influencing distribution and abundance patterns on both local and widespread scales (Newton, 1998).

In urban Warsaw, research has suggested that chlorinated hydrocarbons (insecticides) and poly-chlorinated biphenyls (PCBs) found in the environment through their application in agriculture, sanitary treatments and in industry, could account for the death of a certain number of House Sparrow nestlings (Karolewski *et al.*, 1991). The average level of these insecticides and PCBs were several times higher in the bodies of nestlings than the highest value considered as a background level in the urban environment (Karolewski *et al.*, 1991). The highest insecticide level found in a nestling was 123 parts per million (ppm) and the highest level of PCBs were 3050 ppm. Karolewski *et al.*, (1991) believes that these high levels would probably have affected the health of the nestlings analysed and are indicative of the level of food contamination in the area searched by parents during the breeding season.

Romanowski *et al.*, (1991) found that when studying the concentrations of heavy metals in sparrow nestlings in Poland, the levels of zinc and lead concentrations in the liver were higher in ill and dead nestlings than in healthy ones. Also zinc, cadmium and lead concentrations were higher in the livers of nestlings with delayed development (reduced body weight) as compared to typical weights (Romanowski *et al.*, 1991). Further findings showed that nestlings with higher concentrations of iron or zinc in the liver had slower growth rates after nine days of age. Romanowski *et al.*, (1991) believes this provides evidence that concentrations of heavy metals much lower than those considered as sublethal in the literature, can adversely affect the development and survival of nestlings.

Few studies have considered the influence of calcium and heavy metals on the reproductive capacity of free-living female birds and in particular the impact of heavy metal pollution on clutch size. However Kaminski (1995b), investigated the differences between a polluted and unpolluted area in terms of the concentrations of calcium and heavy metals in the bodies of Tree Sparrows and in the eggs laid. Larger clutches were linked to greater concentrations of iron, magnesium, calcium and zinc in the bodies of females, as well as with lower concentrations of copper, manganese, cobalt, cadmium and lead (Kaminski, 1995b). In unpolluted areas, clutches of five or six were most common, with only three or four in the polluted areas. The small clutches observed therefore, maybe due to excessive concentrations of copper, manganese, cadmium and lead which are related to the pollution of the environment (Kaminski, 1995b).

Further work undertaken by Kaminski (1995a) comparing reproductive parameters such as hatching success, fledging success and nestling growth in an unpolluted area and a polluted area showed that hatching success and fledging success were higher in the unpolluted area than in the polluted area. In the unpolluted area nestlings attained maximum body weight quicker and achieved a higher rate of biomass increase than nestlings in the polluted area (Kaminski, 1995a). Therefore the unpolluted area provided better conditions for the development and reproduction of the Tree Sparrow than the polluted area, indicating that nestlings could be a good indicator of the degree of pollution of urban habitats (Kaminski, 1995a).

Particular heavy metal pollutants were investigated in detail and work by Pinowski *et al.*, (1995b) on House Sparrow nestlings. Upon analysing the effects of heavy metals on the development and mortality of nestlings, lead concentrations in dead nestlings was significantly higher than in healthy ones (Pinowski *et al.*, 1995a; Pinowski *et al.*, 1995b; Pinowski *et al.*, 1995c). This suggests that one of the factors which increases mortality in nestlings could be the levels of lead in the environment (Pinowski *et al.*, 1994; Pinowski *et al.*, 1995a; Pinowski *et al.*, 1995b; Pinowski *et al.*, 1995c).

1.4.6.1 The possible link between pollution and invertebrate abundance

Air pollution may have both direct and indirect effects on avian reproduction (Furness and Greenwood, 1993). Food limitation is known to increase nestling mortality under natural conditions (Martin, 1987) and food limitation has been suggested as being responsible for decreases in bird populations in polluted areas (Furness, 1993). Pollution can either increase or decrease insect population, depending on the species and the degree of pollution (Alstad *et al.*, 1982; Pimentel, 1994). Air pollution (particularly from sulphurous compounds) has been implicated in declines in spiders in London, mites and springtails in Switzerland and overall insect diversity in Poland (McIntyre, 2000).

Eeva *et al.*, (1997) investigated pollution related variation in food supply and breeding success in two passerine species. They found a positive correlation between pollution reduced food supply and breeding performance in the two bird species studied (Eeva *et al.*, 1997). In the case of the Great Tit, a reduction in optimal clutch size in the polluted area was associated with a reduction in arthropod availability (Eeva *et al.*, 1997). Nestlings grew well in the beginning, but suffered increasing mortality later in the nestling stage, i.e. at the time of highest food demand. This pattern would be expected if the available food for nestlings were limited (Eeva *et al.*, 1997). These findings emphasise the importance of indirect, food mediated effects of air pollution on key species (Eeva *et al.*, 1997). Food reduction therefore could be an explanation for the lower breeding success of certain bird species in urban areas.

It has been suggested that emissions from the internal combustion engine, particularly in large conurbations, could be having a detrimental effect on the abundance of key invertebrates such as aphids (Summers-Smith, 1999). One significant difference between large urban centres and rural villages is the density of traffic. A major change associated with traffic was the introduction of unleaded petrol in the 1980s. To maintain the octane rating, tetra-ethyl lead was replaced by oxygenates (mainly methyl tertiary-butyl ether, MTBE) and, with changes in refining techniques, the benzene content increased to about 5%, though an EC Directive subsequently reduced this figure to 1% in 2000 (Summers-Smith, 2000c). The UK Petrol Industry Association cannot give a figure on how much unleaded petrol contains MTBE, though it is probably less than 50 per cent (McCarthy, 2000).

MTBE is a known carcinogen and is water soluble, entering the environment by spillage from filling stations as well as entering the air via exhaust fumes (Achten *et al.*, 2001). The presence of MTBE in urban and rural precipitation in Germany in wintertime has been recorded (Achten *et al.*, 2001). It is unlikely to cause House Sparrow deaths directly but it may be possible that it is responsible for reducing invertebrate numbers in urban areas. Mitschke *et al.*, (1999) found that during studies of breeding House Sparrows in Hamburg, Germany, none of the April broods had chicks that fledged successfully. One of the suggested reasons for this was a lack of insects, in particular aphids, as they are an important food source for nestlings early in the breeding season (Mitschke *et al.*, 1999). Summers-Smith (*pers comm*. 2000a) believes that a pollutant such as MTBE from vehicle emissions could cut down invertebrate numbers such as aphids and therefore have an indirect impact on the survival of young sparrow nestlings. Levels of MTBE are currently not collated in the UK and there is currently no evidence that pollution is contributing to the House Sparrow decline (Summers-Smith, 2000c).

There is no evidence that urban populations of species such as the Blue Tit, Chaffinch or Greenfinch have declined like the House Sparrow. If pollution is having an indirect effect on House Sparrow population decline through reducing invertebrate availability, then it would be expected that these species would also be affected. However, although these species feed their young an invertebrate diet, it could be that the range or variation in the type of invertebrates taken is different compared to the House Sparrow. Further work needs to be undertaken on urban populations of species such as the Blue tit and Chaffinch, to gain a fuller understanding of avian ecology within the urban ecosystem.

1.4.7 Multiple environmental causes

Assessing the causes of mortality in a bird population is itself not straightforward. A bird weakened by food shortage may succumb to disease but just before death it may fall victim to a predator. In this example, food shortage would be the underlying cause of death, while predation is the immediate cause (Newton, 1998). Therefore we cannot assume that a population may be limited by only one factor, such as food shortage, predation or disease. In reality no single factor is likely to account wholly for a given population level. This is because reproduction and survival are seldom influenced by one factor alone, but by several, which may act independently or in combination (Newton, 1998).

Another complication is that different limiting factors may interact, for example, if food were abundant, a bird with many gut parasites might be able to keep itself just as well fed as one without parasites, simply by eating more. However if food were scarce, a parasitised bird, through having part of its intake absorbed by the parasites, might die of starvation, while one without parasites might survive. In this case parasites accentuate the effects of food shortage (Newton, 1998).

Another example is if food were scarce, a bird would have to expose itself for longer each day, reduce its vigilance, feed in less safe place and increase the risk of predation (Newton, 1998). Therefore alterations in either food supplies or predator or parasite numbers could have marked effects on bird numbers. Therefore single factor explanations of mortality may not always be realistic as sometimes one factor might enhance the effect of another, so that their combined impact on population levels is greater than the sum of their individual effects (Newton, 1998).

It has been argued by Ashmole (1963), that some seabird populations may be regulated by localised competition for food, restricted to the vicinity of the colony and limiting production of young. Regulation therefore, is achieved not by numbers of nest sites alone, nor by food supply alone, but by a combination of the two, with local concentrations of nest sites leading to local concentrations of birds, in turn leading to localised food shortage (Ashmole, 1963). This highlights that combinations of multiple environmental factors can contribute to population levels.

If resource limitation can be shown to exist, predation, disease and competition are often assumed to have little or no influence on numbers. This view is possibly too simplistic, and that a common and possibly prevailing pattern in nature is for joint limitation of population levels by both resources and natural enemies, themselves interacting with habitat structure and weather (Newton, 1998). Nest sites, cover, predators or disease can all restrict a species to only parts of an area where food is available, while predators and parasites can reduce rates of food intake and body condition, thereby enhancing the effects of food shortage (Newton, 1998). Therefore it must be acknowledged that any of the environmental factors that have been proposed as possible causes of the decline of the House Sparrow, could combine and interact as a joint limitation to the urban population.

CHAPTER 2

Methodology of Fieldwork

2.1 Establishing the study areas

This study was undertaken in the city of Leicester, the largest city in the East Midlands and the tenth largest in the country. The city has an estimated population size of 300,000 inhabitants and encompasses an area of 73 square kilometres (Leicester City Council, 2004). It stands in the broad, shallow valley of the River Soar at the centre of a network of communications including various major radial and tangential roads.

Although there are a few substantial employers in the engineering and foundry sectors, Leicester in general cannot be described as a ‘heavy’ industrial area. The heavy chemical, engineering and power generation industries are virtually unrepresented within the city (Leicester City Council, 2000). Established industries such as textiles, footwear, engineering and printing have in recent decades been complemented by relatively new industries such as food processing and packaging. Recently there has been a general decline in the footwear and textile industries in Leicester, reflecting the general downward trend in the UK of ‘traditional’ manufacturing industries and the transfer of activity into the service sector. Therefore the key air quality issue in Leicester is emissions from road traffic, rather than from major industry.

Nine study areas were established and I attempted to monitor House Sparrow breeding success in each area for three successive breeding seasons (2001-2003). The locations of the nine study areas in relation to the city centre are shown in (Figure 2.1). A total of 480 nest-boxes were erected within these nine study areas, and a further 139 nest-boxes were erected outside these study areas bringing the grand total of nest-boxes erected to 619. The study areas were chosen to represent different points along an urbanisation gradient, from the city centre (including two industrial/factory type areas), through three suburban areas and three rural areas. Air pollution generally declined along the urban-suburban-rural gradient (Figure 2.2), while building density was greatest in suburban areas and the city centre (Table 2.). All nest-boxes were checked for signs of nesting activity at the start of the breeding season between March and April during 2001-2003. However, due to logistical and time constraints, the 480 nest-boxes that were within the study areas were given priority and checked on a regular basis between March and August.

In this study the city centre (Area 1 in Figure 2.1) was classed as all the area within the inner ring road and was defined as ‘urban’. A total of 70 nest-boxes were erected within this area, on buildings, shop-fronts and housing. The two industrial sites were also defined as ‘urban’ and were situated either side of the city centre. Cobden Street Industrial Estate is located 1km to the east of the city centre (Area 6 in Figure 2.1) and the second industrial site is situated 3km to the west of the city centre (Braunstone Frith Industrial Estate, Area 5 in Figure 2.1). These areas consisted of light plant factories, warehouses and office blocks and were regularly visited by heavy good vehicles. A total of 54 nest-boxes were erected on buildings at these two sites. All of these three urban sites lacked domestic gardens.

Three suburban areas were chosen for this study. Braunstone is a suburb situated 3km southwest of the city centre (Area 2 in Figure 2.1) and consists mainly of privately owned semi-detached housing built in the last forty years, with medium sized gardens. New Parks/Western Park is another suburban area situated 2km west of the city centre (Area 3 in Figure 2.1). The New Parks region of the study area consists mainly of council-owned houses and flats with small gardens. However within the Western Park area, the housing is mainly privately owned semi-detached properties, with larger gardens. The third suburban study area is Thurmaston located 5km northeast of the city centre (Area 4 in Figure 2.1). Most of the houses within this suburb are privately owned semi-detached and detached properties with medium to large gardens.

One of the three rural sites was considered to be a mixture of suburban and rural landscapes. Houghton on the Hill (Area 7 in Figure 2.1) is a village 7km east of the city centre and contains a mixture of housing. The housing density in the centre of the village is equivalent to a suburban semi-detached area while the housing on the edges of the village are mainly detached with large gardens adjacent to farmland. For the purposes of this study, data collected from houses that were more than 200 metres from farmland were classed as coming from a suburban landscape whereas data collected from houses within 200 metres of farmland were classed as coming rural landscape. Approximately 1500 people are estimated to live in Houghton on the Hill (Leicester City Council, 2004). Ninety nest-boxes were erected on houses in this village.

The remaining two rural sites were rural villages situated to the east of Leicester city centre. Both villages were surrounded by mixed arable farming and had only one ‘B’ road running through the village. Keyham (Area 8 in Figure 2.1) is a village 8km northeast of Leicester city centre and 60 nest-boxes were erected on houses within the village. This village has an estimated population of 200 inhabitants (Leicester City Council, 2004). The final study area Hungarton village (Area 9 in Figure 2.1) is 9km north-east of Leicester city centre and has an estimated population size of 250 inhabitants (Leicester City Council, 2004); 35 nest-boxes were erected at this site.

2.2 Field Methodologies

2.2.1 Erection of nest-boxes

Nest-boxes were erected on housing near House Sparrow populations within the nine study areas. The boxes were erected at heights of approximately 4-5 metres with an average of 3 boxes on each house. The dimensions of the nest-boxes were: height 29cms, width 13cms, depth 19cms and two different hole diameters were used, 3.2 cm and 4.0cm. Each nest-box was cleaned out and the old nest removed each autumn.

2.2.2 Nest recording and biometric data collected

Nests were inspected at approximately seven-day intervals from the beginning of April through to mid August during 2001, 2002 and 2003. The following data were collected: the date the first egg was laid, clutch size, the date of hatching, number of eggs hatched and number of chicks fledged. Where first egg lay date was unknown, it was back-calculated from the hatch date, assuming a 12-day incubation period and the laying of one egg per day (Seel, 1968). When nestling age was unknown from observation of hatching, it was estimated by comparing the degree of feather development of nestlings from known age broods.

Nestling mass (to the nearest 0.1g using a 50g Pesola spring balance) and tarsus (to the nearest 0.1mm using a dial calliper) were measured following the procedure of Svensson (1992) during each visit to the nest. Nestlings were ringed when about 8-9 days old with a numbered BTO aluminium ring and a unique colour combination of three plastic rings, sealed using acetone. In order to determine the outcome of nesting attempts, occupied boxes were inspected at least once every 7 days until the nesting attempt was ended.

Nestling sparrows often produced faecal sacs during handling. These were collected and stored in a vial of ethanol in order that diet composition could be analysed (see Chapter 4) using the technique of Moreby (1987). Additionally a feather sample was taken from a limited number of chicks to analyse the dietary composition over a longer time scale using the technique of stable isotope analysis (see Chapter 7).

The analysis of stable isotopes of carbon and nitrogen in feathers can be a powerful analytical tool in the understanding of dietary inputs and trophic relationships (Gannes, 1997). The measurement of stable carbon and nitrogen isotope ratios in bird feathers has the potential to reveal important information on trophic position and sources of prey during feather formation (Hobson, 1999). Isotope signatures of feathers represent the diet at the time of growth and therefore give dietary information over a much wider temporal scale than faecal analysis (Bearhop *et al.*, 1999). The use of stable isotopes also overcomes some of the biases normally associated with conventional dietary analyses, as the isotope signature represents assimilated as opposed to ingested food (Bearhop *et al.*, 1999). Their utility lies in the fact that stable isotope ratios in the proteins of consumers reflect those of the proteins in their diet in a predictable manner (Bearhop *et al.*, 2004).

The stable isotope technique is also useful in situations where two isotopically distinct dietary sources are available to consumers (Hobson and Clark, 1992). This is the case with sparrows as they feed on vegetable material (e.g. seeds, bread etc.) as well as invertebrates, and these two categories of prey are likely to have very different stable isotope ratios (see Chapter 7). In such cases isotopic analysis of tissues provides quantitative information on the relative contributions of each source to the diet (Hobson and Clark, 1992).

2.2.3 Census methodology

In order to estimate the density of breeding House Sparrows in each study area, a census of the number of breeding House Sparrows was undertaken. During 2001, the city centre was the only area surveyed between February and May. However in 2002 and 2003 all nine study areas were surveyed during this period. Surveys of House Sparrows are best conducted at the beginning of the breeding season when males spend a lot of time early in the morning calling at nest sites (Summers-Smith, 2000). A male House Sparrow has a distinctive chirp that it calls persistently in spring to proclaim ownership of its nest-site and to attract a mate (Summers-Smith, 1963) and is therefore detectable. However, surveys in suburban/urban environments may miss a proportion of birds because of the difficulty in gaining access to gardens, or in observing the back of buildings (Bland, 1998). In order to limit background noise levels from traffic obscuring calling birds, all surveys were undertaken before 09:00 (BST).

The survey method was based on that developed by Summers-Smith (2000) for urban House Sparrows. Where the study area was large it was divided up into sections which were visited on successive days. Each study area was surveyed twice during the months of February and May. A census visit constituted six observer hours a day, two people undertaking the census together for three hours each day between the hours of 06:00 and 09:00 (all times are BST). Each person walked the area with a map, marking the positions of calling males. If a female was seen or a male was seen but was not actively calling, these were still marked on the map but with a different colour to the calling males. The total numbers of calling males from the two visits were added and then divided by two to give an average and this count and the area of each site were used to calculate the density of pairs in each study area. It was assumed each male represented a pair and therefore the count was doubled and then divided by the area to give number of birds per hectare (Summers-Smith, 2000) (see Chapter 3).

2.2.4 Habitat selection and utilisation

A key aspect of the House Sparrow's breeding ecology that needed to be investigated was habitat selection by foraging adults. This was undertaken through the recording of foraging observations whilst walking along fixed transect routes once a month during May, June and July to investigate seasonal changes in habitat selection. Transects were selected to cover all key habitats and observations of foraging House Sparrows were recorded for approximately 1.5 hours per transect. Transects were established along the urbanisation gradient and sixteen were set up in rural locations, sixteen in suburbia and twelve in the city centre. The percentage cover of thirteen habitat types (Table 2.2) was mapped 50 metres either side of the transect route during an initial visit. Usage of these habitats by foraging House Sparrows was determined during transect surveys.

The surveying took place at different times of the day in order to reduce the influence of any diurnal variation in foraging behaviour. The following data were recorded: the number of foraging and non-foraging (e.g. calling, bathing, loafing) birds in each habitat type and where possible the species of vegetation the adult was feeding in, the distance of the bird from the observer, the number of juveniles, the period of observation and the weather conditions. The juvenile-to-adult age ratio provided an indirect measure of local productivity for each of the 9 study areas. Age ratios are a useful method for studying annual productivity in multi-brooded passerines, where it is not possible to locate and monitor all nesting attempts (Peach *et al.*, 1996) (see Chapter 8).

2.2.5 Provisioning Watches

Drent *et al.* (1980) give evidence that when feeding young under normal circumstances, parents operate close to a hypothesised energetic limit of four times the basal metabolic rate. Any additional metabolic demands initiated by cold weather or food shortage could force parents to draw on body reserves. There is some evidence that, rather than risk a severe loss of condition, parent birds may simply reduce the feeding rate to nestlings, which might lead to weight loss in nestlings (Drent and Daan, 1980). The rate of provision of food by adult birds could be an important indicator of the amount of food available to feed the young and therefore the nestling’s subsequent survival. Seel (1969) investigated this through assessing the visiting frequencies of adults to their nestlings. The methodology used by Seel (1969) was duplicated in this study, to determine whether there where any variations in feeding rates and the subsequent survival of nestlings across the breeding season and across the urbanisation gradient.

The technique of provisioning watches was undertaken during the breeding season of 2003, at selected nest-boxes to determine the types of food adult House Sparrows were bringing to the nest, as well as the rate of provision. Food type was assessed through direct observation using a telescope trained on the nest-box. In many cases it was possible to identify the food the adults were bringing back to the nest as well as recording the number of visits the adults made. The food type was categorised into six groups: Coleoptera (beetles), Arachnida (spiders), Homoptera (aphids/froghoppers), Diptera (flies/craneflies), artificial food (bread/seed/peanuts), and unknown.

Two observers watched each nest for a standardised period of 1.5 hours and the number of provisioning visits made and food type was recorded. Provisioning watches were carried out at sites along the urbanisation gradient and across the season. After each provisioning watch was completed, the nest site was vacated, before returning between two and three hours later to collect biometric data and faecal samples from the nestlings. In order to establish if diet assessment from the composition of invertebrates from provisioning watches corresponded closely with the overall composition of invertebrate prey remains in faecal samples, the relationship was assessed (see Appendix).

2.2.6 Aphid abundance

Relatively high rates of chick starvation especially in second and third broods (Chapter 5) suggested that the availability of invertebrate prey might have been limiting nesting success. Aphids are known to be an important component of chick diet in some passerine species (Moreby and Stoate, 2001) and especially in the diet of nestling House Sparrows (Seel, 1969; Wilson *et al.*, 1999) in second and third broods. I tested whether nesting success or chick condition were related to the local abundance of Aphids (Aphididae). Although I lacked the resources to estimate the abundance of all chick invertebrate prey, I developed a simple, repeatable method for assessing the relative abundance of aphids within the foraging ranges of provisioning adults. This allowed me to test for relationships between nesting success and chick condition, and local aphid abundance. During the 2003 breeding season, fieldwork was undertaken to establish the relative abundance scores of aphids within the foraging ranges of 29 occupied nest-boxes.

Aphids live on fresh, growing vegetation, on the undersides of leaves and on flower petals and especially the growing tips of green stems. They utilise a wide variety of plants but certain species are more strongly associated with aphid infestation (University of Missouri, 2000) and were therefore given priority in aphid surveys. Aphid densities were recorded in four categories of plants (trees, shrubs, vegetables and grasses/flowers) and within two distance categories of each nest-box (within 50m and 50–100m). Within each distance category I aimed to score aphid abundance on 15-20 deciduous trees, 15-20 samples of deciduous shrubs, 10-15 samples of vegetables and 25-30 samples of flowers and herbs, although in many situations the target samples size for some plant types did not exist within the home range (e.g. vegetables).

For shrubs and trees, aphid abundance was scored at ten regularly spaced locations around the plant. Individual stems, shoots or branches with freshly growing, green vegetation were selected. An aphid abundance score was given using a four-point ordinal rank scale: 0 = no aphids present; 1 = fewer than 15 aphids were counted on the shoot; 2 = between 16 and 30 aphids present; 3 = the sample was heavily infested with more than 30 aphids. By scoring ten locations on a single tree/shrub, the summed score for the whole plant lay between 0 and 30. Each of these ten scores were recorded.

For most small plants (i.e. most vegetables and flowers) the scoring system was applied to the whole plant (i.e. a single score describing the whole plant). For each plant scored, the plant species, each individual aphid score (i.e. ten shoot scores or one whole plant score) and whether or not spittlebugs or froghoppers (Aphrophoridae) were seen on the shoot/plant was recorded. If we were unable to identify the plant species it was recorded as unknown.

Higher priority was given to deciduous trees and shrubs than to coniferous species, which had lower densities of aphids. A widely distributed number of plants were sampled across the home range (i.e. not just from one garden), and an effort was made to ensure that species known to be vulnerable to aphid infestations were sampled. These species included sycamore *Acer pseudoplatanus*, apple *Malus domestica*, elder *Sambucus niger*, bramble *Rubus fruticosus*, field rose *Rosa arvensis*, hawthorn *Crataegus monogyna*, buddleia *Buddleia davidii*, hogweed *Heracleum sphondylium*, thistle *Cirsium arvense* and shepherd’s purse *Capsella bursa-pastoris* (Julien, 1998; University of Missouri, 2000). Only the lower branches were reachable for the taller trees and a ladder was only used if all of the foliage was out of reach.

Aphid abundance scores were summed across plants to give an overall score for the foraging range around each individual nest-box. The score was divided by the maximum possible score available, to give a value out of one. For example if there were only ten shrubs sampled in an area, then the maximum possible score would be 300 (10 x 30). However if the actual total score was 200 (each shrub had a sum score of 20), then it would 200 divided by 300 (actual total score/possible total score) to give an overall score value. The nearer this overall value is to 1, then the greater the density of aphids in the area.

2.2.7 Habitat composition

The habitat composition around an occupied nest-box could be an important predictor of nesting success. Therefore habitat composition was mapped within 70m of each occupied nest-box. House Sparrows will not usually fly more than 200m from their nest site to forage for food (Summers-Smith, 1963). However a 200m radius around each occupied nest-box in a suburban area might contain more than 100 gardens and therefore due to logistic and time constraints, a radius of 70m was adopted. During observations of provisioning rate activity (section 2.2.5) the foraging locations of provisioning adults were determined. Within a suburban area approximately 60% (60/99 observations on 3 broods) of all foraging was undertaken within a 70m radius of the nest-box. Whereas in rural areas, approximately 70% (75/111 observations on 3 broods) of foraging was undertaken within this distance.

An area with a 70m radius was marked around each occupied nest-box on a 1:2500 map. The habitat within this area was then recorded and percentage cover calculated. The same habitat categories used to describe transect routes for the habitat foraging investigation (Table 2.2), were used to map the habitat around nest-boxes. These thirteen variables were reduced to seven prior to analysis. For example all grass habitats such as ungrazed, grazed, mown lawn and weedy patches were combined under one category heading of ‘grass’. There were strong correlations between the areas of the seven habitats recorded across home ranges. Principal Component Analysis (PCA) was used to reduce the seven habitat composition variable to a smaller number of principal components that better summarised variation in habitat composition across home range. PCA was implemented using procedure PRINCOMP of SAS (SAS Institute Inc, 1994).

Eigenvalues are the variances of the derived principal components and an informal rule for choosing the number of components to summarise a set of correlated variables is to use only those components with eigenvalues greater than one (Everitt and Der, 1996; Tabachnick and Fidell, 2001). It can be seen from Table 2.3 that if this rule is followed, then only component 1 and component 2 warrant enough explanatory power to be used. The first component accounts for 0.3987 or 39.87% of total variation in the seven input variables. The second accounts for another 0.2283 or 22.83%. Cumulatively these two components account for 0.6270 or 62.7% of the variation of the seven habitat categories.

Using the eigenvector scores in Table 2.4, the relative influence of different habitats on the different principal components can be assessed (Gnanadesikan, 1997). Thus, the first principal component (PRIN 1) represents variation in habitat across home ranges that is positively associated with area of grass, deciduous shrubs and trees, and negatively associated with area of concrete (Table 2.4). The second eigenvector (or component 2 - PRIN2) has a high positive loading for evergreen habitat and concrete and low scores for arable and grass habitats. Thus, PRIN2 represents variation across home ranges that is positively associated with concrete and evergreen shrubs, and negatively associated with grass and arable habitat. Principal components 1 and 2 (PRIN1 and PRIN2) therefore replaced the seven habitat composition measures in all subsequent analyses involving habitat composition (see Chapter 4, 5 and 6).

2.2.8 Capture and resighting

To investigate over-winter survival, fully-grown House Sparrows were individually colour-ringed at two sites, one suburban (Thurmaston) and one rural (Keyham) during the autumn of 2002. Each bird was ringed with a numbered BTO aluminium ring and a unique colour combination of three coloured plastic rings, which were sealed using acetone. There was an intensive capture period between the end of August and the beginning of October. Birds ringed as chicks during the breeding season only entered the capture-mark-recapture study if and when they were recaptured/resighted during October to March.

Over-winter survival rates were estimated from monthly ‘constant effort’ resightings. A resighting period constituted five observer hours a day, one day a month. Resighting was carried out at the end of each month during November 2002 through to March 2003 (five occasions). Over-winter survival was estimated using the Cormack-Jolly-Seber model which allows for the incomplete sightings/captures of surviving marked birds (Lebreton *et al.*, 1992). The models were fitted using program MARK (White and Burnham, 1999) (see Chapter 9).

2.3 Collecting and processing the air pollution data

Summers-Smith (1999) hypothesised that air pollution levels might be affecting urban House Sparrows, either directly or via their invertebrate prey. We investigated this hypothesis by studying the pollution levels and nesting success across the urbanisation gradient of the study areas.

The 1995 Environment Act legally requires Leicester City Council to monitor and review air quality within the city boundaries (Leicester City Council, 2000). This consists of screening specified sources or background levels of key pollutants. A number of key pollutants are monitored and the concentration of a specific pollutant at a given point is measured. Data are collected from eight monitoring stations situated across the city to provide a continuous assessment of pollutant levels.

A dispersion model interpolates between measuring points to predict air quality levels at all points in space and time across the whole city. The computer modelling system that was used to calculate pollutant values at these points over time, was ADMS-Urban Version 1.6 (C.E.R.E, 1999). This is a PC-based computer system that models dispersion in the atmosphere from pollutants that have been emitted from industrial, domestic and road traffic sources in urban areas. Results can be calculated for specific locations (in this case a nest-box) and can be run for a maximum of ten pollutants at a time. In order to account for changes in weather and changes in traffic flow throughout the day and week, meteorological data and traffic profiles are included in the model to predict pollution levels. The pollutants monitored as part of this scheme are benzene, sulphur dioxide, lead, carbon monoxide, nitrogen dioxide, and PM_{10} particulates (Leicester City Council, 2000).

This was an invaluable resource, as data collected from this scheme were used to investigate pollution levels around each occupied nest-box. The pollutant data that were utilised in this study were sulphur dioxide, nitrogen dioxide and carbon monoxide. Sulphur dioxide arises particularly from combustion plants such as power stations and from the burning of diesel engines (Environment Agency, 2001). Nitrogen dioxide is a toxic gas and in elevated conditions it exacerbates respiratory conditions in humans (Environment Agency, 2001). It is estimated that road traffic accounts for 46% of total UK emissions of nitrogen dioxide (Leicester City Council, 2000). The main source of carbon monoxide in the UK is road transport, which accounts for around 75% of total emissions (Leicester City Council, 2000). Therefore to investigate the hypothesis that air pollution in urban areas are affecting House Sparrows, these three pollutants, as the principal by-products from vehicle emissions, were chosen to be studied in more detail.

A postcode was allocated to each occupied nest-box and a time scale of 1st March to 1st September each year was set and hourly daily levels for each occupied nest-box between these dates were produced. Summer averages of the three pollutants were calculated separately for each year the nest-box was occupied.

The three pollutants that were collected are all in some aspect correlated to one another and when analysing highly correlated independent variables they may produce unstable estimates (Rencher, 1995). I checked for correlations between the three measure of air pollution as they shared common sources like vehicle emissions. Nitrogen dioxide was uncorrelated with sulphur dioxide but carbon monoxide was highly correlated with nitrogen dioxide ($r=+0.83$, $n=87$, $P<0.0001$). However carbon monoxide was excluded from all analyses on the grounds that it is highly correlated with nitrogen dioxide. Nitrogen dioxide was the covarariate used to test for influence of pollution in all analyses.

2.4 Intercorrelations and associations between variables used in multivariate analyses

When multivariate models are developed using the minimum adequate model (MAM) approach (Crawley, 1993) they can have limited power to distinguish between the apparent effects of inter-correlated explanatory variables (James and McCulloch, 1990). To aid the interpretation of the MAMs within this study, I tested for inter-correlations between the following 6 continuous predictor variables: DATE, RAIN (daily total), TEMPERATURE (daily maximum), NO2, PRIN1 and PRIN2. The stronger the correlation between predictor variables, the more cautious the interpretation of its influence needs to be. The 6 predictor variables corresponding with every brood attempted between 2001 and 2003 were tested; therefore data from all 3 years were included but not combined in the testing procedure.

The Pearson's correlation coefficient between all combination of these variables are presented in (Table 2.5). Three significant correlations are apparent. The first significant correlation is a positive relationship between DATE and TEMPERATURE, therefore as date increases i.e. as summer progresses; the daily maximum temperature increases. The second significant correlation is a negative relationship between TEMPERATURE and RAIN, reflecting a general tendency for warm days to be dry. The third significant correlation is between PRIN1 (habitat variable) and NO2. This is a negative association, with PRIN1 reflecting a tendency for the amount of grass, deciduous shrubs and trees within a home range to decrease as NO2 increases.

Analysis of Variance (procedure ANOVA in SAS) (SAS Institute Inc, 1994) to determine whether five of these predictor variables (RAIN, TEMPERATURE, NO2, PRIN1 and PRIN2) differed systematically between PERIOD and LANDSCAPE. It can be seen that RAIN, TEMPERATURE and NO2 all differed significantly between PERIOD (Table 2.6). The amount of daily rainfall peaked in period 2 (June) with periods 1 and 3 being drier. The maximum daily temperature significantly increases across the summer, with the highest daily temperatures being in July (period 3). Nitrogen dioxide levels peaked in period 2 and were lowest in period 3 (Table 2.6).

The variables, NO2, PRIN1 and PRIN2 all differed significantly between home ranges in different landscapes (Table 2.6). Nitrogen dioxide levels were much higher in urban areas than in rural or suburban areas. The variable PRIN1 (representing relatively large areas of grass, deciduous shrubs and trees) was highest in rural areas and lowest in urban areas (Table 2.6). PRIN2 (representing relatively large areas of concrete, evergreen shrub and small areas of grass and arable) was highest in urban areas and lowest in rural areas.

Table 2.1 Details of various characteristics of the nine study sites

Name	Landscape	Area (ha)	Dwelling per hectare[1]	**Average summer air pollution levels[2]**			**No. boxes occupied/available**		
				NO^2 (µg/ m^3)	SO^2 (µg/ m^3)	CO (mg/ m^3)	**2001**	**2002**	**2003**
1. City Centre	**Urban**	**336**	**23.19 (dwelling & retail units)**	**32.7**	**1.29**	**0.1**	**0/62**	**0/70**	**1/70**
2. Cobden Industrial Estate	**Urban**	**56.25**	**0.8** **(industrial units)**	**32.9**	**4.46**	**0.1**	**0/0**	**0/26**	**0/26**
3. Braunstone Industrial Estate	**Urban**	**112.5**	**0.3** **(industrial units)**	**25.6**	**2.96**	**0.05**	**0/0**	**0/30**	**0/30**
4. Braunstone	**Suburban**	**100**	**15.53**	**27.5**	**0.37**	**0.05**	**0/18**	**8/65**	**19/65**
5. New Parks/Western Park	**Suburban**	**100**	**15.89**	**29.2**	**0.35**	**0.05**	**0/7**	**0/50**	**2/50**
6. Thurmaston	**Suburban**	**156**	**11.15**	**22.4**	**0.37**	**0.03**	**1/12**	**16/55**	**21/55**
7. Houghton on the Hill	**Rural/ Suburban**	**50**	**8.44**	**19.0**	**0.20**	**0.02**	**1/90**	**6/90**	**11/90**
8. Keyham	**Rural**	**25**	**3.2**	**18.1**	**0.23**	**0.02**	**0/55**	**3/60**	**6/60**
9. Hungarton	**Rural**	**37.5**	**2.67**	**17.1**	**0.17**	**0.01**	**0/0**	**1/35**	**3/35**
						Total	**2/254**	**34/480**	**63/480**

[1] Data obtained from Leicester City Council

[2] Data obtained from Leicester City Council using ADMS-Urban v1.6 modelling software on data collected from monitoring stations across Leicester

Table 2.2 List of habitat category types

Habitat categories

1. Building/roads/concrete
2. Weedy patches
3a. Ungrazed mown lawn (lawns)
3b. Ungrazed grass
4 Grazed grass
5. Evergreen hedge/shrub
6. Decidious hedge/shrub
7. Ornamental shrubs
8. Tilled land (flowerbeds/allotment)
9. Woodland/spinneys
10. Individual trees
11. Arable farmland
12. Water bodies (ponds, lakes, rivers)
13. Farmyard/farm buildings

Table 2.3 The principal components analysis eigenvalues of the seven habitat categories

	Eigenvalues of the correlation matrix			
	Eigenvalue	Difference	Proportion	Cumulative
1	2.79083939	1.19266385	0.3987	0.3987
2	1.59817553	0.73027490	0.2283	0.6270
3	0.86790063	0.06941325	0.1240	0.7510
4	0.79848738	0.27322949	0.1141	0.8651
5	0.52525789	0.13874025	0.0750	0.9401
6	0.38651764	0.13874025	0.0552	0.9953
7	0.03282153	0.35369611	0.0047	1.0000

Table 2.4 The eigenvectors produced from the principal component analysis of the seven habitat categories; Key: Conc=concrete; Grass=grass habitats; Decid=deciduous shrubs; Evergr=evergreen shrubs; Orn/fb=ornamental shrubs & flowerbeds; Tree=trees; Arable=arable farmland

	Eigenvectors						
	Prin1	**Prin2**	**Prin3**	**Prin4**	**Prin5**	**Prin6**	**Prin7**
Conc	-0.5324	0.3103	-0.0845	0.1721	0.1117	0.0034	0.7557
Grass	0.4547	-0.3536	-0.1864	-0.3136	-0.4434	0.0160	0.5816
Decid.	0.4532	0.1302	-0.3267	0.2414	0.4499	-0.6309	0.1106
Evergr	0.2348	0.4693	0.0704	-0.6775	0.4198	0.2817	0.0715
Orn/fb	0.2712	0.2765	0.8360	0.1660	-0.2040	-0.2343	0.1644
Tree	0.4193	0.2026	-0.1363	0.5689	0.0264	0.6607	0.0605
Arable	0.0048	-0.6511	0.3590	0.0598	0.6082	0.1760	0.2065

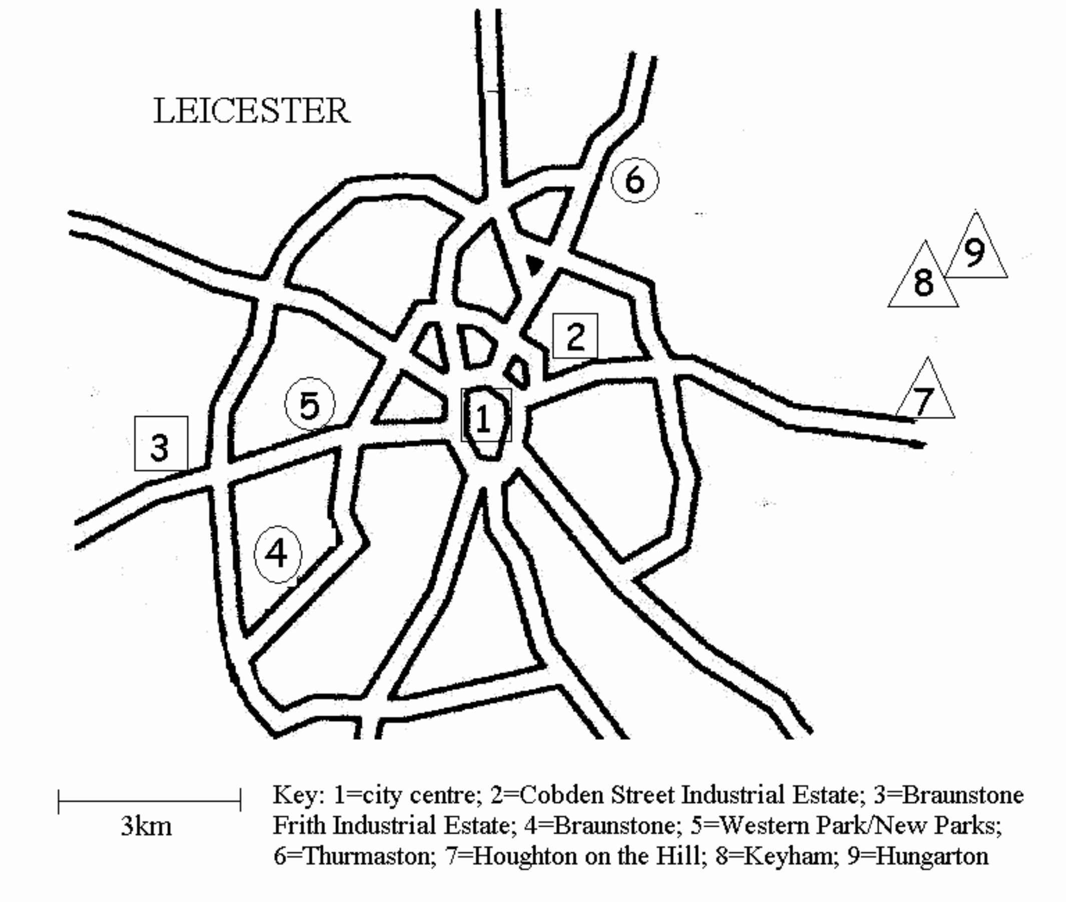
Table 2.5 Inter-correlations between predictor variables used in the multivariate analyses undertaken in this study [R=Pearson's correlation co-efficient] (significant associations between variables are printed in bold)

Variables	DATE	RAIN	TEMP	NO2	PRIN1	PRIN2
DATE		R = 0.043 *P* = 0.437 n=323	**R = 0.582** ***P* <0.0001** **n=323**	R = -0.096 *P* = 0.093 n=310	R = 0.099 *P* = 0.129 n=236	R = -0.014 *P* = 0.8354 n=236
RAIN			**R = -0.192** ***P* = 0.0005** **n=323**	R = 0.06 *P* = 0.293 n=310	R = 0.031 *P* = 0.640 n=236	R = -0.033 P = 0.6126 n=236
TEMP				R = -0.073 *P* = 0.198 n=310	R = 0.037 *P* = 0.575 n=236	R = 0.043 *P* = 0.507 n=236
NO2					**R = -0.499** ***P* <0.0001** **n=235**	R = 0.122 *P* = 0.063 n=235
PRIN1						R = 0.01 *P* = 0.877 n=236
PRIN2						

Table 2.6 ANOVA analysis results showing whether the dependent variables used in this study differed significantly between PERIOD and LANDSCAPE. Non-significant differences are shown in shaded areas. [Values are predicted means]

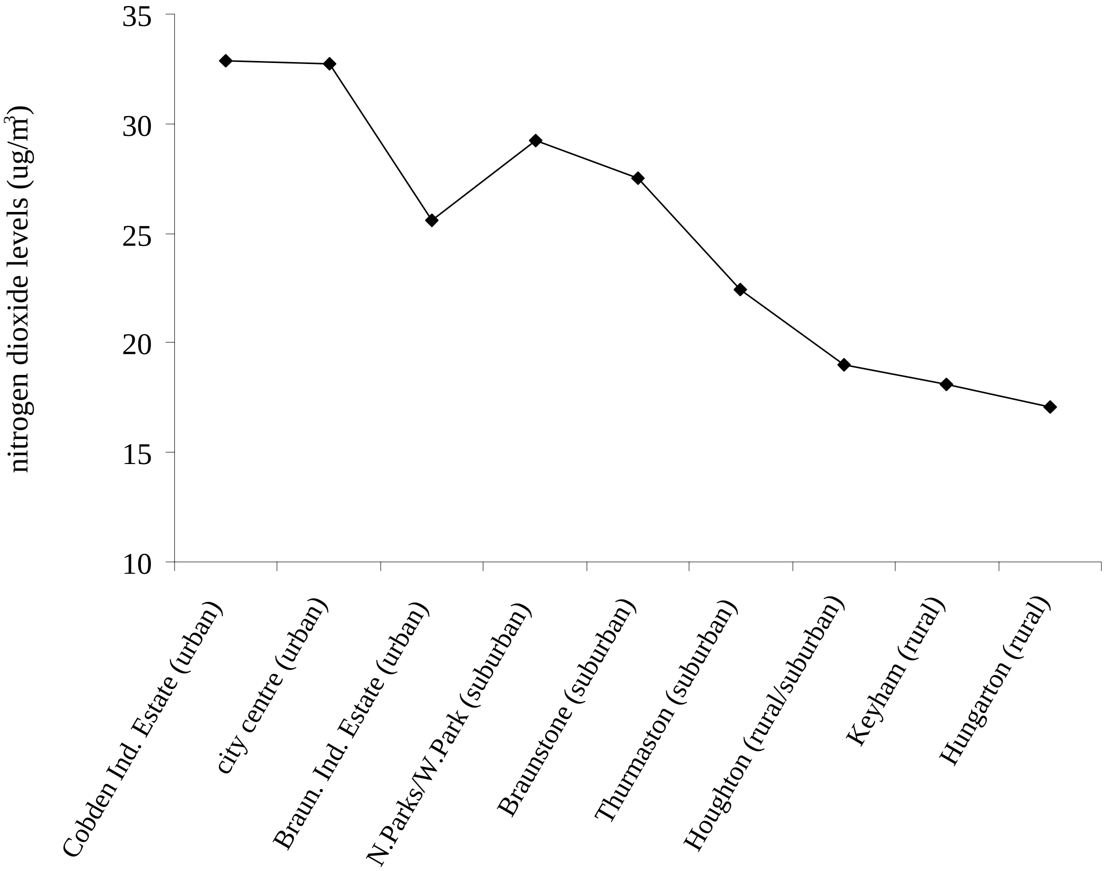
	PERIOD (predicted means)			**LANDSCAPE (predicted means)**		
Dependent variable	**1**	**2**	**3**	**Rural**	**Suburban**	**Urban**
RAIN (daily total) *P*=0.019	1.6	3.11	1.54			
TEMPERATURE (daily maximum) *P*<0.0001	15.57	17.81	21.13			
NITROGEN DIOXIDE *P*=0.04 (PERIOD) *P*<0.0001 (LANDSCAPE)	24.75	25.53	23.13	18.6	24.6	34.7
PRIN1 *P*<0.0001				1.57	-0.67	-2.24
PRIN2 *P*<0.0001				-0.95	0.23	1.52

Figure 2.1 A map of Leicester showing the locations of the nine study areas; squared areas=urban landscape; circular areas=suburban landscape; triangular areas=rural landscape



Key: 1=city centre; 2=Cobden Street Industrial Estate; 3=Braunstone Frith Industrial Estate; 4=Braunstone; 5=Western Park/New Parks; 6=Thurmaston; 7=Houghton on the Hill; 8=Keyham; 9=Hungarton

Figure 2.2 Summer averages of nitrogen dioxide levels at each of the study areas



CHAPTER 3

The status of House Sparrow *Passer domesticus* populations across a number of study areas within Leicester between 2001 and 2003

Abstract

Although there is evidence of substantial declines in House Sparrow *Passer domesticus* numbers in several UK conurbations, there is little quantitative information documenting changes in numbers or in demographic traits in urban-suburban habitats. I surveyed breeding House Sparrows in 9 study areas across Leicester and surrounding villages during 2001, 2002 and 2003. Across all sites chirping males declined by 9% between 2001 and 2002 and by 22% between 2002 and 2003. The average annual rate of decline differed significantly between sites in urban (+3.7%), suburban (−16.5%), and rural (−24.6%) landscapes. Although a change in the timing of surveys might have influenced apparent changes between 2001 and 2002, methodology was standardised between 2002 and 2003.

3.1 Introduction

Large declines in House Sparrows in the UK during the last twenty-five years have led to its inclusion of the UK ‘Red List’ of species of conservation concern (Gregory *et al.*, 2002). The UK House Sparrow population was not monitored adequately by the Common Bird Census (CBC) until 1976, partly because that scheme did not target urban areas and gardens (Crick *et al.*, 2004). Since 1994 the Breeding Bird Survey (BBS) has covered a larger variety of UK habitats and regions. Incorporating both the CBC/BBS data for the period 1976 until 2002 there has been a population change of –69% (Baillie *et al.*, 2005). Since 1994, the largest regional declines have occurred in London (60% decline between 1994 and 2004), south east England (–29%) and eastern England (–20%) whilst numbers have increased significantly in the East Midlands (+20%) (Raven *et al.*, 2005).

Long term changes in abundance as measured by the Garden Bird Feeding Survey (GBFS) show that sparrow populations in rural areas have decline by 47% since the mid 1970s, whereas those in urban and suburban gardens have declined by about 60% (Siriwardena *et al.*, 2002; Robinson *et al.*, 2005). The main reasons for undertaking these surveys was to provide background context to declining populations, as there must have been some environmental or demographic problem and secondly to explore the variation in population changes across sites in order to identify correlates of population change.

3.2 Methods

3.2.1 Census methodology

The difficulties of carrying out censuses of birds in urban developments might explain the paucity of studies on urban bird communities and populations (Mason, 2003). There are problems in the surveying of a suburban/urban environment, as counts may miss a proportion of birds because of the difficulty in gaining access to gardens, or in observing the backs of buildings (Bland, 1998). Householders also have a natural wish to preserve their privacy, therefore making the act of carrying notebooks, maps and binoculars in some areas an uncomfortable activity (Mason, 2003).

Chirping males were surveyed twice in each of the 9 study areas during 2001, 2002 and 2003. As the 9 study areas were not fully established until the summer of 2001, only the city centre was surveyed between February and April 2001. The eight remaining study areas were established and surveyed twice between May and July 2001. In 2002 and 2003 all 9 study areas were surveyed twice between February and May, the period when chirping males are most evident and detectable (Summers-Smith, *pers. comm.*).

A census visit constituted approximately six observer hours a day, two people undertaking the census together for three hours each day between the hours of 06:00 and 09:00 (all time is BST). Where the study area was large it was divided up into sections which were visited on successive days. Due to the difficulty in gaining access to gardens in the suburban and rural areas, the survey routes in all 9 areas were along roads and pathways. The observer walked slowly along the route with a map, marking the positions of calling males using both visual and audible cues. If a female was seen or a male was seen but was not actively calling, these birds were still marked on the map but with a different colour to the calling males. The weather conditions were recorded for each survey. However if on the morning of the survey it was raining, the survey was postponed due to unfavourable and unacceptable weather conditions.

3.2.2 Statistical analysis of the census data 2001-2003

The number of males in each study area from the two visits were added and then divided by two to give a mean average count in each year. The first analysis used the raw data to investigate the percentage changes in male counts between years and overall population changes at each study area. I wanted to investigate whether abundance had changed over the course of the three years. The basic statistical framework employed was that of a generalised linear model (GLM) with a log link function and a Poisson error distribution, as is appropriate for count data (Crawley, 1993). The expected count is modelled as the product of categorical ‘year’ and ‘site’ effects which become additive on a logarithmic scale. The count data were not overdispersed (deviance/d.f. = 0.81).

A further analysis to establish whether there was a trend in the count data was undertaken. In this model, year was treated as a continuous variable to provide an average rate of change in counts over the three years. Finally I tested whether average rates of House Sparrow counts differed between sites in urban, suburban and rural landscapes. In this model, the expected count was a product of a categorical site effect, a continuous year effect and interaction between the year effect and a 3-level categorical landscape effect. Thus, the expected count at site i (=1 to 9) in year j (=2001 to 2003) is denoted by μ_{ij} and the log-linear model with site and year effects is: $\ln(\mu_{ij}) = \alpha_i + \beta_j$ where α_i is the effect for site i, and β_j is the effect for year j. This additive model assumes temporal changes in counts are homogenous across sites.

3.3 Results

3.3.1 Population change at each site over the study period

Raw counts of chirping House Sparrow males in the 9 study areas over the three years are presented in Table 3.. The number of adult males recorded in each study area, are presented along with the percentage changes between years. The density of House Sparrows within Leicester city centre (Table 3.) is comparable to other cities like Edinburgh, Glasgow, London and Hamburg that have experienced population declines (Mitschke *et al.*, 1999; Sanderson, 1999; Dott and Brown, 2000; Summers-Smith, 2000c).

Although House Sparrow density appears to be relatively low in the city centre of Leicester, numbers appear to be fairly stable with only a 2% decline over three years (Table 3.1). The relatively small numbers of House Sparrows at two industrial sites increased slightly during the study period (Table 3.1). All suburban study areas showed a decline in House Sparrow numbers (Table 3.1). House Sparrow counts declined by 19-37% at suburban study sites and by 42-45% in the two rural areas (Table 3.1). Across all 9 study areas, counts of male House Sparrows declined by 9% between 2001 and 2002, and by 21% between 2002 and 2003. This gives an overall decline of 28% in House Sparrow numbers between 2001 and 2003 (Table 3.1).

The relationship between nesting success and population decline (2001-2003) at each of the study sites was tested but was found to be not significant (P=0.337). The relationship between the proportion of juveniles seen on transects and population decline (2001-2003) at each of the 9 study sites was also tested and found to be not significant (P=0.205).

3.3.2 Temporal changes in relative abundance

The Poisson GLM indicated that the relative abundance of House sparrows, differed significantly between sites and years (Likelihood Ratio Test: year: χ^2=1427.9; df=8; *P*<0.001; site: χ^2=37.2; df=2; *P*<0.001). The 'year' parameters from the GLM confirmed that counts fell by 28.3% between 2001 and 2003 (and by 9% between 2001-2002 and 22% between 2002-2003). The smaller decline between 2001-2002 might have been influenced by the change in timing of census work between 2001 and 2002. Declaring year as a continuous variable in the GLM indicated the decline in abundance was statistically highly significant (LRT: year: χ^2=32.1; df=1; *P*<0.001; site: χ^2=1318.03; df=8; *P*<0.001), and indicated an average rate of decline of 15% per annum.

The interaction between year and landscape was significant (Likelihood Ratio Test (LRT): year*habitat: χ^2=13.6; df=2; *P*=0.0011;) indicating that trends in abundance differed between landscapes. The annual rate of change in abundance was weakly positive for urban sites (+3.7% p.a.) and strongly negative for rural (–24.6% p.a.) and suburban (–16.5% p.a.) sites. The trends did not significantly differ between rural and suburban sites (LRT: χ^2=1.6; df=1; *P*=0.21;). There was a tendency for population declines to be larger at greater distances from the city centre (Figure 3.1). The distance from the city centre and population decline was a highly significant positive relationship (correlation coefficient=0.853; *P*=0.003; n=9). Therefore as the distance increased from the city centre, the population decline also increased.

3.4 Discussion

3.4.1 Population changes of House Sparrows within Leicester

The city of Leicester and its suburbs have no historical House Sparrow survey data, therefore we do not know if House Sparrow numbers changed before 2001. Consequently the population change data presented in this chapter are the only available for House Sparrows in Leicester. The data indicate a large decline in the abundance of House Sparrows in suburban and rural areas between 2001 and 2003. The decline was largest during 2002-2003 and the average annual decline was 15% p.a. House Sparrow counts in Leicester City centre remained stable while small populations on industrial sites showed small absolute increases.

It is not obvious why House Sparrows should have decreased drastically in Leicester in just two years. House Sparrows now have a discontinuous distribution throughout suburban Leicester with some areas having isolated pockets of birds, next to streets that have none (Vincent, *per. obs.*). Although the selected study areas are not a random sample of the city and its surrounding villages, these data do suggest that House Sparrows may be declining across suburban areas of Leicester.

The pattern of largest population declines being seen in sites furthest away from the urban city centre, is an interesting one. The relatively low densities of House Sparrows close to the city centre might reflect stable low-density populations after a substantial decline. Using the BBS data for London, it was found that densities of House Sparrows in 2003 were lowest in the urban centre, and this is where the declines were greatest during 1994-2001 (Peach, *pers.comm.*) Therefore in London big declines have resulted in lower densities in the centre. This highlights the need for continued survey work to be carried out in urban areas over a much longer timescale.

However Guisborough, a market town in the north of England, has a much higher density of House Sparrows compared to cities that have experienced a decline in numbers (Summers-Smith, 2000c; 2000d). The density of sparrows in Berlin (Table 3.2), a city that has not experienced a decline (Witt, 1996), can be equated to House Sparrow levels in a town such as Guisborough (Summers-Smith, 2000c; 2000d). Density estimates as measured from BBS show a regional variation with regard to suburban and urban habitat, with the northwest England showing the lowest urban and suburban density (Table 3.2).

In garden habitats in winter, the GBFS data show that the sparrow population in Britain has declined by some 58% since 1970 (Siriwardena *et al.*, 2002). The population was largely stable until 1983, with a continuous decline ever since. This overall pattern of a period of population stability in the 1970s and early 1980s, with a subsequent continuous decline since 1983, is evident in both rural and urban gardens (Siriwardena *et al.*, 2002). Although it must be noted that populations in rural gardens have experienced a lesser decline (48%) than those in suburban gardens (60%) (Siriwardena *et al.*, 2002). The population declines in the wider countryside, as shown by CBC farmland occurred mainly between 1979 and 1983, prior to that observed in gardens. Nevertheless the population in this habitat has been fairly stable, although at a lower level since the mid-1990s (Siriwardena *et al.*, 2002).

Much has been made of declines in some inner cities, such as London (Sanderson, 1996) and Edinburgh (Dott and Brown, 2000). The BBS data (1994-2004) highlights the variability of decline across the UK in that London has shown a population decline of 60%, the south-east of England a decline of 29%, whereas the north-west of England has seen a much lower decline of 16% (Raven *et al.*, 2005). This pronounced regional variation maybe a feature of the decline that may help identify correlates relating to the change in House Sparrow population in the UK.

Table 3.1 Number of adult male sparrows recorded in each study area 2001-2003

	Number of adult chirping males in each study area									
	CC	**BIE**	**CIE**	**BRA**	**NP**	**THU**	**HO**	**KEY**	**HU**	**Total**
Landscape	Urban	Urban	Urban	Suburb	Suburb	Suburb	Sub/Rur	Rural	Rural	N/A
Area (ha)	336	112.5	56.25	100	100	156	50	25	37.5	**973.25**
2001	52	6	10	119	81	212	75	27	40	**622**
2002	51	7	8	108	71	206	65	20	31	**567**
2003	51	8	14	75	66	147	47	15	23	**446**
% change 2001-2002	-1.9	+16.7	-20.0	-9.2	-12.4	-2.8	-13.3	-25.9	-22.5	**-8.8**
% change 2002-2003	0.0	+14.3	+68.8	-30.6	-7.0	-28.6	-27.7	-25.0	-25.8	**-21.4**
% change 2001-2003	-1.9	33.3	+35.0	-36.9	-18.5	-30.7	-37.3	-44.4	-42.5	**-28.4**
Area (ha)	336	112.5	56.25	100	100	156	50	25	37.5	**973.25**
Density (chirping males/ha) in 2003	0.2	0.07	0.3	0.8	0.7	0.9	0.9	0.6	0.6	**0.5**

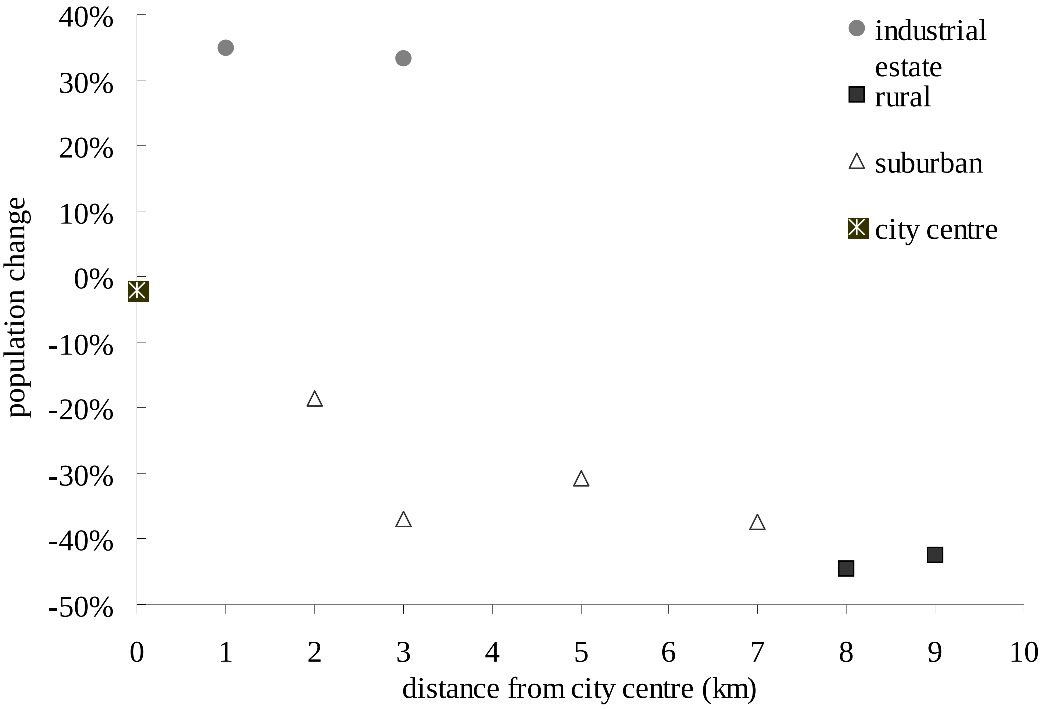
Key: CC = city centre; BIE = Braunstone Industrial Estate; CIE = Cobden Street Industrial Estate; BRA= Braunstone; NP = New Parks/Western Park; THU = Thurmaston; HO = Houghton; KEY = Keyham; HU = Hungarton;

Table 3.2 House Sparrow densities estimated from surveys across Europe

Location	Year	Area (ha)	Density (birds/ha)	Source
Leicester - City Centre	2001-2003	336	0.30	This study
Leicester – Suburban	2003	356	1.57	This study
Leicester – Rural	2003	112.5	1.32	This study
London (all areas)	1975-1996	326.2	0.22	(Sanderson, 1999)
Bristol	1996-1999	13,800	1.45	(Bland, 1998)
Glasgow: Maxwell Park	1959-1997	35	0.06	(Summers-Smith, 1999)
Dublin	2000	229	0.20	(Summers-Smith, pers. comm)
Edinburgh (City Centre)	1997-1999	350	0.20	(Dott and Brown, 2000)
Guisborough Town	1998	120	5.40	(Summers-Smith, 2000b)
North West England (Suburban)[1]	1994-2000	Unknown	2.6	(Siriwardena *et al.*, 2002)
North West England (Urban) [1]	1994-2000	Unknown	1.6	(Siriwardena *et al.*, 2002)
Central East England (Suburban) [1]	1994-2000	Unknown	4.4	(Siriwardena *et al.*, 2002)
Central East England (Urban) [1]	1994-2000	Unknown	2.4	(Siriwardena *et al.*, 2002)
South East England (Suburban) [1]	1994-2000	Unknown	3.4	(Siriwardena *et al.*, 2002)
South East England (Urban) [1]	1994-2000	Unknown	1.8	(Siriwardena *et al.*, 2002)
South West England (Suburban) [1]	1994-2000	Unknown	3.3	(Siriwardena *et al.*, 2002)
South West England (Urban) [1]	1994-2000	Unknown	2.3	(Siriwardena *et al.*, 2002)
Hamburg	1997-1999	3052	0.75	(Mitschke *et al.*, 1999)
Zurich	1980's	172,900	0.82	(Mitschke *et al.*, 1999)
Berlin	1989-1991	91,500	4.37	(Witt, 1996)

N.B. [1] BBS data include juveniles within counts

Figure 3.1 Population changes at the nine study areas between 2001-2003 and the distance of each site from the centre of Leicester



CHAPTER 4

Factors affecting the diet of House Sparrow *Passer domesticus* nestlings in rural and suburban habitats

Abstract

The diet of nestling House Sparrows was assessed by examining 204 faecal samples collected from 155 broods within Leicester and neighbouring villages between 2001 and 2003. The main prey of Araneae, Homoptera, Diptera and Coleoptera accounted for 80% of all invertebrate remains found in the faeces of nestling sparrows. The main factors associated with variation in the composition of invertebrate remains in nestling faeces were ‘PERIOD’, ‘LANDSCAPE’ and ‘CHICK OUTCOME’. The relative proportion of dietary components changed during the breeding season, with Coleoptera (beetles) and Diptera being most prominent during April and May and aphids being most prominent during June, whereas ants were most prominent during July and August. Faeces from urban localities contained a higher proportion of Homoptera than those from suburban or rural localities, whereas Diptera was more common in rural localities than in suburban or urban areas. Ants constituted a higher proportion of prey remains in faeces collected from chicks that subsequently died than in faeces from chicks that subsequently fledged. The amount of vegetable material in nestling faeces was greatest during July and August and was greater in faeces from chicks that subsequently died compared to those that went onto successfully fledge. A high proportion of vegetable material within faecal samples might indicate a general lack of invertebrate prey, possibly leading to malnutrition and starvation. Availability of suitable invertebrate prey may be an important factor limiting nesting success of suburban House Sparrows.

4.1 Introduction

Detailed knowledge of diet is critical to the study of avian biology. Numerous methods have been used to assess the composition of insectivorous diets. Techniques range from direct visual observations, to the use of neck ligatures and the analysis of stomach contents and faecal remains (Calver and Wooller, 1982; Rosenberg and Cooper, 1990; Moreby and Stoate, 2001b). In the case of nestling House Sparrows, all these techniques are useful for assessing nestling nutrition, as invertebrates form a major component of the diet (Summers-Smith, 1988; Wilson *et al.*, 1999).

Quantitative estimates of the composition of bird diet are often made by counting prey remains in faeces. Analysis of faecal samples represents a relatively non-invasive method of determining nestling diet (Moreby and Stoate, 2000). The method confirms that items have been ingested and samples may be collected with minimal stress to nestlings (Brickle and Harper, 1999). The method is also free from the problems of identifying small items by direct observation (Moreby and Stoate, 2001b). Although faecal analysis is itself associated with some bias against small soft-bodied groups (such as Hemiptera and Collembola) the bias is not always large (Moreby and Stoate, 2000). For example, estimates of the diet of Skylark *Alauda arvensis* nestlings based on neck collar and faecal samples from the same broods did not differ significantly (Poulsen and Aebischer, 1995).

4.2 Methods

4.2.1. Collection and inspection of faeces

Nestling mass (to the nearest 0.1g using a 50g Pesola spring balance) and tarsus (to the nearest 0.1mm using a dial calliper) were measured following the procedure of Svensson (1992) during each visit to the nest. Chicks commonly produced faecal sacs when handled. Faecal samples were collected during the breeding seasons (April to August) 2001-2003, from nestlings aged between 2-16 days.

The faecal samples were stored in vials of 70% alcohol until they were analysed in the laboratory. The contents of each faecal sample were deposited into a custom made petri-dish (following Green and Tyler, 1989; Gruar *et al.*, 2003). This was a 75mm diameter glass lid inverted and cemented on to the centre of a 115mm base, giving an annular channel of 20mm. The underside of the dish was scored with radial lines at 10^o intervals giving 36 equal segments. The contents of each faecal sample were placed into this circular channel with a small amount of ethanol, spread evenly across the 36 segments and inspected at 30x magnification using a binocular microscope. By rotating the dish through 360^o it was possible to search the entire contents and the prey items found in each section were recorded.

Much of the material present in the faeces consisted of fragments of insect cuticle and other debris that was difficult to attribute to particular taxa, however where possible the prey remains were identified to order and in some cases family. Recent literature, reference material (Calver and Wooller, 1982; Ralph *et al.*, 1985; Moreby, 1987b) and field guides were used to aid identification. The number and type of each body part, such as leg or mandible were recorded. For each of the main invertebrate groups encountered the following body parts were counted:

Coleoptera (beetles) – mandibles, legs, heads, elytra;

Diptera (flies) – heads, wings;

Lepidoptera (butterflies/moths) – wings, mandibles;

Homoptera (bugs such as froghoppers) – heads, legs;

Aphidae (aphids) – heads, siphunculi (paired dorsal tubes on abdomen);

All larvae such as lepidoptera and sawfly larvae– heads, mandibles;

Formicidae (ants) – heads, mandibles, legs, petioles;

Araneae (spiders) – chelicerae, fangs, pedipalps, leg tips;

The relative abundance of the different invertebrate groups was scored according to the numbers of body parts counted. For example, if a faecal sample contained three spider leg tips then that sample would be scored as containing 0.375 spider units, and a sample containing two ant legs would be scored as containing 0.33 ant units. This approach overcomes the common mistake of rounding prey fragments up to the nearest whole number (Sutherland, 2004).

The faecal samples were analysed for both invertebrate content and plant material content. The invertebrate abundance scores were summed into seven taxonomic groups for statistical analysis. These were spiders, adult beetles, Diptera (adult flying insects, mainly Tipulids and Culicidae), insect larvae, Homoptera (aphids and froghoppers), ants and others. A handful of samples contained mites but they were excluded from the analysis because they were probably ingested during preening or ingested accidentally on soil particles stuck to other prey items, as was the case in Gruar *et al.*,(2003).

An index of the relative proportion of vegetable material was estimated for each faecal sample. Vegetable material included mainly peanuts, bread and seed, along with genuine bits of plant vegetation too. The amount of vegetable material within each of the 36 segments was given a score out of ten reflecting the percentage cover of plant material within the segment (i.e. 0=0%, 5=50%, 10=100%) segment scores were summed to give a sample score between 0 and 360.

The proportion of vegetable material was analysed separately from the invertebrate data, as the two scoring methods were not directly comparable.

4.2.2. Data analysis

The reconstruction of the true diet of the House Sparrow was not possible, as there is no information on the relative passage rates and detectability of the various prey items from ingestion to defecation. However an analysis was undertaken of variation in the relative proportions of different prey groups between faecal samples collected from chicks of different ages, different study areas, and throughout the breeding season. To avoid pseudo-replication, data collected from different chicks of the same brood and of the same age were pooled, as samples from the same brood are not independent. As some broods were visited more than once, it was possible to use data from the same brood on different dates to compare changes in diet with chick age. The number of samples analysed was 204, of which 40 were collected in 2001, 46 in 2002 and 118 in 2003 (Table 4.21).

The counting of prey remains in faeces is one way to quantify the composition of the diet. Direct observation was also undertaken through watching provisioning adults at the nest with the aim to establish the validity of faecal analysis for estimating the composition of diet. The relationship between the overall composition of invertebrate prey remains in faecal samples and the composition of invertebrates from provisioning watches was assessed (see Appendix).

4.2.2.1. Statistical analysis of invertebrate composition within diet

Compositional analysis (Aebischer *et al.*, 1993) was used to identify factors and covariates influencing the composition of invertebrate prey remains in faecal samples. This technique was chosen because the proportions of individual prey groups in the diet summed to one (i.e. were linearly dependent). Compositional analysis (CA) specifically recognises this problem and overcomes it using a log-ratio transformation (Aitchison, 1986). Compositional analysis was used to identify factors influencing variation in the relative proportions of the seven prey groups in the faecal samples. This involved converting the seven proportions to six log ratios, the category ‘other’ being used as the denominator (analytical results are independent of the category used as the denominator). However log-ratios cannot be calculated if either proportion equals zero, therefore following Aebischer *et al.*, (1992), all zero proportions were changed to 0.0001. These log ratios were then treated as dependent variables in a multivariate analysis of variance (MANOVA, Tabachnick and Fidell, 2001).

I investigated the influence of several possible factors and covariates on the composition of nestling diet. These were:

chick AGE (3 level factor: 1 [1-5days], 2 [6-10days], 3 [>11days])

PERIOD (3 level factor: early [April & May], middle [June], late [July and August])

YEAR (3 level factor: [2001, 2002, 2003])

RAIN (continuous variables in the form of daily rainfall on the day the sample was collected)

TEMP continuous variables in the form of maximum temperature on the day the sample was collected)

TIME OF DAY (3 level factor: early [before 11:00hrs], middle [11:00 to 14:59hrs], late [15:00hrs onwards])

LANDSCAPE (3 level factor: rural, suburban, urban)

CHICK OUTCOME (2 level factor: subsequently died or fledged)

NO2 (continuous variable of nitrogen dioxide [pollution levels])

PRIN1 (continuous variable of the principal component describing habitat composition within 70m of the nest) (see section 2.2.7)

PRIN2 (continuous variable of the principal component describing habitat composition within 70m of the nest) (see section 2.2.7)

In the village of Houghton on the Hill, faecal samples collected from nests more than 200m from farmland, were defined as coming from a suburban landscape, while those less than 200 metres from farmland were considered rural. Low temperatures and high rainfall probably reduce invertebrate activity and hence availability to predators like birds (Pimentel, 1994; Frampton *et al.*, 2000; Bradbury *et al.*, 2003). Therefore rainfall and maximum temperature on the day of sample collection were included as continuous variables. The daily weather data were collected at a weather station situated at Cosby, approximately 6km south west of Leicester City centre. The time of day when the faecal samples were collected was also tested, as diurnal variation in the availability of invertebrates (Pimentel, 1994), might influence the composition of the diet.

As well as testing the influence of all factors, the interactions between factors and covariates were tested. However for MANOVA to be valid there must be more observations in each cell of the analysis than the number of dependent variables (six in this case) (Tabachnick and Fidell, 2001). The numbers of faecal samples analysed from each month in each year and from each landscape category are presented in Table 4.1. There are relatively few data from the urban landscape due to the low occupancy of nest boxes and lack of accessibility of nest-sites in the 3 urban study sites (Table 2.1 in Chapter 2).

Faecal samples from the same brood were pooled but if the individual chicks had different outcomes (i.e. one subsequently died but the other survived) the samples were analysed separately. All analyses of faecal invertebrate composition were carried out using the GLM procedure of SAS (SAS Institute Inc, 1994) and each faecal sample had a weighting which was the square root of the sum of the prey items in that sample. Samples containing the remains of many prey items therefore had more influence on the analysis than samples containing relatively few prey items. A minimum adequate model (MAM) explaining variation in invertebrate composition was developed by retaining in the model independent variables that caused the largest and statistically most significant reduction in model deviance. This ‘step up’ procedure continued, until no remaining independent variables could explain further significant amounts of model deviance (Crawley, 1993).

Once the main predictors of the composition of invertebrate prey remains had been established using MANOVA, univariate analysis of covariance (ANCOVA) was conducted on each of the six log ratios to identify predictors of variation in individual log ratios. The same set of predictor variables identified in the MANOVA MAM were initially entered into the model, and any non-significant predictors ($P>0.1$) were then dropped. Due to the multiple ANOVA’s there is an inflated Type 1 error rate (Tabachnick and Fidell, 2001), and therefore more stringent alpha levels are required. A Bonferroni-type adjustment was therefore applied to reduce the likelihood of Type 1 error (Tabachnick and Fidell, 2001). The Bonferroni-adjusted significance level of 0.008 was adopted for all univariate ANOVAs. As there were six dependent variables, this equates to an overall experiment-wise significance level of approximately 0.05 (Tabachnick and Fidell, 2001). However I also report effects significant at the $P < 0.015$ level (equivalent to an experiment-wise level of $P < 0.1$).

4.2.2.2. Statistical analysis of abundance of vegetable material within diet

The correct application of some statistical techniques assumes that samples have been drawn from populations that are normally distributed. However this is often not the case as, for example, many samples of ‘count’ data are from populations that are strongly skewed (Fowler and Cohen, 1997). If a distinct skew exists, statistical techniques that assume normally-distributed data may only be applied without risk of error, once the data have been ‘normalised’ by transformation (Tabachnick and Fidell, 2001). Of several transformations tested, the arcsine came closest to normalising the proportion of vegetable material data. These data were therefore analysed using a standard GLM assuming a normal error distribution. However, since the transformed data had a slight positive skew I checked the residuals from the final MAM were normally distributed.

The following covariates and factors were investigated as potential predictors of the proportion of vegetable material within nestling faecal samples:

chick AGE (3 level factor: 1 [1-5days], 2 [6-10days], 3 [>11days])

PERIOD (3 level factor: early [April & May], middle [June], late [July and August])

YEAR (3 level factor: [2001, 2002, 2003])

RAIN (continuous variables in the form of daily rainfall on the day the sample was collected)

TEMP continuous variables in the form of maximum temperature on the day the sample was collected)

TIME OF DAY (3 level factor: early [before 11:00hrs], middle [11:00 to 14:59hrs], late [15:00hrs onwards])

LANDSCAPE (3 level factor: rural, suburban, urban)

CHICK OUTCOME (2 level factor: subsequently died or fledged)

NO2 (continuous variable of nitrogen dioxide [pollution levels])

PRIN1 (continuous variable of the principal component describing habitat composition within 70m of the nest) (see section 2.2.7)

PRIN2 (continuous variable of the principal component describing habitat composition within 70m of the nest) (see section 2.2.7)

4.3 Results

4.3.1. Invertebrate composition in diet

Beetles, spiders, Diptera and aphids dominated the diet of nestling House Sparrows (Table 4.2). The invertebrate composition of faecal samples varied significantly between PERIOD, AGE, YEAR, LANDSCAPE and according to CHICK OUTCOME (Table 4.3). Although NO2 was only a marginally significant ($P<0.1$) predictor of invertebrate composition, it was retained in the model because of a significant interaction term involving NO2.

It can be seen from Table 4.3 that the relationship between chick age and diet composition differed between landscapes. The nature of seasonal (monthly) changes in diet differed between years and according to chick fate (Table 4.3). The nature of yearly changes in diet also differed between nitrogen dioxide levels and between the outcome of the chick (Table 4.3). The partial R^2 values indicate that the strongest predictors of invertebrate composition were PERIOD, LANDSCAPE (9%) and chick AGE (8%) (Table 4.3).

4.3.1.1. Seasonal and annual variation in diet composition

PERIOD was the strongest predictor of invertebrate composition in faecal samples with the relative proportions of beetle, Diptera, ants and Homopterans showing the strongest evidence of seasonal variation (Table 4.3). Ants were proportionately commonest in late summer (Figure 4.1 & Figure 4.2). Homopterans (aphids and froghoppers) accounted for a higher proportion of the invertebrate diet during June than earlier or later in the breeding season (Figure 4.1). The relative importance of beetles and Diptera decreased through the nesting season, with April and May being the most important (Figure 4.1). Although the pattern of seasonal variation in invertebrate composition varied between YEAR and according to CHICK OUTCOME (Table 4.3) neither of these interactions was a significant predictor (in univariate ANCOVAs) of variation in the proportions of any of the six invertebrate groups. The composition of the invertebrate remains differed significantly between years (Wilk's lambda $\Lambda=0.8552$; $P<0.05$,). Ants were proportionately commoner in 2002 than in 2001 and were scarce in 2003 (Table 4.3).

4.3.1.2 Differences in prey composition between different ages of chicks and between chicks that fledged and chicks that died in the nest

Invertebrate composition differed significantly according to AGE (Wilk’s lambda $\Lambda=0.844$; $P=0.005$,), however there was no single prey group whose relative composition significantly differed between age groups (Table 4.3). The only invertebrate group that came closest to significance was spider $P<0.1$. The relationship between chick AGE and invertebrate composition differed between LANDSCAPE (Wilk’s lambda $\Lambda=0.752$; $P=0.0028$,) but there was no single prey group whose relative composition differed with age and landscape.

Whether the chick died or survived (CHICK OUTCOME) was a significant predictor ($\Lambda=0.797$, $P=0.0002$) for diet composition (Table 4.3). Ants accounted for a significantly greater proportion of the diet in chicks that died compared to those that survived (Figure 4.3), as well as being more abundant in samples collected in July and August (Table 4.3). Thus, a relatively high proportion of ants in the diet of nestlings during the second half of the breeding season was associated with a higher risk of chick mortality (Figure 4.2). Spiders however accounted for a significantly greater proportion of the diet in chicks that survived compared to those that died. Therefore spiders appear to be more beneficial and nutritious to growing nestlings.

4.3.1.3 Differences in diet between study landscapes

The influence of landscape on invertebrate composition was significant ($\Lambda=0.831$, $P<0.003$). Diptera and Homoptera were both highly significant prey groups with regard to variation between landscapes ($P<0.001$). Homoptera accounted for a significantly higher proportion of the diet in urban areas than in suburban or rural areas (Figure 4.4), whereas a higher proportion of Diptera was found within the diet in rural areas compared to suburban and urban areas

(Figure 4.4). Diptera (mainly adult tipulids) are likely to be highly profitable prey while Homopteran bugs (mainly aphids) are not. This pattern probably reflects lower availability of Dipterans in urban/suburban landscapes and may be part of the reason the birds do less well there and are reliant on lower quality prey like aphids.

4.3.1.4 The influence of nitrogen dioxide levels on invertebrate composition in faeces

The influence of nitrogen dioxide on invertebrate composition varied significantly between years (Λ=0.849, *P*=0.007) (Table 4.3). This effect was evident for only one of the invertebrate groups, ants (*P*=0.0012) (Table 4.3). In 2001 and 2003, ants compromised a higher proportion of invertebrate remains at locations with relatively high nitrogen dioxide levels, while in 2002 there was no significant relationship between the proportion of ants and NO_2 levels (Figure 4.5).

4.3.2. Vegetable material in diet

Chick outcome (Wilk's lambda Λ=0.964; *P*=0.019), period (Wilk's lambda Λ=0.939; *P*=0.001), year (Wilk's lambda; Λ=0.972; *P*=0.05) and time of day (Wilk's lambda Λ=0.960; *P*=0.01) were significant predictors of the amount of vegetable material found within a faecal sample (Table 4.4).

4.3.2.1 Seasonal and annual variation in the relative abundance of vegetable material

The interaction between year and period showed a significant interaction when predicting vegetable material abundance in nestling diet (Wilk's lambda Λ=0.951; *P*=0.03) (Table 4.4). The relative abundance of vegetable material generally increased through the breeding season although in 2002 the relative abundance of vegetable material peaked during June, and declined thereafter (Figure 4.6). The proportion of vegetable material was highest in 2001 and lowest in 2002 (Figure 4.6).

4.3.2.2 Effect of chick fate and time of day on the amount of vegetable material ingested

The proportion of vegetable material was significantly greater in faecal samples from chicks that subsequently died than in samples that fledged (Wilk's lambda Λ=0.964; P=0.019) (Figure 4.7). A significant interaction between time of day of faecal collection and chick outcome (Λ=0.923; P=0.0023) suggests that a relatively high proportion of vegetable material in samples collected late in the day (after 15:00 hrs) was not associated with a higher risk of subsequent death (Figure 4.8).

4.4 Discussion

In this study it was found that nestlings are fed a large variety of invertebrate prey species and these vary with season. More ants and plant material were found in nestling faeces during late summer, with more aphids and froghoppers found in faeces during mid-season and beetles and Diptera being more prominent during April and May. The most important and most common prey species in this study were aphids, spiders, Diptera and adult beetles. In Oxfordshire, Seel (1969) also found that the most important invertebrate prey for nestling House Sparrows were aphids, Diptera and beetles. The composition of nestling diet within Seel's study also changed considerably during the breeding season, with dipterous flies especially Tipulids being most numerous until mid-May, and aphids first appearing in the diet in June but becoming more numerous in July (Seel, 1969). This seasonal variation in the diet of nestling House Sparrows is probably a consequence of variation in the availability of the more suitable foods in the environment, either because certain prey were easier to locate and catch at some times than others or because abundance varied.

Work undertaken by Seel (1969) over thirty years ago, found that plant material and bread was prominent in the diet of nestlings in June and July. The seasonal variation in nestling survival was best explained by variation in the availability of invertebrate prey (Seel, 1969). Bread was available to sparrows throughout the season, but was only taken later in the breeding season when prey like aphids and Diptera became relatively scarce. The seasonal variation of prey items like aphids and the problem of scarcity of aphid numbers later in the season are reflected in my data. Like Seel (1969), I also found there was an increase in the abundance of plant material during the later months of summer. Seel (1970) found that approximately one third of all broods completely failed and attributed these failures to nutritional deficiencies related to the consumption of unsuitable food, such as bread and vegetable material, as a consequence of a seasonal shortage of key invertebrate prey.

The prominence of plant material within the diet of chicks that subsequently died probably reflects a shortage of invertebrate prey. Seeds and grain do not contain essential amino acids such as Lysine which are found in animal protein and which are vital for rapidly growing nestling passerines (Ricklefs, 1983). Therefore nestling sparrows are fed substantial amounts of invertebrates because of the greater nutritional benefit compared to just feeding seed (Summers-Smith, 1988). However plant material may acquire an importance when invertebrate food is scarce. Therefore if there is a high proportion of plant material within the diet compared to invertebrate prey, this may indicate a general lack of available invertebrate food, leading to inadequate provision of food and hence starvation. High levels of chick starvation were observed in this study during June and August (see Chapter 5). In Seel's (1969; 1970) study, food shortage seemed to be the only important factor causing complete or partial failure of broods. These findings highlight that invertebrate food availability may be a key factor influencing the proportion of House Sparrow nestlings that successfully survive to fledging age and beyond.

The secondary analysis of the relationship between faecal sample composition and provisioning watch data during the preceding 2-3 hours (see Appendix) highlights that the reconstruction of the true diet of the House Sparrow is still not clear cut. Further research is needed to gain information on the relative passage rates and detectability in House Sparrow faecal remains, of the various prey items from ingestion to defecation.

Table 4.2 Numbers of faecal samples broken down by year, landscape and period*

		Time Period			
Year	**Landscape**	**Early**	**Middle**	**Late**	**Total**
2001	Urban	3	2	4	9
	Rural	5	2	7	14
	Suburban	8	2	7	17
2002	Urban	0	1	2	3
	Rural	0	6	9	15
	Suburban	4	6	18	28
2003	Urban	2	0	0	2
	Rural	17	9	14	40
	Suburban	25	22	29	76
Totals		**64**	**50**	**90**	**204**

* Early = April to mid-May; Middle = mid-May to end June; Late = July-Aug

Table 4.2 Total number of invertebrate prey units found in 204 analysed faecal samples split by landscape. See section 4.2.1 for an explanation of invertebrate prey units

Major prey groupings[1]	**Urban**	**Suburban**	**Rural**
Spiders			
Araneae (spiders)	19.95	9.19	10.14
Acarina (Mites)	0.00	1.60	0.00
Opilione (Harvestmen)	0.00	0.31	0.23
Beetles			
Coloeoptra Un-Specified	5.77	6.78	11.14
Carabidae (Ground Beetles)	3.12	3.04	6.23
Curculionidae (Weevils)	14.65	6.80	6.71
Staphylinidae (Rove Beetles)	2.53	0.63	1.59
Scarabidae (Dung Beetles)	0.00	1.60	1.57
Elateridae (Click Beetles)	0.00	0.29	1.06
Coccinellidae (Ladybirds)	0.00	0.69	0.40
Insect Larvae			
Coleoptera Larvae	6.45	0.69	2.25
Sawfly Larva	2.35	0.40	0.53
Diptera larv	0.00	0.57	0.60
Lepidoptera Larvae	0.00	3.08	1.99
Neuroptera larv	0.00	0.06	0.27
Un-Specified Larvae	0.00	0.06	0.00
Diptera			
Diptera	5.87	5.83	19.63
Tipulidae	0.00	1.77	8.04
Culcidae	0.00	0.11	2.65
Homoptera			
Homoptera (Bugs)	1.17	0.69	0.34
Aphid	20.53	39.74	8.75
Froghopper	6.44	0.65	2.03
Formicidae (Ants)	8.99	5.28	10.56
Others			
Heteroptera	0.00	0.11	0.00
Collembola	0.00	0.00	0.27
Isopoda	0.00	0.09	0.00
Nabidae (Damsel Bugs)	0.00	0.09	0.13
Nitidulidae/Chrysomelidae	0.00	0.91	0.53
Dermaptera (Earwigs)	0.00	0.00	0.27
Orthoptera (Grasshoppers etc)	0.00	0.00	0.05
Unidentified	1.94	1.26	3.00
Hymenoptra (Sawflies etc.)	0.00	1.63	2.25
Adult Lepidoptera	0.00	0.11	0.40
Adult Zygoptera (Damselflies)	0.00	0.06	0.27
Snails (Mollusca)	0.23	0.62	1.43

[1] Analytical units in compositional analyses

Table 4.3 Summary of multivariate and univariate analyses of factors affecting the invertebrate composition of House Sparrow chick faecal samples. Significance levels are uncorrected for multiple testing but are not listed under univariate ANCOVAS unless P < 0.015 (equivalent to experiment-wise significance level of 0.1). See section 4.2.2.1 for definitions of factors such as PERIOD, AGE, LANDSCAPE etc.

Compositional analysis[1] (MANOVA)	Partial R^2 (%)[3]	Prey groups showing significant effects in univariate ANCOVAS[2]
PERIOD***	17.0	Beetle*** (early>middle>late) Diptera* (early>middle>late) Ant*** (late>>early>middle) Homopteran*** (middle>early>late)
AGE**	8.1	
YEAR*	7.5	Ant** (2002>2001>2003) Other** (2002>2003>2001)
LANDSCAPE**	8.8	Diptera*** (rural>>sub>urban) Homoptera*** (urban>suburban>>rural)
CHICK OUTCOME***	6.9	Spider** (unknown>survived>died) Ant** (died>>unknown>survived)
NO2 (*)	5.1	Ant** (+ve)
PERIOD x YEAR*	5.7	Beetle***
LANDSCAPE x AGE**	6.9	
CHICK OUTCOME x PERIOD*	5.5	Ant***
CHICK OUTCOME x YEAR*	8.2	
NO2 x YEAR**	7.9	Ant*** (2001: +ve, 2003: +ve, 2002: no relationship) Other ** (2001: –ve, 2002: –ve, 2003: +ve)

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[1] MANOVA significance levels: ***P<0.001, **P<0.01, *P<0.05, (*)P< 0.1

[2] ANCOVA significance levels: ***P<0.001 (experiment-wise P<0.01), **P<0.008 (experiment-wise P<0.05), *P<0.015 (experiment wise P<0.1).

[3] Derived from Wilks' lambda using formula 9.9 on page 339 of Tabachnick and Fidell (2001)

Table 4.4 Summary of multivariate analyses of factors affecting the plant material composition of House Sparrow chick faecal samples. See section 4.2.2.1 for definitions of factors such as PERIOD, AGE, LANDSCAPE etc.

Independent Variables[1]	Partial R^2 (%)[2]	Direction and magnitude of the effect
YEAR*	2.8	2001>>2003>2002
PERIOD***	6.1	Late>>Middle>Early
TIME OF DAY*	4.0	Middle>>Late>Early
CHICK OUTCOME(*)	4.9	Died>>Survived>Unknown
YEAR x PERIOD*	2.6	2001: Late>Middle>Early 2002: Middle>Late>Early 2003: Late>Middle>Early
TIME OF DAY x CHICK OUTCOME**	7.7	Early: Died>>Survived>>Unknown Middle: Died>>Unknown>Survived Late: Survived>Unknown>Died

[1] Significance levels: ****P*<0.001, ***P*<0.01, **P*<0.05, (*)*P*< 0.06

[2] Derived from Wilks' lambda using formula 9.9 on page 339 of Tabachnick and Fidell (2001)

Figure 4.1 Weighted mean back-transformed arcsine proportions of (a) Diptera, (b) Homoptera and (c) ants in the diet of nestling House Sparrows during the early, middle and late nestling season

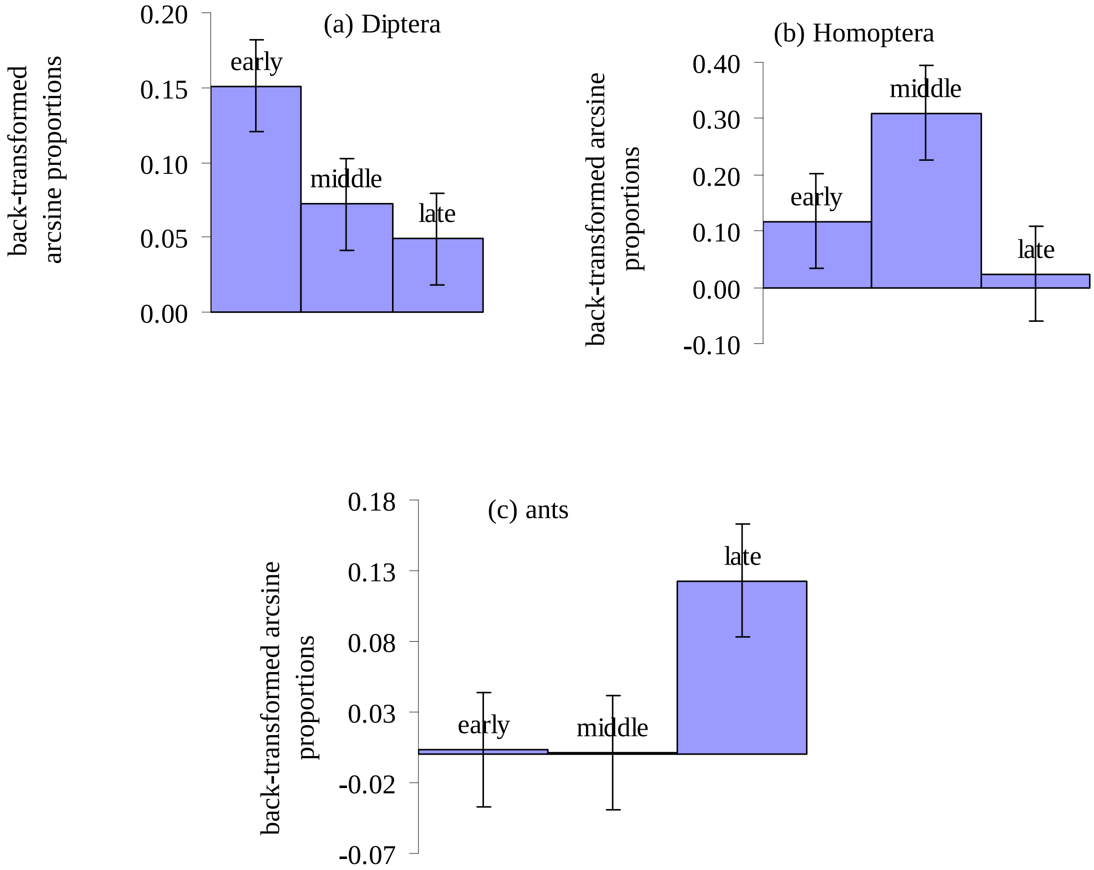


Figure 4.2 Effects of seasonality and chick outcome on the relative proportion of ants found in nestling faecal samples (n=204).

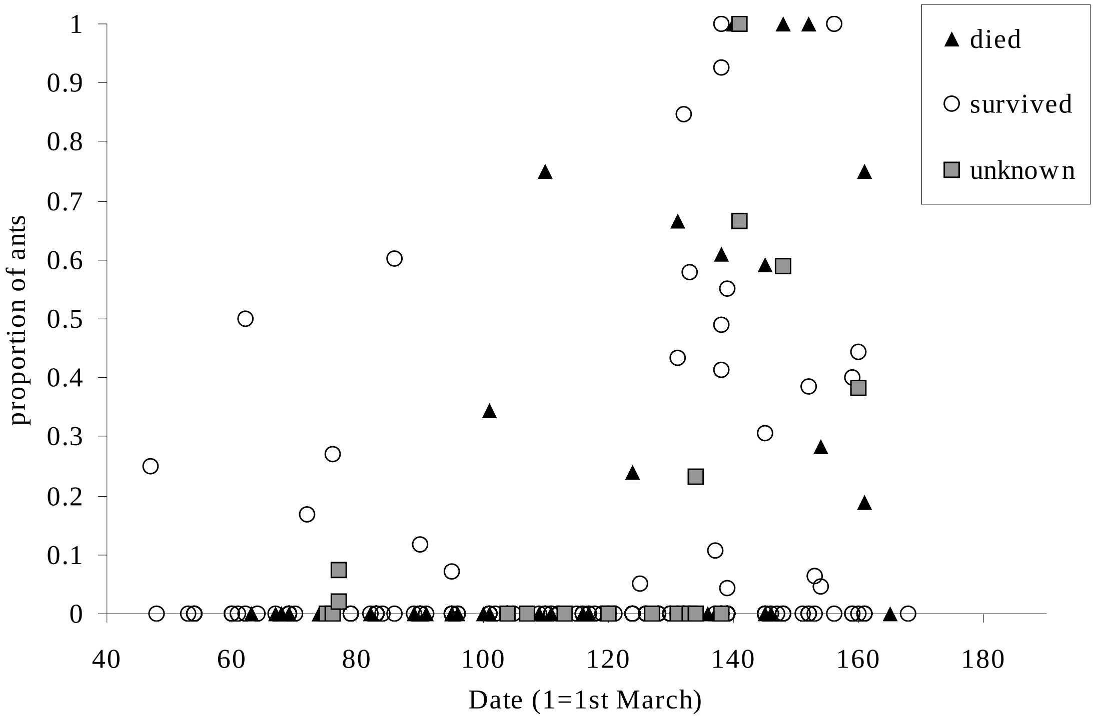


Figure 4.3 Weighted mean back-transformed arcsine proportions of nestling invertebrate diet comprising of (a) ants and (b) spiders in the diet of nestling House Sparrows with differing fates

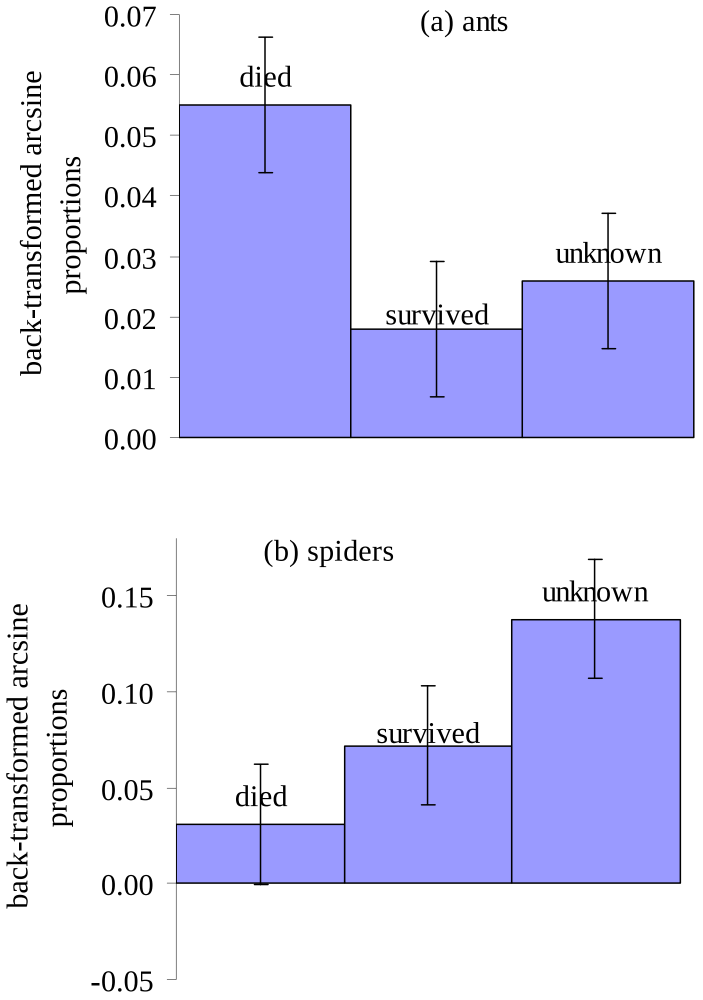
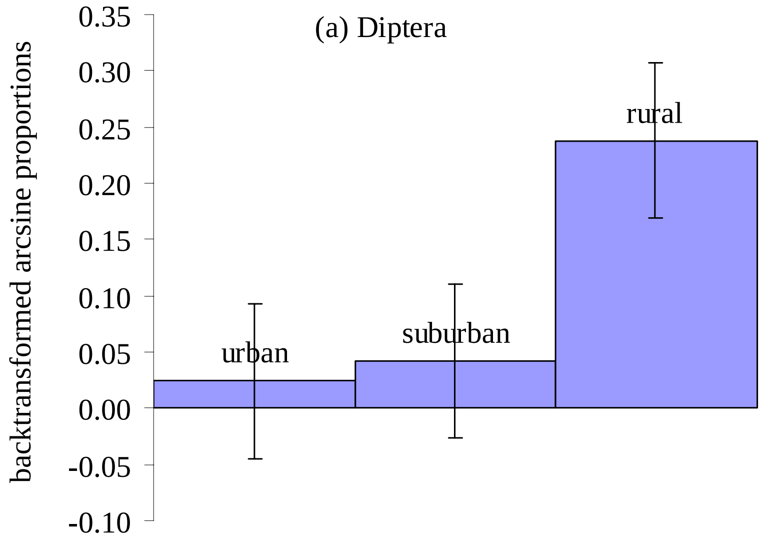


Figure 4.4 Weighted mean backtransformed arcsine proportions of nestling invertebrate diet comprising of (a) Diptera and (b) Homoptera in urban, suburban and rural landscapes



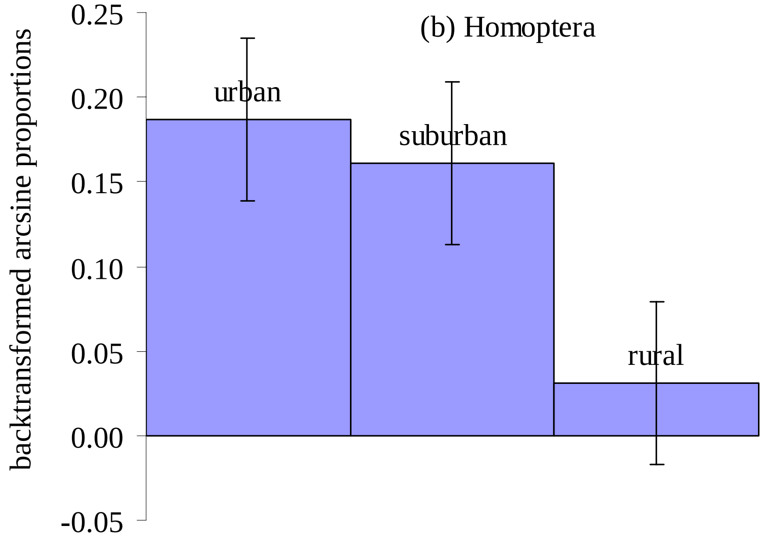


Figure 4.5 Effects of nitrogen dioxide levels and year on the relative proportion of ants found in nesting faecal samples (n=204)

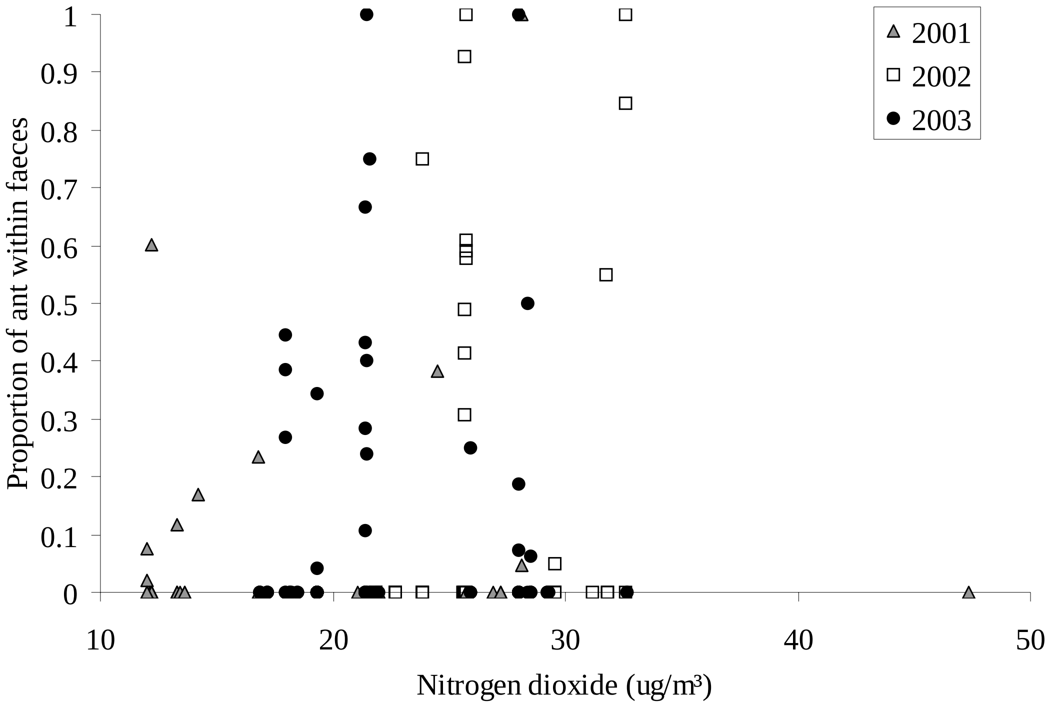
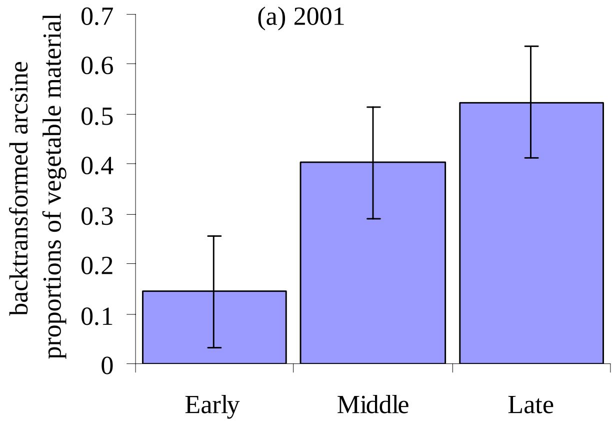
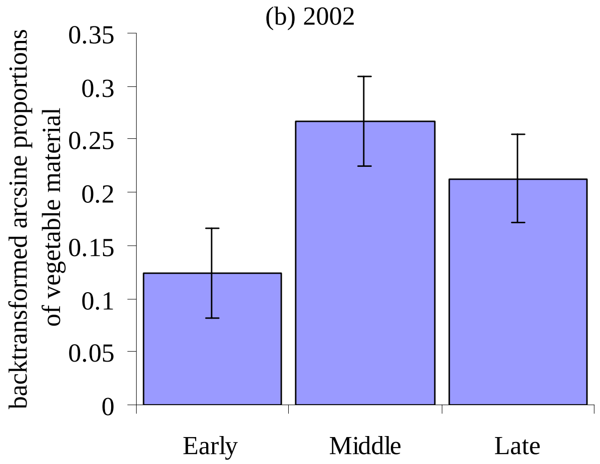


Figure 4.6 Seasonal changes in the backtransformed arcsine proportions of vegetable material in nestling faeces


(a) 2001


(b) 2002

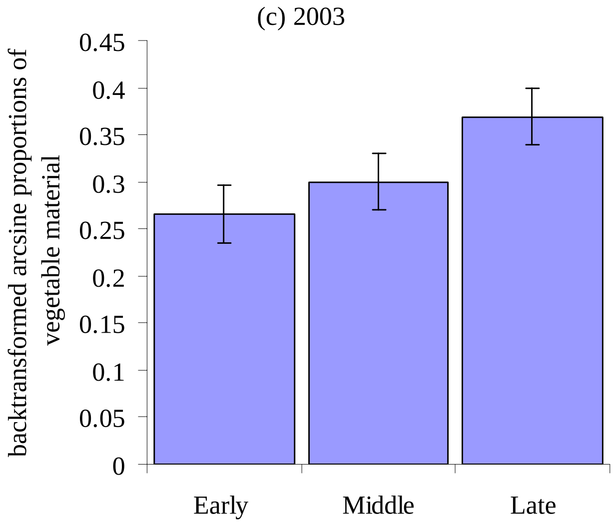

(c) 2003

Figure 4.7 Seasonal changes in the proportion of vegetable material in nestling faecal samples in relation to subsequent fate of the chick. Each point relates to a faecal sample collected from a single brood (n=200)

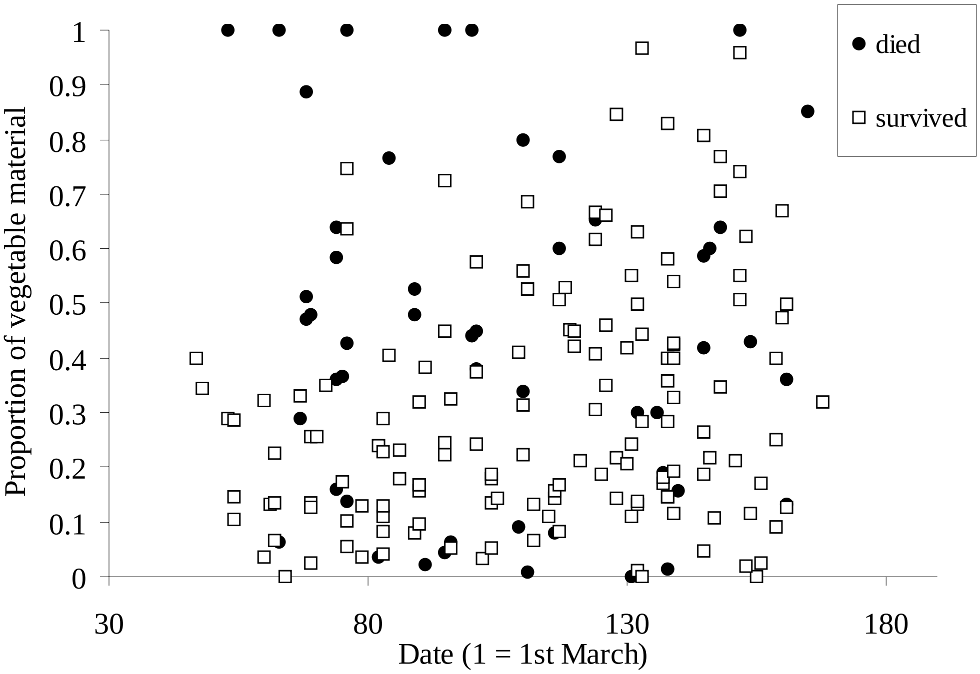
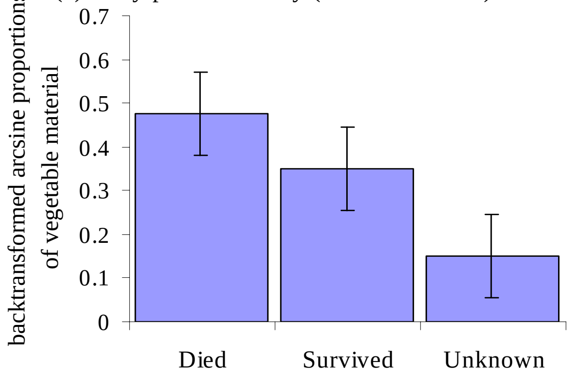


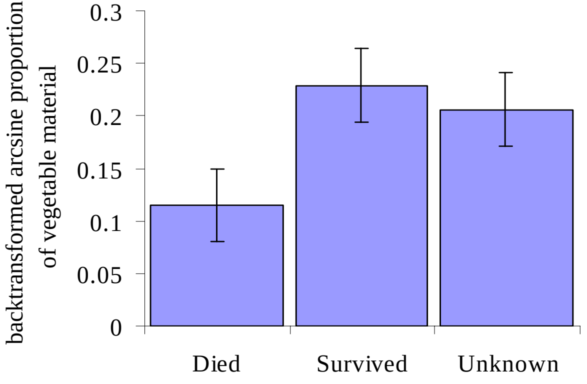
Figure 4.8 Mean backtransformed arcsine proportions of vegetable material in nestling faeces in relation to the subsequent fate of the chick and time of day the sample was collected

(a) Early part of the day (before 11:00hrs)



(b) Middle part of the day (11:00 to 15:00hrs)

(c) Late part of the day (after 15:00hrs)



CHAPTER 5

Factors affecting the breeding performance and productivity of the House Sparrow *Passer domesticus* in rural and suburban habitats

Abstract

The estimation of reproductive success is fundamental to the understanding of the causes of animal population declines. Breeding performance variables for suburban House Sparrows were investigated to establish possible causal factors behind the population decline. Seasonal variation in the number of young fledged per attempt was pronounced with the fewest number of young fledging from late summer nesting attempts. The number of young successfully fledging per nesting attempt was greater in home ranges with higher proportions of grass, deciduous shrubs and trees, and relatively little concrete. During June and July, there was evidence of more young fledging from home ranges with a high abundance of aphids. Fewer young fledged from broods that were fed a plant-dominated diet. The high rate of chick and whole-brood starvation during June and July, especially in broods, whose diet was dominated by plant material, has not been reported in previous studies. The availability of key invertebrate prey probably limited chick survival in the suburban study areas.

5.1 Introduction

Nesting success is a key variable in demographic studies of birds. The estimation of natality is fundamental to the understanding of the population dynamics of a species such as the House Sparrow. It is important to know the proportion of nests that succeed in producing at least one fledged young in addition to the average size of broods at fledging. From nest initiation this can be achieved in studies using nest boxes (Clobert and Lebreton, 1990).

The provision of nest boxes in this study allowed the measurement of various aspects of breeding ecology including first egg date, clutch size, hatching and fledging success and daily nest failure rates before and after hatching. Each weekly nest visit enabled the collection of nest history data, along with information describing chick condition, across the nine study areas. These breeding variables were used to estimate the productivity of House Sparrows in different landscapes or habitats and years. There have been many studies on the nesting ecology of House Sparrows (Summers-Smith, 1963; Seel, 1968; 1970; Summers-Smith, 1988) but very few within a suburban environment.

Most nests were not found at the same stage and this needs to be taken into account when estimating nesting success. Mayfield (1975) devised a method for estimating daily whole nest survival rates that takes into account the number of days of observation of each nest, and produces an unbiased estimate of the average daily nest survival rate for a sample of nests. My aim in this chapter is to estimate a range of breeding variables for suburban House Sparrows, and to identify environmental factors that influence reproductive success in suburban House Sparrows. The approach adopted is correlative, and seeks to relate natural variation in breeding parameters across nesting locations to variation in environmental factors.

5.2 Methods

5.2.1 Data collection

The number of nest boxes that were occupied during the first year of this study was low (less than 10), so I used a remote inspection camera to check ‘natural’ nest sites in roof spaces in order to obtain as much information on breeding performance as possible. The miniature camera was approximately 3cm wide and was attached to the end of a 2m length flexible cable and was inserted into access holes for roof nests. The black and white image from the camera could be seen on a monitor held by the person inserting the camera into the hole. However, most nests were either ‘out of range’ or inaccessible to the camera probe, however I was able to record 25 nest histories within urban roofs using this method. Therefore I was forced to limit my study to nests in artificial boxes during 2002 and 2003.

A total of 619 nest-boxes were erected within this study. All were checked at the start of the breeding season between March and April each year. However due to logistical and time constraints, the 480 nest-boxes that were within the nine study areas were given priority and checked on a regular basis between March and August.

Nests were inspected at approximately seven-day intervals from the beginning of April through to mid-August between 2001 and 2003. The following data were derived: the date the first egg was laid (first egg date), clutch size, date of hatching, number of eggs hatched and number of young fledged. Where first egg date was unknown, it was back-calculated from the hatch date, assuming a 12-day incubation period and the laying of one egg per day (Seel, 1968). Where nestling age was unknown from observation of hatching, it was estimated by comparing the degree of feather development of nestlings from known age broods (Hole, 2001).

5.2.2 Parameters investigated

First egg date was defined as the mean first egg date of the first 30% of clutches, in order to reduce the influence of second and replacement clutches (Bradbury *et al.*, 2000). I tested whether the distribution of first egg dates differed between rural and suburban landscapes or between years using the Kolmogorov-Smirnoff two sample test (Siegel and Castellan, 1988). The length of breeding season was estimated as the interval between the fifth and ninety-fifth percentiles of the first egg date distribution (Hole, 2001) across all years, as well as within each landscape type. It was assumed that multiple clutches at a single nest-site were all made by the same female (Summers-Smith, 1963; McGillivray, 1983) and therefore the inter-clutch interval could be estimated as the number of days between the laying of the first egg in successive successful clutches.

Daily whole nest failure rates were estimated during the ‘egg stage’ (the time between laying of first egg to hatching) and the ‘nestling stage’ (the time between hatching and fledging) using an extension of the Mayfield method (Aebischer, 1999; Hole, 2001). Mayfield considers only whole nest survival and ignores partial losses, therefore if 4 young die from a brood of 5, the nest is still considered to have survived. The number of days that the nest was exposed to the risk of failure (exposure days) during the egg and nestling periods were calculated as the mid-points between the maxima and minima possible given the timing of nest visits (Siriwardena *et al.*, 2000). For nests that failed, date of failure was estimated as the mid-point between the date the nest was last known to be active and the date on which it was found to have failed. Exposure days did not include days prior to the date when the nest was first found to be active (Aebischer, 1999; Hole, 2001).

Analyses to determine environmental factors influencing variation in nesting parameters across nests were modelled using Generalised Linear Models in software SAS (SAS Institute Inc, 1994). Daily survival rates were modelled using logistic regression (binomial errors and a logit link), with nest fate (failure = 1, success to hatching or fledging = 0) as the binary response variable and the number of exposure days as the binomial denominator (Aebischer, 1999; Siriwardena *et al.*, 2000; Hole, 2001).

The proportion of eggs hatched and the proportion of young fledged from each nest were also modelled with a logit-link and binomial errors, with the number hatched and number fledged as the binary response variables and clutch size and number hatched as the binomial dominators respectively. Clutch size was modelled with identity links and normal errors (Crick *et al.*, 1993; Siriwardena *et al.*, 2000; Hole, 2001) with the distribution of the residuals from the final model inspected to check for normality. The number of chicks that fledged was modelled as being Poisson distributed, which is appropriate for count data where mean (2.1) is approximately equal to the variance (2.1). These count data were not overdispersed (deviance/df = 1.35)

I tested for relationships between nesting variables and the following seasonal and environmental factors:

- PERIOD [this date always relates to first egg date] (3-level factor: early [April to mid May], middle [mid May to mid June], late [mid June onwards]),
- YEAR (3-level factor: 2001, 2002, 2003),
- RAIN (continuous variable in the form of cumulative daily rainfall),
- TEMP (continuous variable in the form of mean maximum temperature),
- LANDSCAPE (3-level factor: rural, suburban, urban),
- PMAT (the amount of plant material in nestling diet) (see Chapter 2 for further details),
- APHID (the amount of aphids present in nestling diet) (see Chapter 2 for further details),

- NO2 (mean summer nitrogen dioxide levels around each box) (see Chapter 4 for further details),
- PRIN1 and PRIN2 (principal components of habitat composition around each nest box) (see Chapter 2 for further details).

To estimate the number of attempts made in a season by an individual female, it was assumed that multiple attempts at a single nest-site were all made by the same female (Summers-Smith, 1963; McGillivray, 1983; Hole, 2001). From observations in the field this was a reasonable assumption to make. However, Hole (2001) found that where colour-ringed females could be followed throughout the breeding season, a high rate of movement between boxes was observed between successive attempts (43% between first and second attempts; 33% between second and third). Unfortunately in this study adult birds occupying nest boxes were not colour-ringed due to the logistical problems of doing so.

The mean number of young fledged per attempt can be used as an overall measure of breeding success but this assumes an unbiased sample of nests and that early failing nests have not been overlooked or missed. This is a reasonable assumption given that nest boxes were checked weekly and therefore abandoned eggs were likely to be found due to the low incidence of predation. However, to avoid this bias caused by the missing of early failed nests would be to calculate the average productivity per nest. Productivity per nesting attempt was estimated using the following formula (Hole, 2001):

$P = \phi . \sigma . \beta$ Equation 1.

Where P = *productivity*; ϕ = *survival rate over the whole nest period*; σ = *mean number fledged per successful attempt;* β = *mean number of breeding attempts per female*. Cumulative errors around the productivity estimate were calculated, assuming day to day and nest to nest independence (Hensler, 1985; Crick and Baillie, 1996), using the following formula (Mood *et al.*, 1982).

$$SE(\delta) = \sqrt{[SE(\gamma)^2 \ .\theta^2] + [SE(\theta)^2 \ . \ \gamma^2] + [SE(\gamma)^2 \ . \ SE(\theta)^2]} \qquad \text{Equation 2.}$$

Where δ is the product of γ and θ; and γ and θ are two independent random variables. Substituting γ and θ for ϕ and σ from equation 1 gives the SE of an intermediate product δ. The process is repeated using SE(δ) and SE(β) (from equation 1) to give SE(P).

5.2.3 Establishing counts of young seen across study sites during transect fieldwork

The recording of adults and juveniles along 44 fixed transects was undertaken once each month during May, June and July. The number of foraging and non-foraging (e.g. calling, bathing, loafing) birds, as well as the number of juveniles, were all recorded. The number of adults and the number of juveniles recorded on the three occasions were summed giving a total number of adults and number of juveniles within each of the nine study areas for each year. An observation of a juvenile was only recorded if an obvious yellow gape was evident around the beak of the bird to confirm it had recently fledged. Due to the low occupancy of nest boxes and problems of assessing nests in natural nest sites, a relatively smaller number of nest histories were obtained from the urban landscape (n=29) compared to suburban (n=213) and rural (n=71) landscapes (Table 5.3). Therefore this juvenile-to-adult ratio provided an alternative indirect measure of local productivity for each of the nine study areas.

5.3 Results

5.3.1 Breeding phenology

The length of the breeding season varied between habitats (Table 5.) being greatest in suburban landscapes (93 days), intermediate in rural ones (87 days) and shortest in urban areas (72 days). The first egg date distribution did not differ significantly between landscapes (*P*=0.455; n=284) or years (*P*=0.089; n=235) (Table 5.2 & Figure 5.3). However the frequency histogram of first egg date distribution suggests there were fewer late broods in rural areas compared to suburban areas (Figure 5.2).

The mean first egg date was significantly different between the three landscapes (T=2.44, *P*=0.0012) with a ten day difference mean between urban areas (28th April) and suburban areas (18th April) but only a seven day difference mean between urban and rural areas (21st April). However the mean first egg dates for suburban and rural and urban and rural landscapes were not significantly different from one another (*P*>0.05).

The inter-clutch interval between first and second attempts was not significantly different between rural and suburban landscapes (Table 5.3) or between years. The second to third attempt inter-clutch interval was also not significant between rural and suburban landscape or between years.

5.3.2 Factors affecting clutch size

Clutch size varied between one and six eggs with the mean clutch size being 4.0 (n=242) (Table 5.3). The factor PERIOD was the only significant predictor of clutch size (*P*<0.0001; n=242). The seasonal variation in clutch size is illustrated in (Figure 5.3), with the largest clutches during the mid-season and smaller clutches seen at the beginning and end of the breeding season. The predicted mean clutch sizes were 3.9, 4.3 and 3.9 for early middle and late breeding attempts respectively.

5.3.3 *Factors influencing the proportion of eggs that successfully hatched*

Investigating the proportion of eggs that successfully hatch provides a more complete assessment of egg stage losses, as partial and complete losses are considered. Significant predictors of the proportion of eggs that hatched were LANDSCAPE and NO2 levels around each nest box (Table 5. & Figure 5.). Hatching rates were highest in urban nests (86.9%) intermediate in rural nests (84.3%) and lowest in suburban nests (72.5%). The change in model deviance value, within Table 5.4, provides a measure of relative strength of the independent variables. Therefore if the independent variable has a low change in deviance then the effect on the dependent variable will be weak. There was a weak positive relationship between the proportion of eggs that hatched and predicted local concentrations of nitrogen dioxide (Table 5.4 & Figure 5.4). It should be noted, that the majority of nests did not have PRIN1 data accompanying each nest history (due to the time constraints of mapping each home range, see section 2.2.7), but as there is a high negative correlation (r= -0.5 [see section 2.4 & table 2.5]) between NO2 and PRIN1, NO2 was preferred.

5.3.4 *Factors influencing the proportion of chicks that successfully fledged*

The factors significantly affecting the proportion of chicks that fledged were YEAR and PERIOD, as well as the PERIOD*YEAR interaction (Table 5.4). In 2001 and 2002, fledging success was lowest in late season broods (late June onwards), and in 2003 fledging success was relatively low throughout the breeding season (Table 5.5).

5.3.5 *Factors influencing Mayfield egg stage daily survival rates*

The only environment factor to influence daily whole nest survival rate (DSR) at the egg stage was YEAR (*P*<0.0001; n=240) (Table 5.6). Daily whole nest failure rates were 0.59% in 2001, 0.12% in 2002 and 1.02% in 2003. Thus, egg stage failure rates were nearly ten times higher in 2003 than during 2002.

5.3.6 *Factors influencing Mayfield chick stage daily survival rates*

During the chick stage the factors that influenced the rate of whole nest daily failure were YEAR, PERIOD and YEAR*PERIOD interaction, with YEAR producing the greatest change in deviance and therefore showing the strongest effect (Table 5.6). Chick stage whole nest failure rates were much higher than failure rates at the egg stage. Chick stage failure rates were highest during late breeding attempts and across the whole breeding season in 2003 (Table 5.7).

5.3.6.1 Mayfield chick stage daily survival rates and the influence of vegetable matter in brood diet

Through the analysis of dietary composition in Chapter 4, it was shown that the proportional amount of plant material in brood diets influenced whether chicks survived and fledged or died. I therefore tested for an influence of the proportional amount of plant material in the diet on daily whole nest failure rates. The dataset for this analysis was smaller (n=119 [excluding 2001]) because dietary information was not available for all broods. I first incorporated into the model the previously identified significant predictors of chick survival rate (i.e. YEAR, PERIOD, YEAR*PERIOD interaction), and then tested the influence of the proportional amount of plant material on brood survival rates. A few nest histories from 2001 (n=13) were excluded because the lack of any mid-season nests in this year, prevented the YEAR*PERIOD interaction being fitted.

The amount of plant material in chick diet was a highly significant positive predictor of whole nest failure rate (*P*=0.0006) (Table 5.6). The sensitivity of daily failure rates to the amount of plant material in the diet is highlighted in Figure 5.. When there was no plant material in the diet, the daily failure rate is predicted to be low, increasing about 3-5 fold when the proportion of plant material increases to 50% (Figure 5.5). When the diet consists entirely of plant material the daily whole nest failure rate is predicted to reach approximately 8% (Figure 5.5). The implications of these failure rates over the entire chick period (14 days) are summarised in (Table 5.). Thus, 19% of broods are predicted to fail completely when plant material accounts for 50% of the diet, and 70% of broods will fail when plant material accounts for 100% of diet. Chick diets dominated by plant material were not unusual, as of the 119 broods considered, plant material accounted for 100% of dietary items in 4 cases, and greater than 75% of dietary items in 9 cases.

The above relationship is one based on the predicted daily failure rates and the proportion of plant material in faeces from the model. The observed relationship between the proportion of plant material found in brood faeces for successful nests and failed nests across the season are highlighted in Figure 5.6. During periods 1 (*P*=0.017; n=39) and 2 (*P*=0.0071; n=36) plant material constituted a much higher proportion of dietary items in broods that subsequently died than in broods that fledge at least one chick (Figure 5.6). However, the same pattern was not evident in late season nests (period 3: *P*=0.49; n=44) when broods that died appeared to have similar proportions of plant material in their diets (Figure 5.6). Despite this problem, the interaction PERIOD*PMAT was not significant (*P*=0.54) in the chick stage failure rate GLM.

The key points to emerge from the Mayfield analyses are that whole nest failure rates at the egg stage were low, though they were higher in 2003. Failure rates were much higher during the chick stage, with late summer and 2003 having the highest daily failure rates. There was also evidence of much higher whole nest failures at the chick stage when brood diet was dominated by plant material.

5.3.7 *Factors affecting the number of fledglings produced per attempt*

The mean number of fledglings produced per successful attempt was 2.75 (n=196). The number of young fledged per nesting attempt (n=258) varied seasonally and across years (Table 5.9 & Figure 5.). The interaction between PERIOD and YEAR was not significant, so in all three years, the numbers of fledglings produced per nesting attempt was greatest during June, and lower during July and August. Productivity per nest was greatest in 2002 and lowest in 2003.

Habitat composition within the home range of each nest also influenced the number of young fledged. There was a positive relationship between the number of young fledged and PRIN1 (Table 5.9) Thus, home ranges with a high proportion of grass, deciduous shrubs and trees tended to produce more fledged young than home ranges with larger areas of concrete.

The predicted number of fledged young was determined by back transforming the parameter estimates from the Poisson GLM confirming that the middle period of the breeding season (mid May to mid June) is the most productive, with the greatest number of young fledged (Table 5.10). The early part of the season (April to mid May) although not as productive as June does produce more fledged young than later months (July and August). Lower productivity during late summer was pronounced with 2003 being the poorest year (Table 5.8). This pattern of seasonal and annual variation in nesting success closely matches that already described for the proportion of chicks that successfully fledge and the Mayfield chick stage results.

I repeated these analyses for two subsets of data; one for those broods which had diet composition information from faecal samples and one for those broods for which I had estimates of aphid density within 100m of the nests (see section 2.2.6).

5.3.7.1 The number of young fledged and the influence of vegetable matter in brood diet

The proportion of plant material found within brood faecal samples was taken as a measure of diet quality. Dietary information was not available for every brood therefore a smaller dataset (n=136) was analysed to determine whether brood diet, in the form of the proportion of plant material, was a significant predictor of the number of young fledged. I tested for an influence of the proportion of plant material in the diet of young fledged by including this variable in a Poisson model including the three significant predictors identified from the full dataset (i.e. PERIOD, YEAR, PRIN1). Having allowed for these effects the proportion of plant material in chick faecal remains was a significant (P=0.011) negative predictor of the number of young fledged (Table 5.9 & Figure 5.8). Thus, fewer young fledged from broods that were fed a relatively high proportion of plant material. The significant PERIOD*PMAT interaction indicated that the negative relationship between the number of young fledged and PMAT was confined to broods in early and middle of the breeding season. The proportion of plant material in the diet did not influence the number of young fledged in nests initiated during July and August.

5.3.7.2 Number of young fledged and the influence of aphid abundance within home range

Aphids are an important component of nestling diet (Chapter 4) and therefore I investigated the hypothesis that nesting success (number of young fledged per attempt) is related to local abundance of aphids. The relationship between number of fledged young and the relative abundance of aphids within the locality of nest boxes during June and July of 2003 was tested. The analysis was restricted to 32 broods that were active at approximately the same time as aphid abundance was recorded. Previously identified predictors of the number of young fledged were retained in the model (irrespective of their significance) prior to testing for an influence of aphid abundance. Having allowed for significant effects of PERIOD and PRIN1, the number of young fledged per attempt was significantly (*P*=0.0185) positively related to aphid abundance (Table 5.9 & Figure 5.9). Thus, more young fledged from territories with a greater abundance of aphids (Figure 5.9).

Thus, to summarise, the main factors affecting the number of young fledged are: seasonal productivity which is highest during mid-May to mid-July; year effects, habitat composition (PRIN1) around the nest box; the amount of vegetable material in the diet (however it must be noted that plant material is only important in early and middle periods); and the proportion of aphids in the diet of late broods (however only had APHID data for late nests; mainly period 3 (n=28) and a few in period 2 (n=4)).

5.3.8 *Number of breeding attempts by individual females*

The number of attempts made by individual females was not known precisely due to the lack of colour-ringed breeding adult females in this study. Therefore in order to estimate the number of breeding attempts made in a season, it was assumed that multiple attempts at a single nest-site were all made by the same female (McGillivray, 1983; Summers-Smith, 1988), as in Hole's (2001) study in period one when there were no detailed colour-ring observations. Within this study a large number of nest boxes were regularly checked during the season. The proportion of these nest boxes that were occupied and active between April and August for 2002 and 2003 is shown in Figure 5.10. This gives an overall impression of the number of boxes that had multiple nesting attempts across the season as well as highlighting annual variation.

The mean number of breeding attempts per box from all landscapes was 2.06 (n=123), which shows little variation with Hole’s (2001) value of 2.14 attempts per female. However the mean number of attempts per year varies between landscape types as well as year (Table 5.11). In 2002, suburban boxes showed a lower value (1.8) in the number of attempts per year than in rural boxes (2.1), yet in 2003, rural boxes exhibited a lower number (1.7) of attempts per year than suburban boxes (2.2). In this study, the percentage of second attempts that were replacement clutches for failed first attempts was 9.1%. The percentage of breeding pairs that had two attempts with both broods being successful was 66.7%. Of the number of third attempts, 16.2% were replacement clutches for failed second attempts and less than half (45.9%) of pairs had three successful broods.

5.3.9 *Productivity per nesting attempt*

The mean number of fledglings per successful nest was 2.75 (n=196), the egg stage daily survival was 0.9929 and the chick stage daily survival was 0.9875. The predicted numbers of young fledged per attempt from the GLM were calculated for each period and year and compared against the observed number fledged per attempt (Table 5.10). The mean number fledged per successful nest multiplied by the Mayfield survival rate over the whole nest period was also calculated. The observed mean number of young fledged per attempt and the Mayfield estimate of mean number fledged from successful nests are highly correlated (r=0.78) (Table 5.10). Therefore the observed number of young fledged per attempt do not appear to be bias and give a reasonable overall measure of breeding success.

The productivity per nesting attempt can be determined by multiplying the Mayfield survival estimate over the whole nest period with the mean number fledged from successful nests. The productivity per nesting attempt within suburban and rural areas was investigated to determine annual and seasonal variation (Table 5.12). In 2003 the productivity per nesting attempt was much lower for both landscapes compared to 2002, particularly during the middle and late part of the summer (period 2 and 3) (Table 5.12). The difference in the two landscapes was also evident, with suburban areas showing a lower productivity per nesting attempt compared to rural areas (Table 5.12). Therefore to summarise, productivity per nesting attempt was lower in 2003 than 2002, lowest in late summer in 2002 but even lower in middle and late summer in 2003, with suburban areas showing a lower productivity than rural areas (Table 5.12).

The annual productivity of a female (and by inference pair, as House Sparrows are generally monogamous [(Summers-Smith, 1988)]) can be determined by multiplying the mean number of breeding attempts per female (2.06, [n=123]), with Mayfield survival overall nest period estimate and the mean number fledged from successful nests. Using equation 1 and assuming a 14-day egg period and a 12-day chick period, the average productivity by each female per year for all nests would be:

$2.75 \text{ X } 0.9929^{14} \text{ X } 0.9875^{12} \text{ X } 2.06 = 4.41$ young produced by each female each year (all nests)

Therefore the annual overall productivity of a breeding pair of House Sparrows between 2001 and 2003 within Leicestershire was 4.41 young. In suburban areas the annual productivity for this period was 4.21 whereas it was slightly higher in rural areas at 4.67 (Table 5.13)

5.3.10 Comparing counts of young seen across study sites during transect fieldwork

The proportion of juveniles were recorded during May, June and July in all study areas (including urban areas), when undertaking foraging observations. Therefore the proportion of juveniles could possibly be used as an index of the number of young fledged in areas where direct data was unobtainable. The annual variation in the proportion of juveniles seen in each study area is shown in Figure 5.11. During 2002 the proportion of juveniles seen in each study area was on average slightly higher than in 2003. Of all the study areas, Cobden Street Industrial Estate, an urban landscape, had the highest proportion of juveniles seen, followed by a suburban area, Western Park/New Parks. The study area to have the lowest proportion of juveniles seen during 2002 was Houghton on the Hill. However apart from these three study areas, there is consistency in the proportion of juveniles seen across all landscapes in 2002. It is illustrated in Figure 5.11, that in 2003, a lower proportion of juveniles were seen across the season, in all areas compared to 2002. The two areas with the highest proportion of juveniles seen were again Cobden Street Industrial Estate and Western Park/New Parks with Thurmaston and Houghton on the Hill showing the lowest levels of juveniles. Nevertheless, it is still evident that the three urban areas do not differ greatly to the suburban and rural areas in the proportion of juveniles seen in each area (Figure 5.11).

The variation across the season is illustrated in Figure 5.12, with all but two sites (Cobden Street Industrial Estate and Western Park/New Parks), showing an increase in the percentage of juveniles seen across the summer, with a peak in July. However, Cobden Street Industrial Estate shows a high proportion of juveniles during May compared to other areas, decreasing in June before returning to comparative levels for all areas in July. The suburban site of Western Park/New Parks does not follow the expected increase over the summer of juveniles seen but levels within this area peak in June before slightly declining in July. Although two of the nine study areas do not show a seasonal increase in juvenile numbers, the majority of study areas do show this seasonal pattern. Therefore the lack of variation in juvenile levels across each of the three landscapes show that urban sites had similar productivity to other sites in this study.

5.4 Discussion

5.4.1 *Comparison of breeding variables with other studies*

The breeding variables found within this and a number of other studies are presented in (Table 5.13). The mean clutch size for all nests within this study was 4.1, which is similar to UK means from BTO nest record cards (Summers-Smith, 1988; Crick and Siriwardena, 2002). Mean first egg date in Leicester gardens were approximately 14-21 days earlier than Hole's farmland population and approximately 10 days earlier than Seel's (1968) suburban/farmland populations (Table 5.11). One possible explanation of this is that birds lay eggs earlier due to climate change (Crick *et al.*, 1997).

The length of breeding season in this study varied between landscapes. However, it must be highlighted that the difference between landscapes in this study may be due to the smaller sample size in the urban category, compared to the rural and suburban categories. Although the length of breeding season within Hole's (Hole, 2001) study is very close to suburban Leicester, the season in Oxfordshire didn't start until the beginning of May but lasted until the end of July whereas the suburban and rural Leicester season started mid April and finished in the second week of July (Table 5.11). Nests in suburban Leicester showed a lower proportion successfully hatching (73%) than in any other studies (Table 5.13), indicating that partial losses were much more common. Although the hatching success within suburban areas appear low in comparison to more rural areas, the rate is similar to that found by studies undertaken by Summers-Smith (1988).

The Mayfield survival rate is an important factor to establish the breeding success of nests in different habitat types and regions. Hole (2001) found that in rural nests in Oxfordshire the Mayfield survival rate at the egg stage was 95%. This is higher than the survival rates at the same stage in rural (86%) and suburban Leicester (91%) (Table 5.13). There were no signs of predation in any of the nests in Leicester which was probably due to the nest boxes being sited on the walls of houses, making it inaccessible to ground-moving predators. Therefore the cause for failure at the egg stage was probably due to the eggs not hatching either through abandonment or being infertile.

The Mayfield survival rate over the nestling stage was much lower than the egg stage in Leicester. In Oxford (during the 1960s and 90s) the survival rate was 87% (Hole, 2001), whereas in rural Leicester the survival was slightly higher at 90% (Table 5.13). In suburban Leicester the survival rate at the chick stage was much lower at 83% than rural nests in Leicester or rural nests in Oxford (Table 5.13). This low survival rate can be attributed to the high number of nests where chicks died, particularly during July. This high mortality rate of chicks in suburban nests is not seen in any of the other studies. The survival rate over the whole nest period is much lower in this study compared to rural Oxfordshire in the 1990s. In rural Oxfordshire the overall survival rate was 82% (Hole, 2001) whereas in rural Leicester it was 78%, with suburban nests showing an even lower rate of 75% (Table 5.13).

The mean number of chicks that fledge per successful attempt and the number of breeding attempts found in each study contribute to the seasonal productivity calculation. The mean number of chicks that fledge per successful attempt is a major difference between studies. The BTO suburban study has a mean number of young fledged per successful attempt of 3.82, whereas in this study the mean number of young fledged per successful attempt is 2.65 in suburban areas (Table 5.13). The main differences in breeding parameters between studies are the survival rate over the whole nest period, the mean number of fledged per successful attempt and therefore the seasonal productivity with suburban Leicester showing the lowest seasonal productivity of all studies.

The seasonal productivity value is the number of chicks produced per pair per year. In suburban Leicester the value was 4.21 whereas it was a little higher in rural areas at 4.67 (Table 5.13). Nevertheless, seasonal productivity in both these areas was lower than the studies in rural Oxfordshire where the seasonal productivity was nearer 6 chicks produced per pair, per year (Hole, 2001). The lower productivity of pairs in Leicester could be due to the lower survival rate across the nesting period but in particular during the nestling stage compared to nests in Oxford (Table 5.13).

5.4.2. *Environmental correlates of breeding variables*

The House Sparrow is a multi-brooded species and Crick *et al.* (1993) has shown that multi-brooded species show a seasonal pattern of increase and then decrease in mean clutch size, with a mid-season peak. In this study there was a seasonal change in clutch size with a mid-season peak, with no significant annual or local variations in clutch size. Studies of House Sparrows at Oxford (Seel, 1968; Hole, 2001) and across the UK (Summers-Smith, 1988) as well as in North America (Murphy, 1978; McGillivray, 1983) have also showed this lack of annual or local variation, along with a mid-season peak in mean clutch size. The delay in the laying of eggs by females in urban areas in Leicester suggests a poorer habitat, as it is possible the females are taking longer to attain breeding condition.

There was a marked seasonal variation in the number of young fledged per attempt with late summer showing the lowest number of young fledging. However, the number of young fledging was found to be greater in home ranges with lots of grass, deciduous shrubs and trees, whereas fewer young fledged in home ranges with lots of concrete. This suggests that the available invertebrate food supply in the environment surrounding the nest is very important. During June and July there is evidence of more young fledging from territories with a high abundance of aphids. Seel (1970) found that later in the season the consumption of aphids accounted for the increase in survival of nestlings reared at this time. This again suggests a good invertebrate food supply within the habitat surrounding each nest makes an important contribution to the survival of young. One possible reason why there was no landscape effect on the number of young fledging may have been due to density dependence in urban areas where the population sizes were known to be smaller.

There also appears to be fewer young fledging from broods that are fed a plant-dominated diet. Seel (1969) found that plant material and bread were prominent in the diet of nestlings in June and July. Therefore this low productivity late in the summer could be linked to high levels of plant material in the diet at this time (Chapter 4: Figure 4.7). These findings highlight the potential importance of the quality of the surrounding habitat around each nestsite and the contribution that it makes by providing a much greater invertebrate food source, which is vital in order that more chicks fledge successfully. Therefore this seasonal variation in number of young fledged seems to be best explained by the varying availability of suitable foods.

During the chick stage the whole nest failure rates were much higher than during the egg stage, with rates varying during the summer months and across years. Seel (1970) found that complete failures of the brood occurred at all stages of the breeding season, with the majority happening from the end of June onwards. In this study, the period of late summer (late June onwards) showed the greatest rate of whole brood failure, with broods whose diet was dominated by plant material showing very high chick stage failures. One possible explanation could be a seasonal decline in the quality of invertebrate diet, with the availability of high quality invertebrates early on in the season causing the need for plant material in the diet to be high in order to affect bird survival. This consolidates the evidence that high levels of late summer mortality is associated with increased vegetable matter in diet.

It was common for young to die in the nest, with losses occurring mostly in the first half of the nestling period (*pers obs*.). The fledging rates varied across years and season with the worst fledging rates appearing in 2003. The losses seen in this year are high but are similar to that found in the study undertaken by Seel (1968; 1970) which were attributed to the variation in the availability of suitable foods. Further studies on Blue and Great Tits in suburban gardens have shown that both species suffered a reduction in breeding success with most of the reduction due to nestling mortality from starvation (Cowie and Hinsley, 1987).

5.4.3 *Conclusion*

It has been shown that there is intercorrelation between NO2 and the habitat variable of PRIN1 (see chapter 2). Therefore for every model where either NO2 or PRIN1 was found to be significant, the addition of the opposing variable was added to the final MAM to determine any confounding effects. However for the models where this was the case, (proportion of eggs that hatched and number of young fledged [all models]) the added variable did not become significant and the original variable remained significant. Therefore highlighting there were no confounding effects between the variables PRIN1 and NO2 within any models explaining breeding parameters.

It has been suggested that brood reduction results from preferential feeding of some young in the brood at times when all of the young cannot be adequately provisioned (Lack, 1954). Therefore the high levels of brood reduction, in particular during the latter part of the breeding season within this study, indicates a problem with food availability. Lack of food seems to be the only important factor causing complete or partial failure of broods, either through the inadequate provision of food due to poor quality habitat surrounding the nest, or the provision of unsuitable food resulting in nutritional deficiency or starvation of the brood. This seasonal variation in nestling survival, along with evidence linking vegetable dominated diet with complete brood failures, emphasises the lack of suitable food available for nestlings to be a problem for House Sparrow nests in suburban habitats.

Table 5.3 Number of nest histories obtained from each landscape type between 2001-2003

	Urban	**Suburban**	**Rural**	**Total**
2001	25	37	12	74
2002	2	69	21	92
2003	2	107	38	147
Total	29	213	71	313

Table 5.2 Fifth and 95th percentiles of first egg date distributions detailing the length of the breeding season as well as mean first egg date for the three landscape types

	5th percentile	95th percentile	Length of season (days)	Mean first egg date (of the first 30% of clutches)
All nests	12th April	12th July	91	20th April
Rural	14th April	11th July	87	22nd April
Suburban	10th April	13th July	93	18th April
Urban	20th April	1st July	72	28th April

Table 5.3 Mean values for breeding phenology parameters such as interclutch interval and mean clutch size for all nests as well as each landscape type (all values are taken from the raw data)

Parameters	All nests	SE (n)	Rural	SE (n)	Suburban	SE (n)	Urban	SE (n)
Interclutch interval (1st to 2nd attempts)	40.22 days	0.73 (69)	40.06 days	1.23 (16)	40.26 days	0.88 (53)	N/A	N/A
Interclutch interval (2nd to 3rd attempts)	37.72 days	1.12 (18)	38.00 days	3.00 (2)	37.69 days	1.23 (16)	N/A	N/A
Mean clutch size	4.00	0.06 (242)	4.14	0.02 (58)	3.96	0.07 (178)	3.67	0.21 (6)

Table 5.4 Summary of GLM analyses of factors affecting the proportion of eggs that hatch and the proportion of chicks that fledge

Dependent variables	Independent Variable[1]	Direction & Magnitude of effects	Change in model deviance
Proportion of eggs that hatched (n=242)	LANDSCAPE *** NO2 *	Urban>Rural>Suburban +ve	29.4 5.38
Proportion of chicks that fledged (n=248)	YEAR *** PERIOD ** YEAR x PERIOD ***	2001>2002>2003 Middle>Early>Late 2001: Middle >Early>Late 2002: Middle>Early>Late 2003: Late>Early>Middle	11.12 30.74 32.9

[1] Significance levels: ****P*<0.001, ***P*<0.01, **P*<0.05

Table 5.5 Percentages of chicks that fledge predicted for different seasons and years from a GLM

	Predicted percentage of chicks that fledge		
	Early	Middle	Late
2001	81.5	83.3	73.9
2002	52.1	70.5	49.0
2003	56.3	50.6	58.1

Table 5.6 Summary of GLM analyses of factors affecting daily whole nest failure rate (DFR) at the egg and chick stages

Whole nest daily failure rates	Independent Variables[1]	Direction & Magnitude of effects	Change in model deviance
Egg Stage (n=240)	YEAR ***	DFR: 2003>2001>2002	
Chick Stage (n=304)	YEAR ***	DFR: 2003>2002>2001	27.57
	PERIOD (*)		5.25
	YEAR x PERIOD **	2003: early>middle>late 2002: late>middle>early 2001: late>middle=early	18.27
Chick Stage with dietary information (n=119 excluding 2001)	YEAR (NS)		3.2
	PERIOD (NS)		1.1
	YEAR x PERIOD (NS)		1.7
	PMAT ***	+ve	11.9

[1] Significance levels: ****P*<0.001, ***P*<0.01, **P*<0.05, (*)*P*<0.08, NS=not significant

Table 5.7 Observed daily nest failure rates (%) at the chick stage (n=304) showing seasonal and annual variation (data are observed and real failure rates and not those predicted from the model)

Daily Whole Nest Failure Rates (Chick Stage)			
	Early	Middle	Late
2001	0	0	0.28
2002	0	0.68	2.18
2003	2.88	2.02	1.52

Table 5.8 The predicted relationship between whole nest failure rates at chick stage and the proportion of plant material within brood diet

	Percentage plant material in brood diet			
	0	50	75	100
Whole nest daily failure rate (%)	0.3	1.5	3.5	8
Predicted survival over 14-day chick period	4.1	19.1	39.3	68.9

Table 5.9 Summary of Poisson GLM analyses of factors affecting the number of young fledged per nesting attempt. See 2.2 and 5.2.2 for definitions of independent variables

Sample of nests	Independent variables[1]	Direction & magnitude of effect	Change in model deviance
All nests (n=258)	PERIOD ***	Middle>Early>>Late	15.94
	YEAR *	2002>2001>>2003	9.2
	PRIN1 *	+ve	4.5
Nests with faecal samples (n=136)	PERIOD *	Early>Middle>Late	1.59
	YEAR NS	NS	0.34
	PRIN1 **	+ve	7.65
	PMAT *	–ve	9.04
	PERIOD x PMAT*	Middle>Early	7.09
Nests with aphid scores in 2003 (n=32)	PERIOD **	Late>Middle	6.47
	PRIN1 **	+ve	4.90
	APHID *	+ve	4.17

[1] Significance levels: ***P<0.001, **P<0.01, P<0.05, NS=not significant

Table 5.10 A comparison between the annual and seasonal uncorrected observed mean number of young fledged per attempt, the predicted number of young from the Poisson GLM and the mean number of young fledged per successful nest*Mayfield survival rate over whole nest period

		Observed mean no. fledged per attempt	Predicted no. fledged per attempt derived from Poisson GLM	Mean no. fledged per successful attempt*overall Mayfield survival rate
2001	Early	2.75	2.63	2.75
	Middle	1.67	2.82	2.06
	Late	2.13	2.81	2.66
2002	Early	2.87	2.70	2.58
	Middle	2.93	2.89	2.53
	Late	1.52	1.86	2.11
2003	Early	1.83	2.03	1.82
	Middle	2.02	2.18	1.95
	Late	1.70	1.40	2.03

Table 5.11 The mean number of breeding attempts per box per year for rural and suburban areas in 2002 and 2003.

	2002	2003
Suburban	1.8	2.18
Rural	2.1	1.67

Table 5.12 Productivity per nesting attempt (Mayfield survival rate over whole period*mean number young fledged per successful nesting attempt) subdivided into period and landscape for 2002 and 2003

	2002			2003		
	Early	Middle	Late	Early	Middle	Late
Suburban						
Mayfield survival rate over whole nest period	1.00	0.897	0.738	0.578	0.824	0.663
Mean number fledged per successful nesting attempt	2.67	3.18	2.12	2.63	2.6	2.35
Productivity per nesting attempt	2.67	2.85	1.56	1.52	2.14	1.56
Rural						
Mayfield survival rate over whole nest period	0.764	1.00	0.897	0.722	0.485	0.798
Mean number fledged per successful nesting attempt	2.83	3.5	2.8	3	3.43	2.63
Productivity per nesting attempt	2.16	3.5	2.51	2.17	1.68	2.10

Table 5.13 A comparison of breeding parameters from this study with those from previous studies (where sample number is known it is written in parentheses).

Breeding Parameter	**Oxford 1960s [suburban & farmland]** (Seel, 1968)	**Oxford 1990s [farmland]** (Hole, 2001)	**BTO 1970-2000 [suburban]** (Crick and Siriwardena, 2002)	**BTO 1970-2000 [rural]** (Crick and Siriwardena, 2002)	**Leicester 2001-2003 [suburban]**	**Leicester 2001-2003 [rural]**
Mean Clutch Size	3.98 (831)	4.30 (272)	4.07	4.15	3.96 (178)	4.14 (58)
Mean First Egg Date	1st May	4th May			18th April	22nd April
Length of Breeding Season (days)	94 (21/4-24/7)	92 (1/5-31/7)			93 (10/4-13/7)	87 (14/4-11/7)
Interclutch Interval (1st to 2nd attempt) (days)	40 (94)	40 (84)			40 (53)	40 (16)
Interclutch Interval (2nd to 3rd attempt) (days)	38 (54)	40 (34)			37 (16)	38 (2)
Mayfield Survival rate over the egg stage: 14days	0.88 (369)	0.96(274)	All habitats: 2002: 0.964	1968: 0.859	0.91(194)	0.86(42)
Mayfield Survival rate over nestling stage: 12 days	0.88 (322)	0.87 (266)	All habitats: 2002: 0.965	1968: 0.843	0.83 (215)	0.90 (51)
Mayfield Survival rate over whole nest period	0.77 (370)	0.85 (277)	0.68 (1403)	0.85 (835)	0.75 (409)	0.78 (93)
Proportion eggs that hatched	0.79 (747)	0.85			0.73 (184)	0.84(58)
Proportion of chicks that fledged	0.45 (711)				0.61(176)	0.63 (64)
Mean no. fledged per successful attempt	2.98	3.14 (231)	3.82	3.41	2.65 (138)	3.04 (50)
Mean no. fledge per attempt	2.28	2.58	2.6	2.9	1.98	2.37
Mean no. breeding attempts per female	2.36 (138)	2.14 (35)			2.13 (85)	1.97 (32)
Seasonal Productivity	5.40	5.68			4.21	4.67

Figure 5.3 The distribution of first egg date showing seasonal and annual variation (n=323)

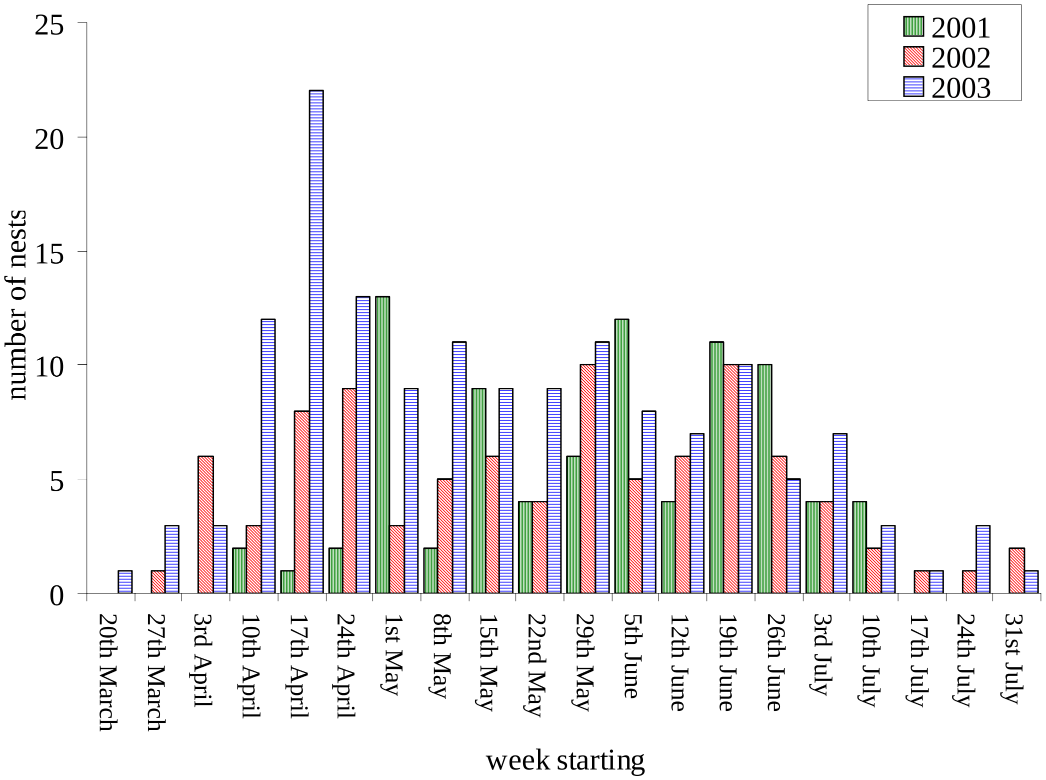


Figure 5.2 The distribution of first egg dates across the season and across landscape (n=323)

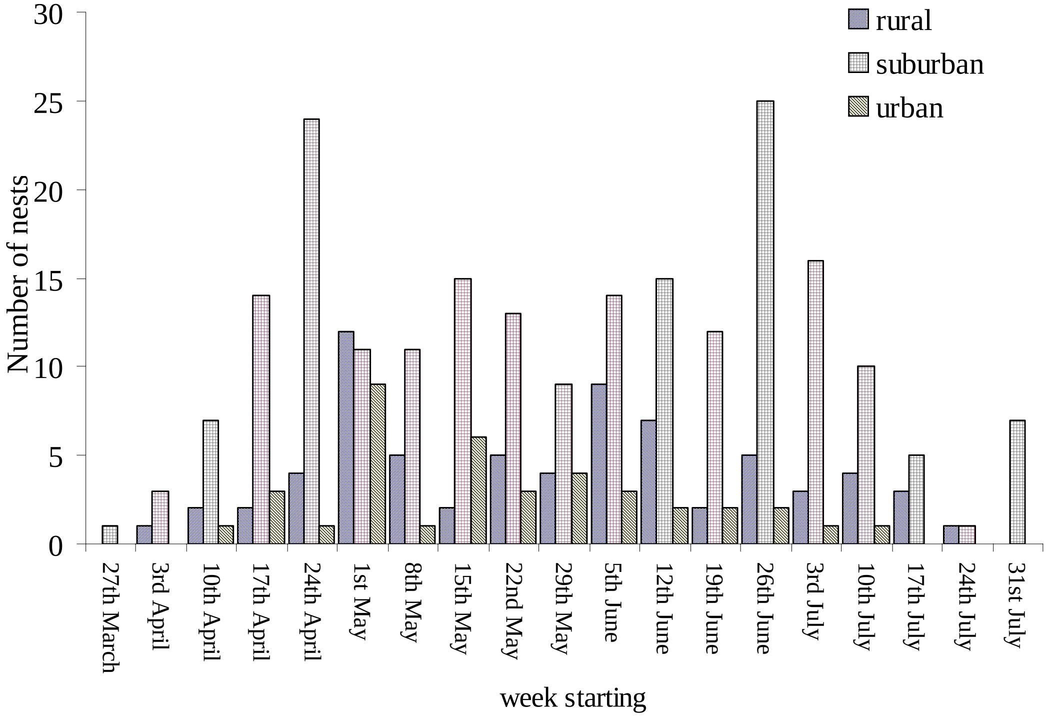


Figure 5.3 Seasonal variation in clutch size (n=242)

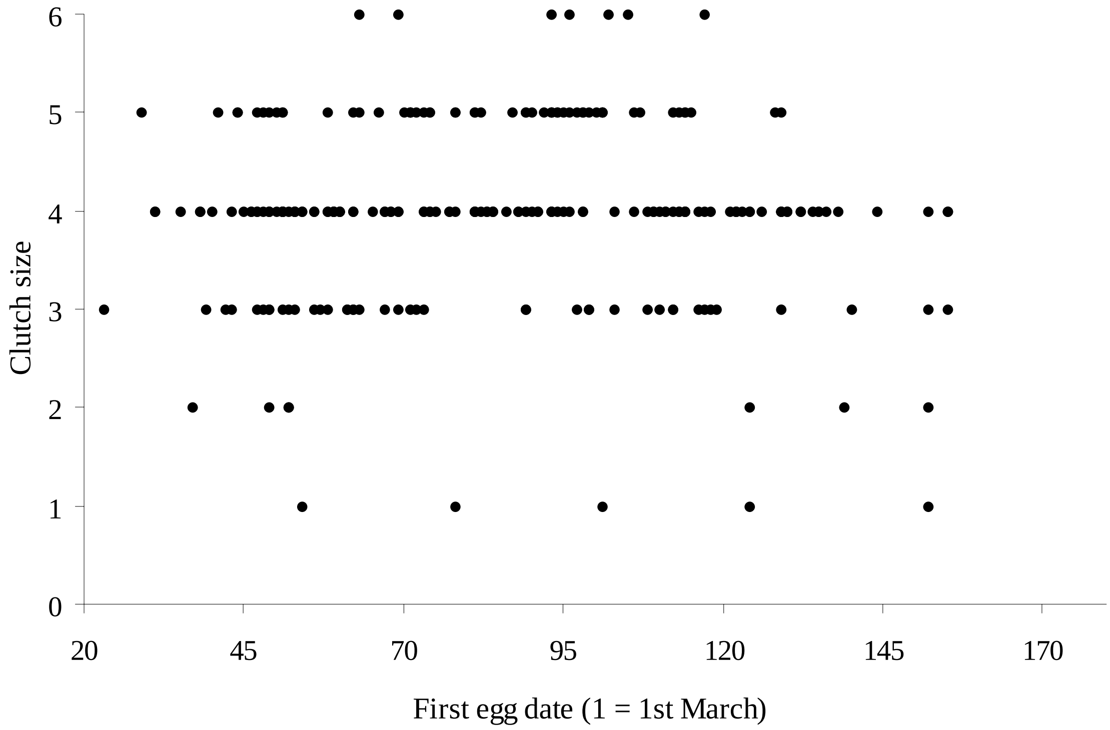


Figure 5.4 The relationship between nitrogen dioxide levels around each box and the proportion of eggs that successfully hatched, shown at the level of landscape

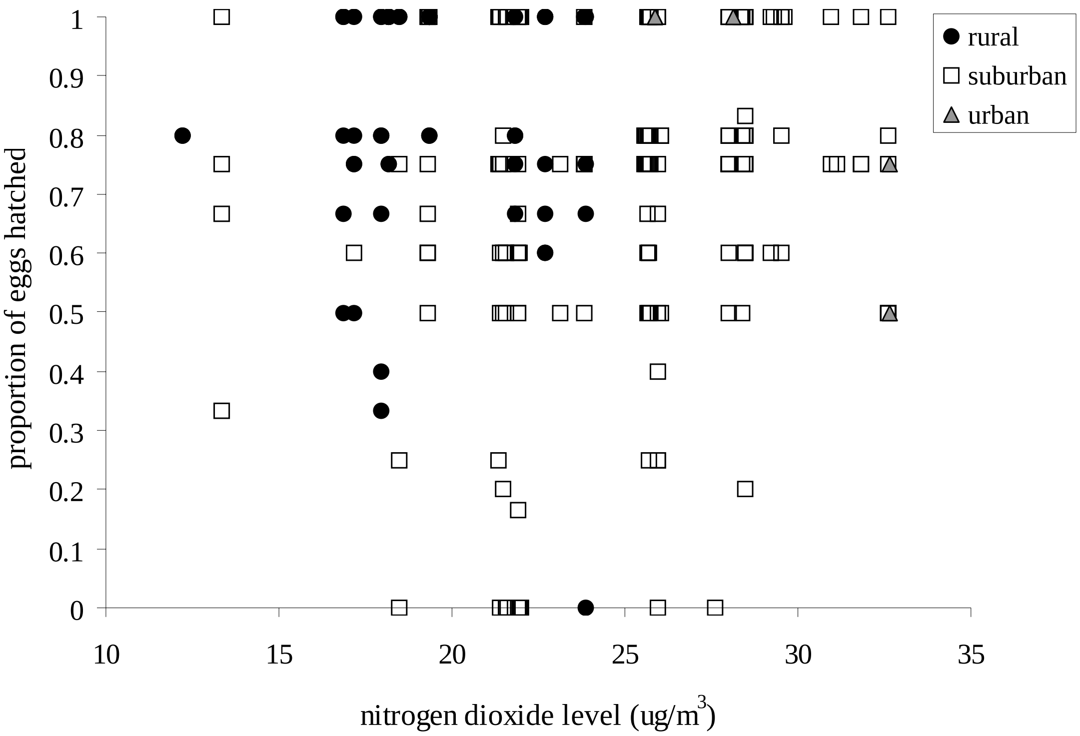


Figure 5.5 The relationship between proportion of plant material in the diet and predicted daily whole nest failure rates at the chick stage

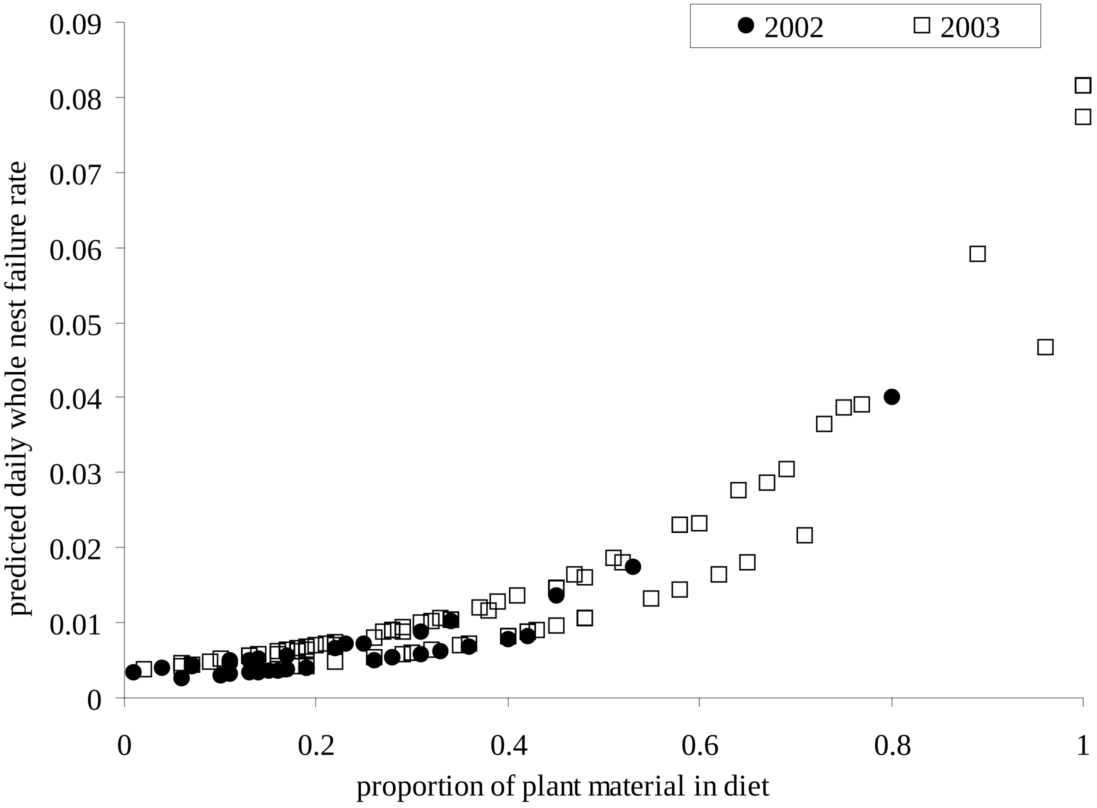


Figure 5.6 A comparison between the proportion of plant material found in brood faeces for successful nests (at least 1 chick fledged) and failed nests across the season (Period 1=April to mid-May, Period 2=mid-May to mid-June, Period 3 = mid June onwards) [n=119]

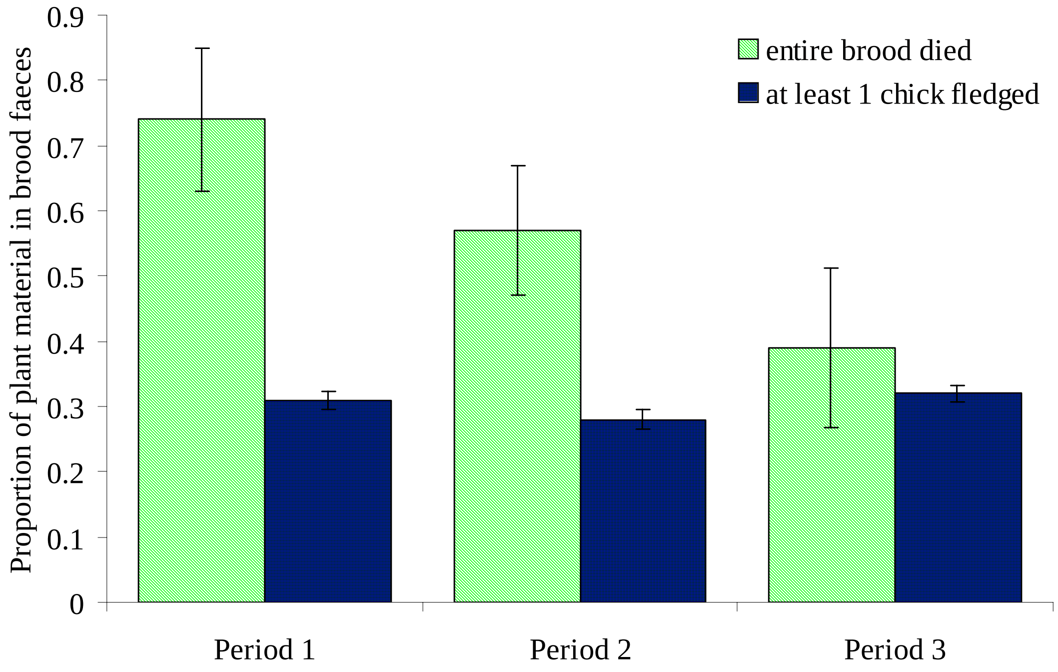


Figure 5.7 Seasonal and annual variation in the number of young House Sparrows fledging from each nesting attempt

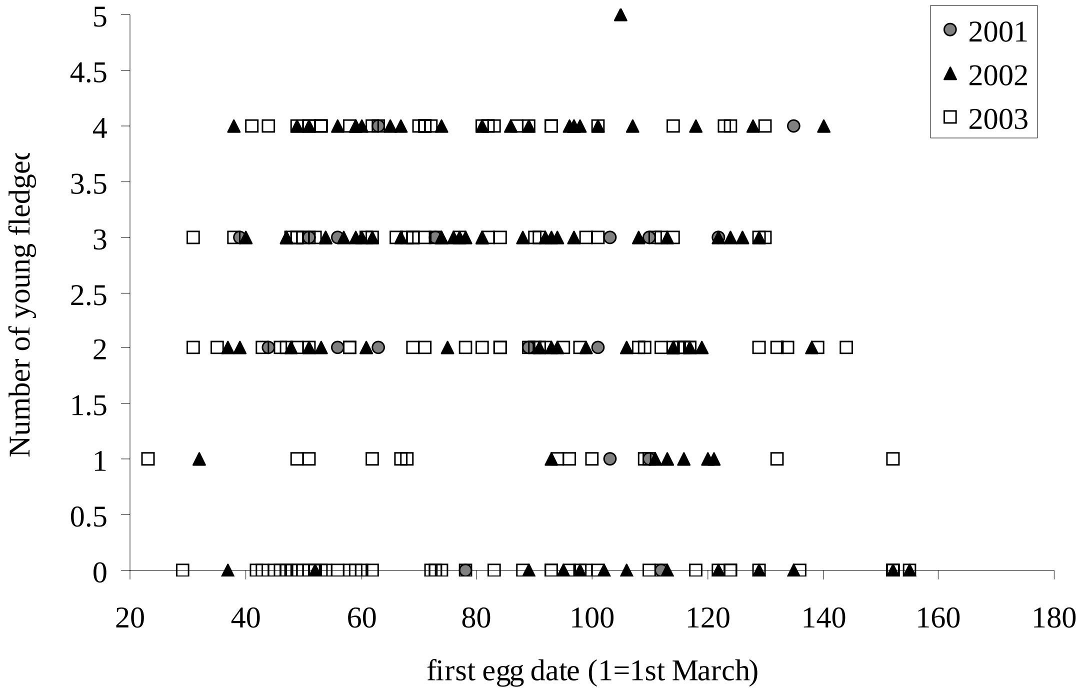


Figure 5.8 Relationship between the proportion of plant material in brood diet and the residual number of young fledged per nesting attempt (having allowed for effects of Period, Year and PRIN1)

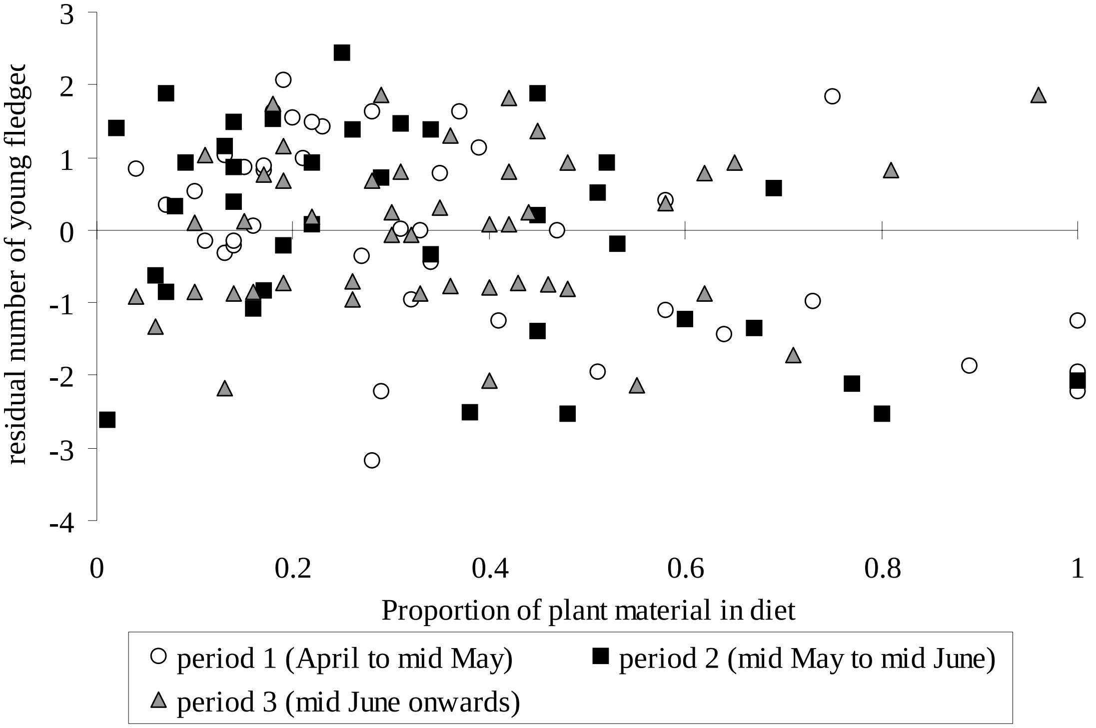


Figure 5.9 The relationship between the number of young fledged per nesting attempt in 2003 and aphid abundance within the home range (for aphid score methodology see section 2.3.6)

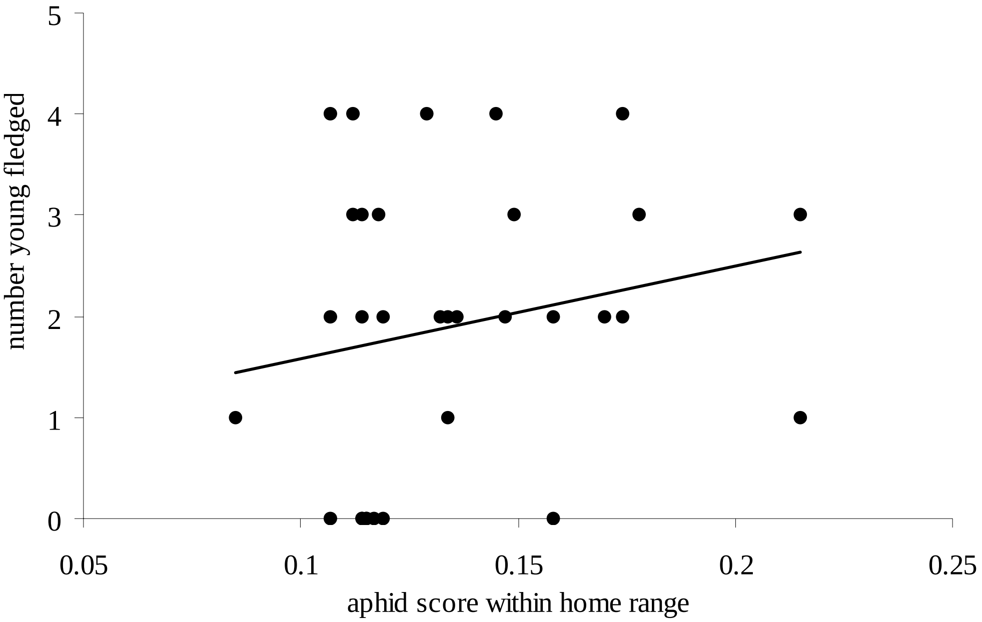


Figure 5.10. The proportion of regularly checked nestboxes that were occupied and active between April and August (n=226)

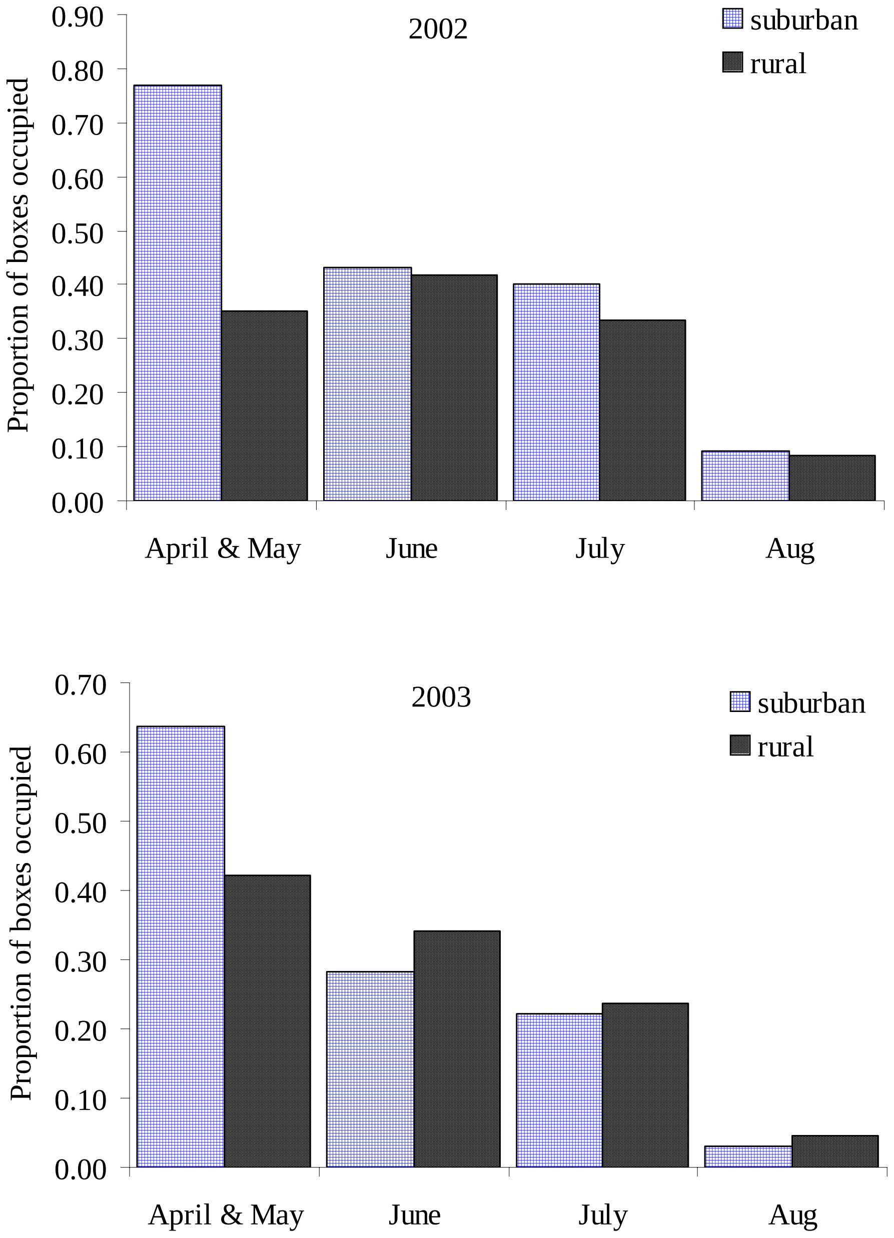


Figure 5.11 The proportion of juveniles seen along transect routes in each study area in 2002 and 2003. [Error bars are +/- S.E.]

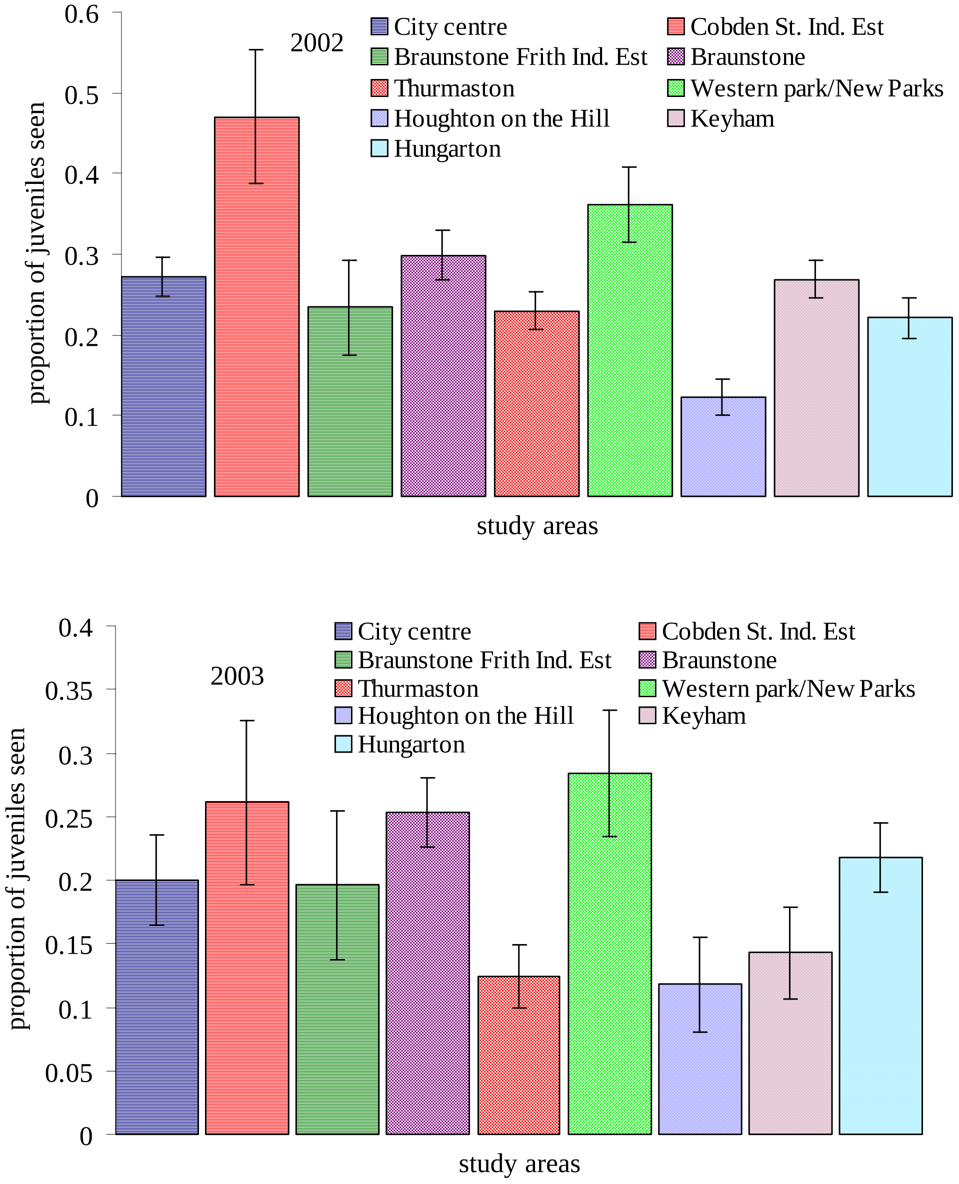
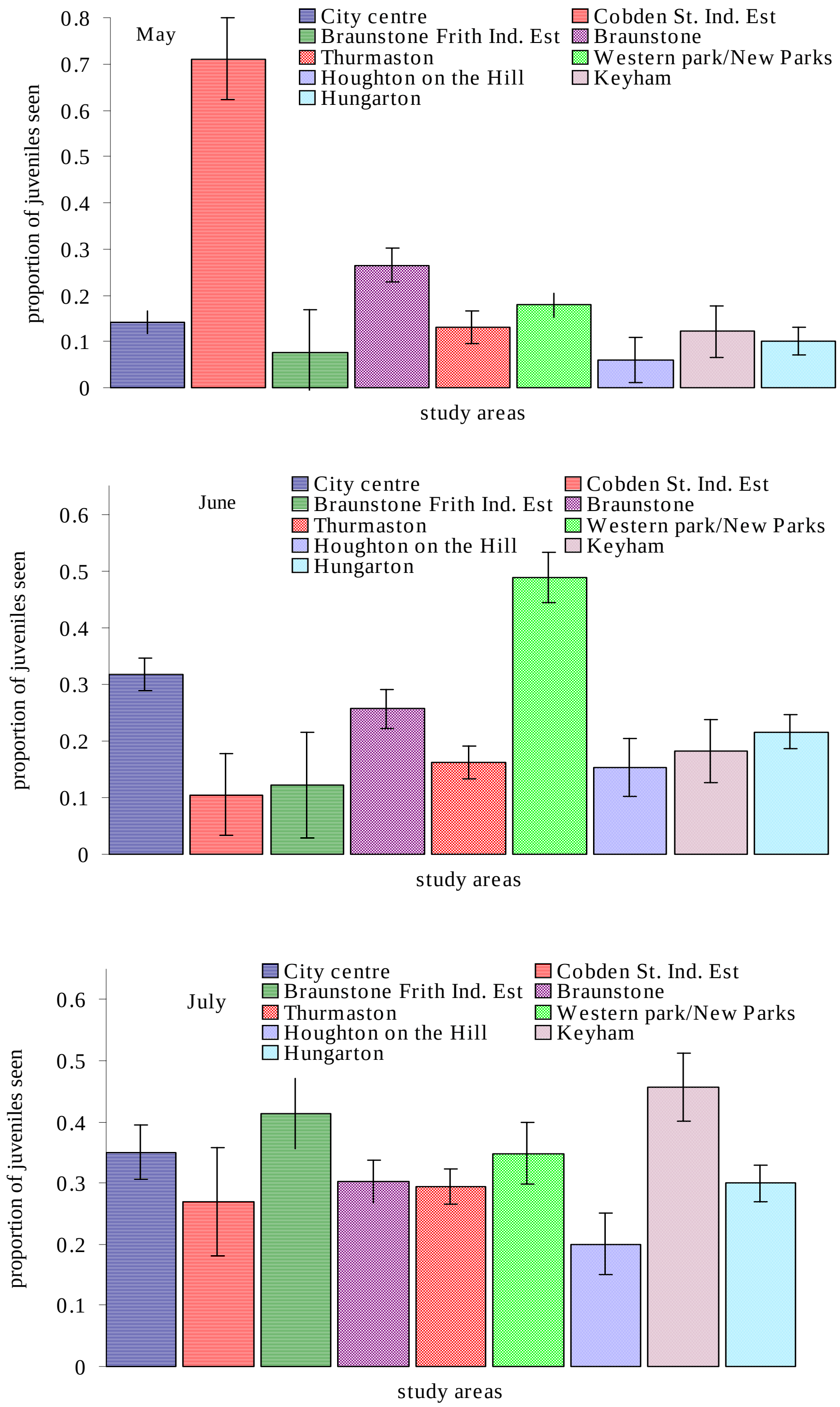


Figure 5.12 The proportion of juveniles seen along transect routes in May, June and July. [Error bars are +/- S.E.]



CHAPTER 6

Factors affecting body condition of House Sparrow *Passer domesticus* nestlings in rural and suburban habitats

Abstract

Factors affecting the body condition and growth rates of nestling House Sparrows were assessed to examine their relationship to the suburban and urban environment. Weather factors such as temperature and daily rainfall were shown to affect brood growth rate, chick condition and brood biomass. The negative effect of rainfall on growth rates, chick condition and brood biomass is consistent with thermoregulatory costs and with reductions in invertebrate availability. Chicks fed a large proportion of Coleoptera had higher body condition indices than those not fed Coleoptera. In areas with high nitrogen dioxide levels, the brood mass at fledging was found to be significantly lower. This relationship has implications in terms of lower expected post-fledging survival being seen. Therefore fledging in higher polluted areas confers a significant survival disadvantage between fledging and independence. The positive relationship between home ranges with high proportions of grass, deciduous shrubs and trees and relatively little concrete, and brood biomass, suggests that local invertebrate availability is sensitive to the habitat quality around the nest. Consequently it is possible that a reduction in the availability of key invertebrate foods (such as Coleoptera), during the breeding season, in a deteriorating environment, is having a detrimental effect on the quality and condition of sparrow nestlings when they fledge.

6.1 Introduction

The effect of food availability on breeding success has been implicated in the declines of Grey Partridge *Perdix perdix* (Potts and Aebischer, 1995), Skylark *Alauda arvensis* (Poulsen *et al.*, 1998) and Corn Buntings *Miliaria calandra* (Brickle et al., 2000). This is in part because of the effect of pesticides on the availability of chick-food invertebrates in cereal crops. As reproductive success is determined by the successful recruitment and breeding of offspring, it may be reduced if parents maintain offspring quantity at the expense of offspring quality (Hochachka and Smith, 1991).

Given that a reduction in insect food availability within the farmland habitat has been demonstrated (Donald, 1998), it is plausible that a similar reduction has occurred in urban habitats (McIntyre, 2000), due to perhaps improved hygiene in gardens and the trend for 'tidier' landscaping of garden areas. In city centres, brown-field sites are likely to be fewer due to inner-city regeneration. The loss of such sites might be important as these weedy areas act as a rich food resource for urban sparrows (Crick *et al.*, 2002).

The abundance of insect prey can have pronounced effects on reproductive success in birds. A superabundant food supply increases productivity in House Sparrows through increased fledging success and shortened intervals between breeding attempts (Anderson, 1977). This has also been backed up by research by Arcese *et al.*,(1988) where upon supplementing food to Song Sparrows, birds produced larger clutches, had higher hatching success and chick survival was higher compared to birds that received no extra food.

Therefore suburban and urban populations of sparrows may be suffering reduced nestling condition and growth rates, as a result of either lowered food intake rates or from a lower quality diet such as more vegetable matter (Borg and Toft, 2000). Nestling body condition is a predictor of post-fledging survival, social status and even lifetime reproductive success (Hochachka and Smith, 1991; McGrath, 1991; Lindstrom, 1999; Hole, 2001). Explaining variation in nestling condition is therefore an important step in understanding the relationship between a declining bird species and its environment. Therefore this aspect of House Sparrow breeding biology needs to be investigated to establish whether food availability at the nestling stage might be contributing to the population decline.

I have already investigated nesting success and annual productivity in urban-suburban and rural areas (see Chapter 5). I now intend to examine the more subtle effects of environmental factors on nestling body condition.

6.2 Methods

6.2.1 Data collection

Nests were inspected at approximately 7-day intervals from the beginning of April through to mid August during 2001, 2002 and 2003. Nestling mass (to the nearest 0.1g using a 50g Pesola spring balance) and tarsus (to the nearest 0.1mm using a dial calliper) were measured on each chick following the procedure of Svensson (1992) during each visit to the nest. In order to determine fledging success, boxes were inspected regularly until the end of the season.

6.2.2 Statistical analysis and parameters investigated

6.2.2.1 Nestling condition

In order to avoid pseudoreplication in the analysis of brood condition, data from only one day were used for each brood (Donald *et al.*, 2001; Bradbury *et al.*, 2003). To maximise usage of available information on brood condition, two separate analyses were undertaken considering different ages of development. Broods aged between two and six days (after hatching) were analysed and classed as 'EARLY', whereas the last measurement taken from each brood (8 to 12 days after hatching) was classed as 'LATE'. The EARLY period was a stage at which many chicks died (mainly through starvation, see Chapter 5), while the LATE period (close to fledging) will have been the stage at which more subtle cumulative environmental effects are most likely to be detected (Bradbury *et al.*, 2003).

The condition of each nestling was estimated as its residual from regression of the natural logarithm (ln) of body mass on the natural logarithm of tarsus length (Jakob *et al.*, 1996). Natural logarithms were used to account for the probable allometric relationship between a measure of mass and a measure of length [mass = a (tarsus^b)]. Due to the measurements used being over a spread of nestling ages, the possible effects of nestling age on the condition index had to be controlled for. This was undertaken through including AGE and the interaction term between nestling AGE and LN TARSUS as predictors of LN MASS (Donald *et al.*, 2001; Hole, 2001; Bradbury *et al.*, 2003). If the interaction had a significant effect on LN MASS, then the residuals from this analysis, which were independent of nestling age, were used as measures of condition. If the interaction was not significant, then the residuals of a regression of LN MASS on LN TARSUS were used as measures of body condition (Donald *et al.*, 2001; Hole, 2001; Bradbury *et al.*, 2003).

Data were collected from all nestlings within all broods, however siblings within broods are not independent in any statistical analysis due to being fed by the same parents and experiencing the same environmental conditions (Bradbury *et al.*, 2003). Therefore variation in the mean brood condition index was analysed as a function of the predictor variables (see below). Broods in which there was chick mortality prior to the measurement used to calculate the condition index, were excluded from analyses (Donald *et al.*, 2001; Bradbury *et al.*, 2003). This ensured analyses were not biased by the effects of differential chick mortality (Shkedy and Safriel, 1992).

Generalised linear modelling (with normal errors), was used to identify factors explaining significant variation in chick condition, along with the inclusion of quadratic terms to test for simple curvilinear effects. A minimum adequate model (MAM) explaining variation in brood condition was developed by retaining in the model independent variables that caused the largest and statistically most significant reduction in model deviance. This ‘step up’ procedure continued until no remaining independent variables could explain further significant amounts of model deviance (Crawley, 1993).

6.2.2.2 Growth rate of mass and tarsal length

Growth rates of individual broods were calculated for nests for which there were two or more sets of biometric measurements. Growth rates for both mass and tarsal length were calculated by dividing the difference between measurements taken on different visits by the interval (in days) between these visits (Evans *et al.*, 1997; Donald *et al.*, 2001; Hole, 2001; Bradbury *et al.*, 2003). The resulting growth rate (in grams of mass, or millimetres of tarsus gained per day) was assigned the age of the nestlings at the mid-point between the two measurements (Donald *et al.*, 2001; Bradbury *et al.*, 2003).

Again only one estimate of growth per brood was included in order to avoid pseudoreplication and any broods in which there was brood reduction prior to the first measurement or between the first and subsequent measurements were excluded from the analysis (Donald *et al.*, 2001; Hole, 2001; Bradbury *et al.*, 2003). Residuals from a linear regression of growth rate on age were used as a growth rate index. Mean brood growth rates (both mass and tarsus) were analysed along with chicks with the smallest growth rate in each brood (both mass and tarsus) (Bradbury *et al.*, 2003). Once indices of mass and tarsal growth rates had been derived, general linear modelling was used to identify environmental factors explaining any significant variation in these two rates (Donald *et al.*, 2001; Bradbury *et al.*, 2003). A minimum adequate model (MAM) was developed by retaining in the model independent variables that caused the largest and statistically most significant reduction in model deviance. This ‘step up’ procedure continued, until no remaining independent variables could explain further significant amounts of model deviance (Crawley, 1993).

6.2.2.3 Standardised brood size (nest biomass)

A standardised brood size (SBS) index was developed to represent the total amount of chick biomass present in the nest at eight to twelve days after hatching. This index reflects the possibility that a given amount of invertebrate prey might sustain two chicks in good condition or four in poorer condition (Brickle and Peach, 2004). The summed observed weights of all chicks in each nest, divided by the predicted weight of a chick that age (derived from a regression of mean weights against age for all broods) produces the SBS index. If the chicks in the nest were all above average weight for their age, then the SBS value will exceed the raw brood count, whereas if the chicks were under weight then the SBS will be less than the raw brood count (Brickle and Peach, 2004). A generalised linear model was used to identify environmental factors that were correlated with this integrated measure of brood size and body condition.

6.2.2.4 Mean brood fledging mass at day 10-12

The mass at the approximate time of fledging (House Sparrow nestlings fledge between 12 and 14 days old [(Summers-Smith, 1988)]), was analysed to determine the environmental effects upon nestling mass at that time. Brood fledging mass was defined as body mass at nestling day 12. However due to limited data, broods of 10-12 days old were included. No broods older than 12 days were included in this analysis because mean brood body mass tended to decline after this time (Figure 6.1). Variation due to age was controlled for by placing an age term into the model during subsequent analyses (Hole, 2001).

6.2.2.5 Parameters investigated

I tested for relationships between brood condition parameters and the following seasonal and environmental factors:

- PERIOD [this date always relates to first egg date] (3-level factor: early [April to mid May], middle [mid May to mid June], late [mid June onwards]),
- FED (first egg date: continuous variable),
- YEAR (3-level factor: 2001, 2002, 2003),
- HATCHED (the number of eggs that hatched),
- RAIN (continuous variable in the form of cumulative daily rainfall),
- TEMP (continuous variable in the form of mean maximum temperature),
- LANDSCAPE (3-level factor: rural, suburban, urban),
- NO2 (mean summer nitrogen dioxide levels around each box) (see Chapter 4 for further details),
- PRIN1 and PRIN2 (principal components of habitat composition around each nest box) (see Chapter 2 for further details).

I also considered the influence of chick diet composition on nestling condition and standardised brood size. I tested the following components of diet composition: proportion of spiders, beetles, Diptera, Homoptera, ants, larvae and proportion of vegetable material (see Chapter 4). However diet composition was not considered when analysing growth rate, as faecal samples do not give dietary information over a temporal scale, but at one point in time and therefore do not relate to growth between two points.

The variables of FED and TEMP were strongly correlated (R=0.582 *P*<0.0001; see section 2.4) and substituted for each other in several models (i.e. when AIC of model with FED was similar to that for model with TEMP). I decided to include TEMP not FED in this situation because TEMP was more likely to directly influence chick condition.

6.3 Results

Mean brood body mass increased with age up to approximately 12 days, after which it tended to decline (Figure 6.1). There were a few cases of chicks older than the usual age of fledging (14 days) remaining in the nest. These broods had a lower mean body mass indicating that these chicks were not as fully developed as they should have been at that age (Figure 6.1).

6.3.1 Factors influencing chick condition at the early nestling stage (2-6 days)

Mean brood condition at 2-6 days old differed significantly between years and was significantly lower in areas with high nitrogen dioxide levels (Table 6.1 & Figure 6.). Weather conditions also appeared to influence brood condition at this early nesting stage. Early brood condition peaked at intermediate temperatures and intermediate rainfall (Table 6.1 & Figure 6.3) and declined during relatively hot or cold, or wet or dry conditions. It has been shown that there is intercorrelation between NO2 and the habitat variable of PRIN1 (see chapter 2). Therefore to determine if NO2 and PRIN1 have confounding effects in models where either one is significant, the addition of the other factor was added to the final MAM and the significance of each variable was assessed. In the brood condition at 2-6days model, NO2 was a known significant factor, therefore PRIN1 was added to the model to appraise any confounding effects. However when PRIN1 was added, it did not become significant (*P*=0.811) but NO2 remained significant within the final MAM (*P*=0.004). Therefore for this model there were no confounding effects between the variables NO2 and PRIN1.

Measures of diet composition from faecal samples were available from 81 broods, but no element of diet composition was a significant predictor of early brood body condition. The proportion of Diptera came closest to being a significant (*P*=0.1), positive predictor of early brood condition, and was significant (*P*=0.051) when NO2 was excluded from the model. This suggests nitrogen dioxide and the proportion of Diptera are inter-correlated, in that a lower proportion of Diptera is found in diets in relatively polluted areas. This fits in with the finding in Chapter 4 (section *4.3.1.3* and Figure 4.4) that Diptera may be lacking in diets from chicks in urban home ranges. Nitrogen dioxide had a negative effect on chick condition at the early nestling stage but dietary factors did not. However it is hard to quantify from this study whether nitrogen dioxide had a direct effect on the health of the chick.

6.3.2 Factors influencing chick condition at the late nestling stage (8-12 days)

Residuals from the regression of LN MASS on LN TARSUS were significantly related to brood age (Table 6.1). The relationship was quadratic with residual weights being lowest at intermediate age, and higher at younger and older ages. Having allowed for the effects of age, late chick body condition was weakly related to the proportion of beetle remains in faecal samples, or alternatively, weakly and negatively related to the proportion of ants or vegetable material in the diet (Table 6.1). However, the proportion of ants became non-significant (*P*=0.12) in the presence of the proportion of beetles, implying inter-correlation between these two dietary items. It was shown in Chapter 4 (section *4.3.1.2. & 4.3.2.2*) that diets dominated by ants or vegetable material are associated with birds that are likely to die or in this chapter, be in poor condition.

6.3.3 Factors affecting mass growth rate of nestlings

Growth rates varied significantly between years and in relation to daily maximum temperature and daily rainfall (Table 6.4). Brood growth rates tended to be lowest in the mid-temperature range (Figure 6.4) and following heavy rainfall (Figure 6.5).

The smallest growth rates within broods were related to the same set of factors on the average brood growth rates (above) plus the number of young hatched (Table 6.2). The number hatched within each brood was a significant negative predictor of the smallest growth rate within each brood, which might have reflected a density-dependent effect of food availability.

6.3.4 Factors affecting tarsus growth rate of nestlings

Temperature was the only significant predictor of variation in mean brood tarsus growth rate (Table 6.2). The form of this relationship is similar to that for mass growth rate (Figure 6.4) with growth rates being smallest in the mid-temperature range and lower during relatively cool or warm conditions. The smallest growth rate in tarsus length for any chick in each brood was negatively related to the amount of rainfall (Table 6.2). Thus, the smallest growth rates within broods were recorded during relatively wet weather.

6.3.5 Factors affecting standardised brood size (nest biomass)

Standardised brood size (SBS) varied significantly between years and declined significantly through the breeding season (Table 6.3 & Figure 6.6). SBS was also significantly greater in home ranges containing relatively high proportions of grass, deciduous shrubs and trees and relatively little concrete (i.e. a high PRIN1 score) (Figure 6.7). Rainfall had a significant negative influence on SBS (Table 6.3).

Due to the habitat variable of PRIN1 being signnificant within the SBS index model and because of the known intercorrelation between NO2 and the habitat variable of PRIN1 (see chapter 2), the addition of the variable NO2 was added to the final MAM of this model to determine any confounding effects. However when NO2 was added, it did not become significant (*P*=0.62) but PRIN1 remained significant within the final MAM (*P*=0.0008). Therefore for this model there were no confounding effects between the variables PRIN1 and NO2.

None of the chick dietary components were significant predictors of SBS, although the modest sample size (n=58) will limit the power of this analysis to detect relationships.

6.3.6 Factors affecting mean brood mass at fledging (day 10-12)

The mean brood mass at fledging can be seen as another indicator of the health of each brood at the time of fledging. The key significant predictors that influence mass at fledging were YEAR and NO2 (Table 6.4). The annual and seasonal variation in mean mass at fledging is presented in Figure 6.8. There is a slight seasonal decline in mean mass suggesting that broods fledging during late summer (e.g. July-August) are slightly lighter, on average, than those fledging earlier in the year. Brood mass at fledging was significantly lower in areas with relatively high nitrogen dioxide levels (Figure 6.9). This apparent effect of air quality on mean brood mass at fledging was large. Mean brood mass was approximately 20grams at nitrogen dioxide levels typical of urban-suburban areas (e.g. 30µg/m^3) compared to 27grams at nitrogen dioxide levels typical of rural villages (e.g. 18µg/m^3) (Figure 6.10). Rainfall had a relatively weak negative influence on brood mass at fledging (Table 6.4). None of the chick dietary components were tested as the sample size (n=32) was too small and would limit the power to detect relationships.

Due to the habitat variable of NO2 being signnificant within the mean mass at fledging model and because of the known intercorrelation between NO2 and the habitat variable of PRIN1 (see chapter 2), the addition of the variable PRIN1 was added to the final MAM of this model to determine any confounding effects. However when PRIN1 was added, it did not become significant (*P*=0.78) but NO2 remained significant within the final MAM (*P*=<.0001). Therefore for this model there were no confounding effects between the variables NO2 and PRIN1.

There were a number of consistent patterns across each of the models analysed (Table 6.5). Weather conditions appeared to influence many aspects of brood growth in that brood condition peaked at intermediate temperatures and intermediate rainfall and declined during relatively hot or cold, or wet or dry conditions. Heavy rainfall had a negative impact on brood condition, mass growth rate and even mass at day 10-12, with smallest growth rates within broods being recorded during relatively wet weather. Yearly patterns were also seen in a number of models, with 2001 being the worst year for chick condition, standardised brood size and the mean mass at day 10-12, and 2002 being the best. However the yearly effect on mass growth rate implied 2001 was the best year and 2001 was the worst. The negative influence of nitrogen dioxide was evident in brood condition at an early age and the fledging mass at day 10-12. This implication that pollution has a detrimental effect on the health of a chick before fledging is an important one.

6.4 Discussion

6.4.1. Condition and rate of growth of nestlings

The decrease in weight of nestlings after the peak on day 11-12 maybe due to consumption of insulating body fat since the peak weight coincides with the achievement of nestling temperature control (Seel, 1969). However there are a few cases where the chicks are above the age of fledging and are still in the nest, indicating that the chicks are probably not in peak condition upon leaving the nest, implicating a possible high mortality rate in post-fledging survival (Hole, 2001). Seel (1970) found that decline in sparrow nestling weight and the number in each brood was linked to starvation therefore the decline in tarsus growth rate with an increasing number of chicks that hatched could possibly be attributed to starvation.

Weather factors such as temperature and daily rainfall were shown to affect brood growth rate, chick condition and even brood biomass. Nestling development can be affected by weather in several ways (Bradbury *et al.*, 2003). These effects act both directly on the bird themselves and indirectly on the food supply (McCarty and Winkler, 1999). Lower temperatures and high rainfall could both chill nestlings and therefore increase their energy demands for thermoregulation, ultimately reducing the availability of resources for the chicks development. Also an increase in thermoregulatory demands as well as low temperatures and high rainfall could reduce nestling development by reducing feeding time for the female, who must brood the nestlings to keep them warm and dry, and hence reducing intake rates. A third effect could be related to invertebrate activity, as low temperatures and high rainfall could all reduce invertebrate activity and availability, resulting in lowered intake rates.

Therefore the negative effect of rainfall on growth rates, chick condition and even brood biomass is consistent with thermoregulatory costs and with reductions in invertebrate availability. Thermoregulatory costs decrease and invertebrate availability increases in warmer conditions, which may explain why brood condition index increased with an increase in daily maximum temperature. Evans *et al.* (1997) determined that rainfall reduced growth rates of nestling Cirl Buntings *Emberiza cirlus*, suggesting that insect prey became harder to find under such conditions, upon which the adult Cirl Buntings switched to foraging for cereal grain instead. Brickle and Harper (1999) found that Corn Buntings nestlings, plant material made up a large proportion of faeces on wet days possibly because invertebrates became harder to find. When studying Skylarks, Donald *et al.* (2001) found that rainfall was an important predictor of chick growth rates and body condition, as it was negatively correlated with chick development.

The positive relationship between the habitat correlate PRIN1, which represents home ranges with high proportions of grass, deciduous shrubs and trees and relatively little concrete, and brood biomass (SBS), suggests that local invertebrate availability is sensitive to the habitat quality around the nest. Areas with high nitrogen dioxide levels such as built up suburban areas appear to have broods with underweight nestlings during the period of fledging. Hole (2001) showed that post-fledging survival is positively related to chick body mass on day 13. Figure 6.10 suggests a difference in mass of about 5-9g between nests in the most polluted and least polluted areas. From Figure 3.1 in Hole (2001), it can be seen that a bird with fledging mass of 25g has a 70% chance of surviving from fledging to independence (10 days out of the nest) compared to approximately 40% for a bird weighing 20g. This is a massive difference in expected survival and highlights the importance of the relationship shown in Figure 6.9 & 6.10.

This relationship has implications in terms of lower expected post-fledging survival in the fledging weights being seen in the more polluted areas. In order to allow for the younger aged birds (day10-12) in this study to be compared to Hole’s (2001) day 13 plot, an average daily rate of mass increase between ages 10-13 was calculated and this correction was then applied to each weight in Figure 6.10. Using Figure 3.1 from Hole (2001), the survival probability was determined using the predicted weight at day 13. This predicted survival probability was then plotted against nitrogen dioxide levels to establish the relationship between the probability of survival to independence in varying polluted areas (Figure 6.). The relationship between the predicted probability of a chick surviving to independence and nitrogen dioxide is negatively significant (correlation coefficient = –0.32; P=0.004; n=78 broods), suggesting that chicks fledging in urban and suburban areas have a much lower chance of surviving to independence than chicks from rural areas. Therefore fledging in higher polluted areas such as urban and suburban landscapes confers a significant survival disadvantage between fledging and independence. This variation in juvenile survival across the landscapes therefore will have repercussions on the population dynamics of House Sparrows in urban and suburban areas.

As high nitrogen dioxide levels are correlated with high proportions of habitat such as concrete, this finding again suggests that local invertebrate availability is sensitive to the habitat quality around the nest. Therefore the surrounding habitat conditions around each nest is a key factor in determining the health and successful development of the chick both during the nestling and the fledging period.

6.4.2 Conclusions

For every model where either NO2 or PRIN1 was found to be significant, the addition of the opposing variable was added to the final MAM to determine any confounding effects. However for the three models where this was the case, (chick condition early, SBS index and mean mass at fledging) the added variable did not become significant and the original variable remained significant. Therefore highlighting there was no confounding effects between the variables PRIN1 and NO2 within any models explaining chick growth.

Only a small proportion of variance in condition, growth rates and brood biomass, (a maximum of 21.5% for mean brood mass at fledging), were explained by all the models. Therefore it could be that parents may be compensating for spatial (i.e. food availability within the foraging range) and temporal (i.e. weather-induced) variations in habitat quality in order to maintain the number of quality of nestlings fledged.

However it must be pointed out that weather and habitat quality surrounding the nest are important key factors that affect nestling condition, growth rate and brood biomass. Both these factors are linked to invertebrate activity and availability. Therefore without high levels of invertebrate availability, sparrow nestlings will not reach peak condition and successfully fledge. It was shown in Chapter 5 that the lack of suitable food available for nestlings is a problem for House Sparrow nests in suburban habitats. The evidence can be taken one step further, in that it has been shown there is a positive relationship with good quality habitat, such as deciduous vegetation that houses more native invertebrates, and an increase in brood biomass. Therefore home ranges with good quality habitat have chicks that fledge in peak condition and are subsequently more likely to survive the crucial post-fledging period. Consequently a reduction in the availability of key invertebrate foods (such as Coleoptera), during the breeding season, such as that shown in a deteriorating environment, is likely to have a detrimental effect on the quality and condition of sparrow nestlings when they fledge.

Table 6.1 Summary of multivariate analyses of factors affecting brood condition at different chick ages

Dependent variable[1] (no. of broods)	Independent Variables	Partial R^2 values	Direction & Magnitude of Event
Chick condition: early (2-6d) (n=156)	***YEAR	10.7	2002>2003>2001
	***NO2	7.1	–ve
	***TEMP	9.2	+ve
	***TEMP^2	8.0	–ve
	*RAIN	4.0	+ve
	***RAIN^2	5.7	–ve
Additional diet predictors (2-6d) (n=81)[2]	(*)DIPTERA		+ve
Chick condition: late (8-12d) (n=134)	*AGE	3.0	–ve
	*AGE^2	3.0	+ve
Additional diet predictors (8-12d) (n=59)[3]	*AGE	3.0	–ve
	*AGE^2	3.0	+ve
	*BEETLE	8.0	+ve

[1] Significance levels: ***$P<0.001$, **$P<0.01$, *$P<0.05$, (*)$P<0.08$

[2] Proportion of Diptera was significant at $P=0.051$ if NO_2 was excluded from the model

[3] Alternative weaker predictors of late chick body condition were the proportion of ants ($P<0.04$, –ve) and the proportion of vegetable material ($P=0.06$, –ve) in the diet. Neither of these predictors was significant in the presence of beetle.

Table 6.4 Summary of multivariate analyses of factors affecting brood growth rate

Dependent variable[1]	Independent Variables	Partial R^2 values	Direction & Magnitude of Event
Mass growth rate (n=75)	*YEAR	11.1	2001>2002>2003
	**TEMP	11.1	-VE
	**$TEMP^2$	10.6	+VE
	*RAIN	5.2	+VE
	*$RAIN^2$	7.4	-VE
Mass growth rate of smallest chick (n=75)	*YEAR	10.1	2001>2002>2003
	*TEMP	5.3	-VE
	*$TEMP^2$	5.3	+VE
	*HATCHED	5.5	-VE
	(*)RAIN	4.3	
	*$RAIN^2$	5.5	-VE
Tarsus growth rate (n=75)	*TEMP	6.1	-VE
	*$TEMP^2$	6.9	+VE
Tarsus growth rate of smallest chick (n=75)	* $RAIN^2$		-VE

[1] Significance levels: ****P*<0.001, ***P*<0.01, **P*<0.05, (*)*P*<0.08

Table 6.3 Summary of significant predictors influencing the standardised brood size (SBS) index

Dependent Variable[1]	Independent Variables	Partial R^2 values	Direction & Magnitude of Event
SBS index (n=133)	***YEAR	10.66	2002>2003>2001
	*FED	4.42	+VE
	**FED^2	5.7	-VE
	***PRIN1	13.61	+VE
	*$PRIN1^2$	3.56	-VE
	*RAIN	3.52	-VE

[1] Significance levels: ****P*<0.001, ***P*<0.01, **P*<0.05, (*)*P*<0.08

Table 6.4 Summary of multivariate analyses of factors affecting mean mass at fledging (day 10-12)

Dependent Variable[1]	Independent Variables	Partial R^2 values	Direction & Magnitude of Event
Mean fledging mass (n=78)	***YEAR	21.5	2002>2003>2001
	***NO2	19.2	–ve
	**AGE	9.3	+ve
	*RAIN	5.9	–ve
	(*)FED^2	4.4	–ve
	FED (NS)	3.9	

[1] Significance levels: ****P*<0.001, ***P*<0.01, **P*<0.05, (*)*P*<0.08

Table 6.5 A summary comparing all significant predictors and relationships within all final models relating to brood condition and growth rate. ✓= the independent variable is significant ($P<0.05$).

	Dependent Variable					
Significant Independent Variable	Brood Condition (Early)	Brood Condition (Late)	Mass Growth Rate	Tarsus Growth Rate	SBS Index	Mean Mass at day10-12
AGE		✓ –ve				✓ +ve
AGE^2		✓ +ve				
YEAR	✓ **02>03>01**		✓ **01>02>03**		✓ **02>03>01**	✓ **02>03>01**
FED					✓ +ve	
FED^2					✓ –ve	✓ –ve
TEMP	✓ +ve		✓ –ve	✓ –ve		
TEMP^2	✓ –ve		✓ +ve	✓ +ve		
RAIN	✓ +ve		✓ +ve		✓ –ve	✓ –ve
RAIN^2	✓ –ve		✓ –ve			
NO$_2$	✓ –ve					✓ –ve
PRIN1					✓ +ve	
PRIN1^2					✓ –ve	
BEETLE		✓ +ve				
DIPTERA	✓ +ve					

Figure 6.1 Mean brood mass against mean brood age (n=312)

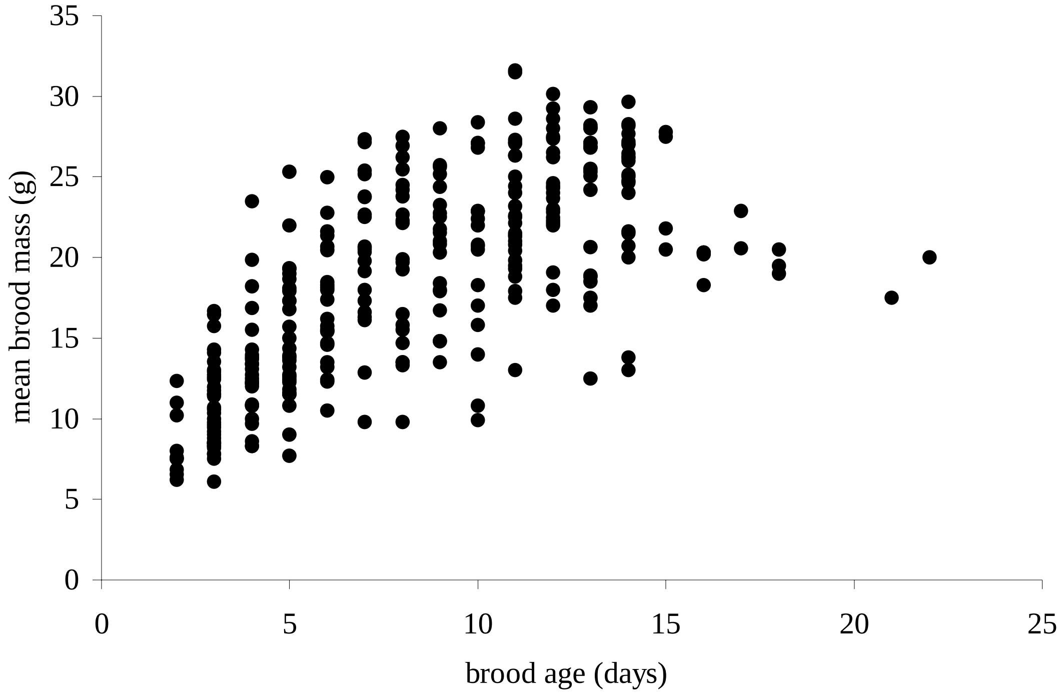


Figure 6.2 The relationship between residual brood condition of chicks (after allowing for year effects) aged between 2-6 days old and local nitrogen dioxide levels (n=156)

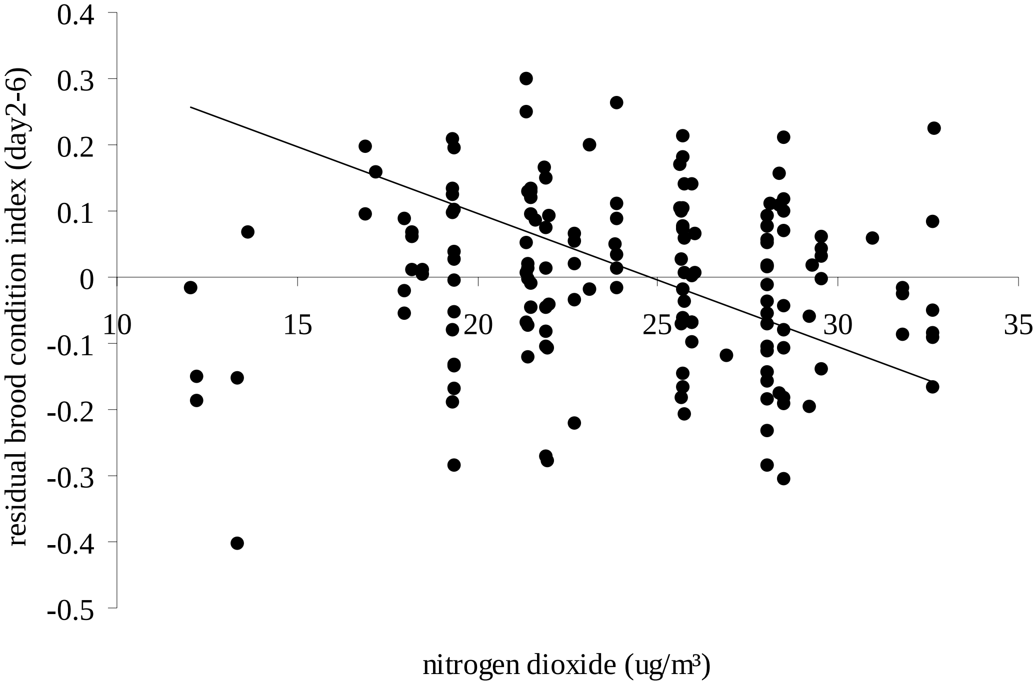


Figure 6.3 The relationship between residual brood condition of chicks (after allowing for year effects) aged between 2-6 days old and maximum daily temperature (n=156)

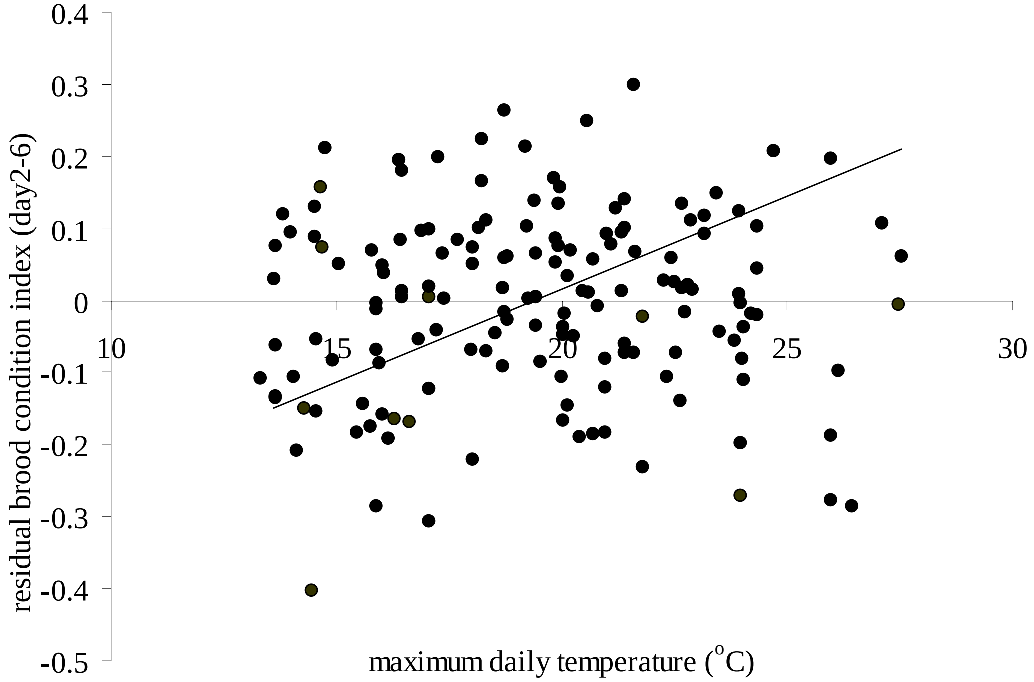


Figure 6.4 The relationship between brood mass growth rate and maximum daily temperature (n=76)

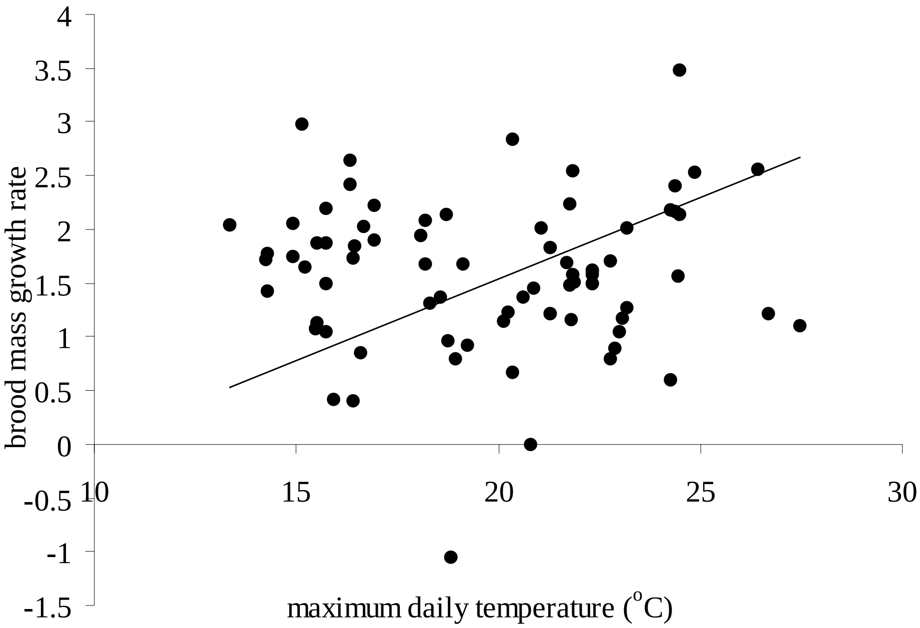


Figure 6.5 The relationship between brood mass growth rate and daily total rainfall (n=76)

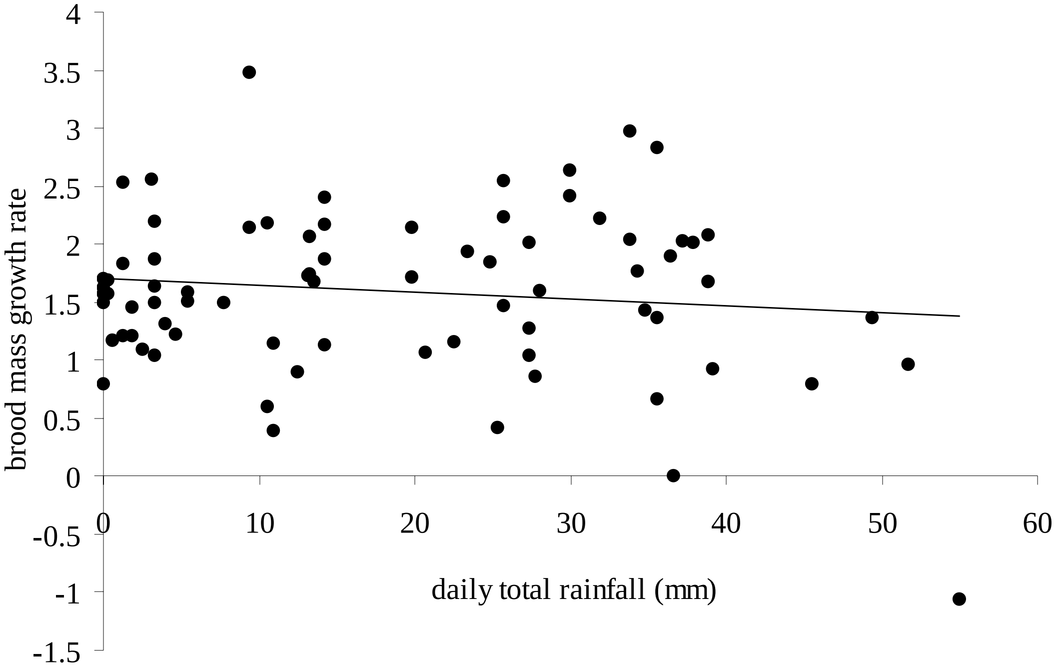


Figure 6.6 The relationship between residual standardised brood size (SBS) and seasonality (n=133 broods)

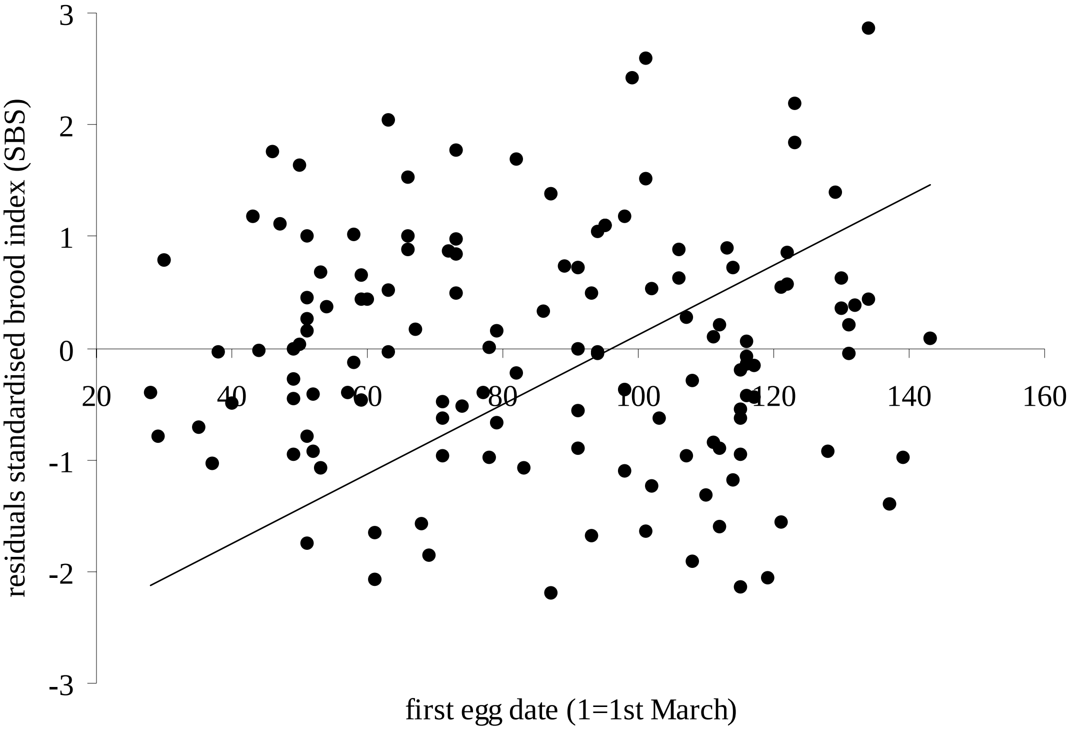


Figure 6.7 The relationship between PRIN1, a principal component of habitat composition [x-axis] and residual standardised brood index (SBS) [y-axis] (n=133)

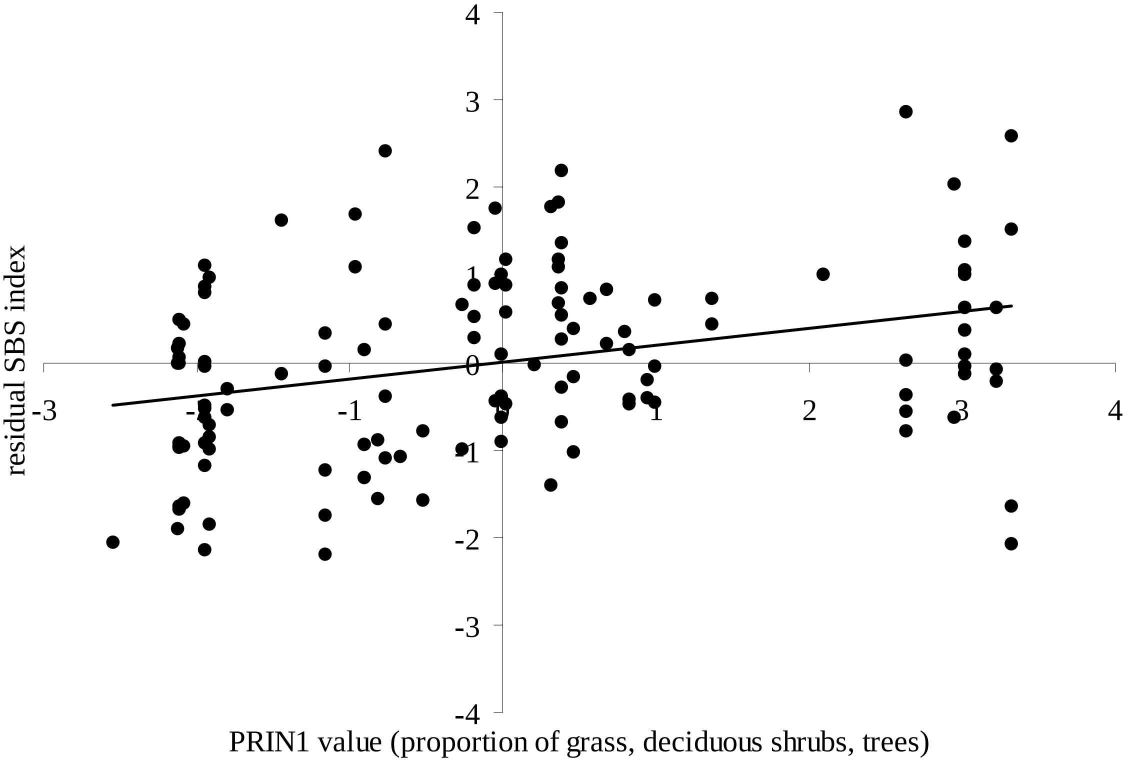


Figure 6.8 The annual and seasonal variation in mean brood mass at age 10-12 days (n=78 broods)

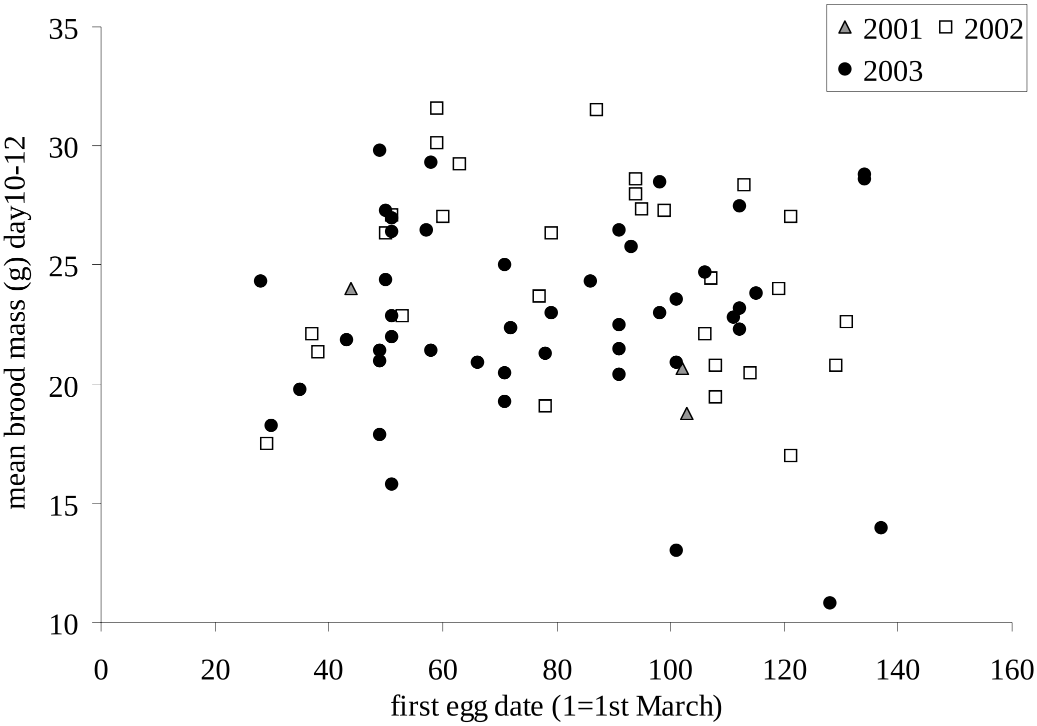


Figure 6.9 The relationship between residual mean brood mass at day 10-12 (allowing for AGE, FED and YEAR effects) and nitrogen dioxide levels around the nest (n=78 broods)

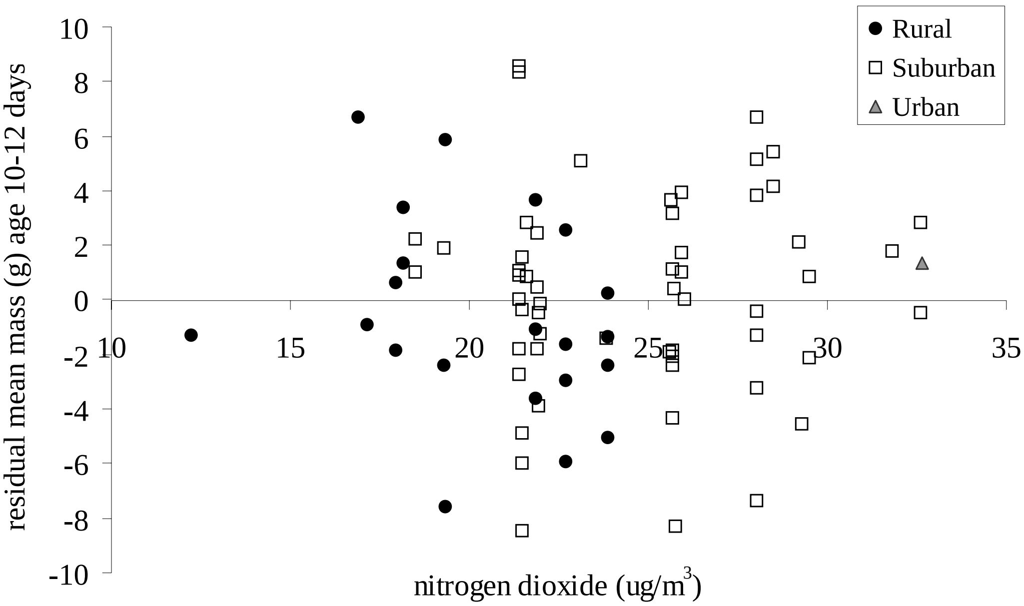


Figure 6.10 The relationship between mean brood mass at day 10-12 and nitrogen dioxide levels around the nest (n=78 broods)

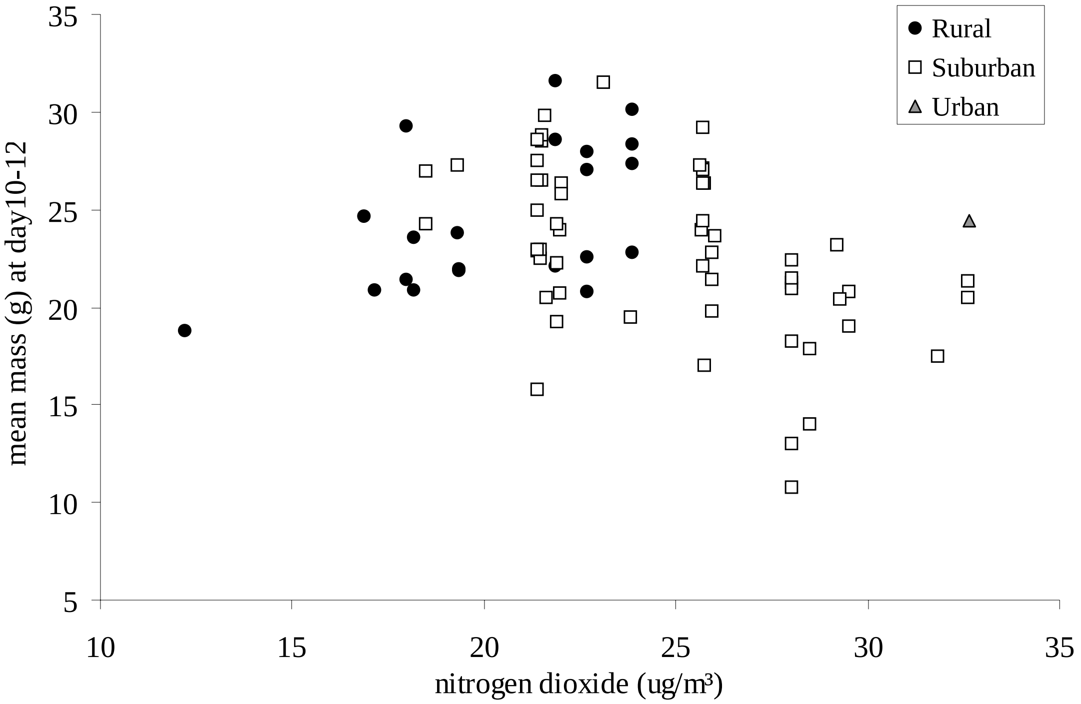
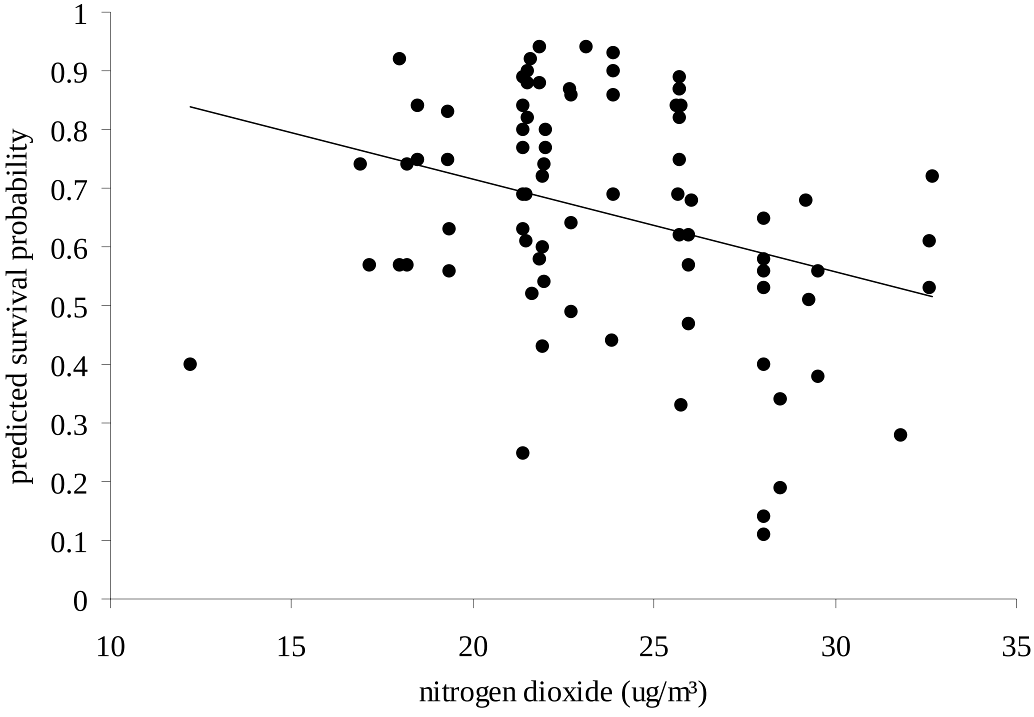


Figure 6.11 An illustration of the effect of nitrogen dioxide levels around the nest box on the probability of chick survival to independence (10 days out of nest). The predicted survival probability was calculated using the relationship evident in Figure 3.1 in Hole (2001) [whereby the average daily rate of mass increase between ages 10-13 was calculated and the correction was applied to each mass in Figure 6.9 and the corresponding survival probability was taken from Figure 3.1(Hole, 2001)].



CHAPTER 7

Stable isotopes in House Sparrow *Passer domesticus* chick feathers as an indirect measure of the quality of nestling diet

Abstract

Stable isotope ratios of carbon and nitrogen in bird tissues may potentially reveal information on diet during the growth of those tissues. Ratios of $^{15}N/^{14}N$ differed markedly between different components of the House Sparrow chick diet. Plant and vegetable material had the lowest scores; vegetarian invertebrate groups (aphids, craneflies and weevils) had intermediate scores and carnivorous invertebrate groups (spiders, ants and beetles) had the highest scores. $\delta^{15}N$ scores from chick feathers collected in 2003 averaged 7.7 (10% and 90% quantiles respectively: 6.4-9.0). If its assumed that diet-feather fractionation of $\delta^{15}N$ averages 3 units for bird feathers (Hobson and Clark, 1992b), the $\delta^{15}N$ values of the ingested sparrow diet would average 4.7 (3.4-6.0). This suggests that chick diet was dominated by plant material and invertebrates with a mainly vegetarian diet (e.g. aphids, weevils and craneflies).

Variation in feather $\delta^{15}N$ values was negatively related to PRIN2 (i.e. $\delta^{15}N$ values were lower from home ranges with relatively large areas of concrete and evergreen vegetation, and lacking in grassland and arable habitats). In 2003, $\delta^{15}N$ values were highest for nests initiated during mid-May to mid-June and lowest for nests initiated before mid-May. Variation in $\delta^{15}N$ levels was not a significant predictor of chick survival or the number of young fledged from a brood, but was a positively related predictor of chick growth rate and chick condition on day 10-11 (i.e. as $\delta^{15}N$ increases so does chick growth rate and chick condition index). This confirms that $\delta^{15}N$ levels are a useful measure of diet quality and that diet quality determines chick growth rate and condition.

7.1 Introduction

Avian diets are usually determined by foraging observations or faecal analysis. However, these approaches often only provide ‘snapshot’ dietary information covering relatively short time periods (e.g. less than a day in the case of a faecal sample). Conventional dietary information, if it is not collected intensively over an extended period, is likely therefore to only reflect short-term diet (Bearhop *et al.*, 1999). Stable isotopes in animal tissues have the potential to provide information on the composition of assimilated foods (not just ingested foods) integrated over longer time periods (Pearson *et al.*, 2003).

In various eco-chemical reactions, stable isotopes of bio-elements react at different rates, resulting in different values in various biogeochemical reservoirs (Mizutani *et al.*, 1992). The measurement of these isotope compositions provides information of ecological interest (Thompson and Furness, 1995). They can be used to reconstruct diet because stable isotopic composition of heterotroph tissues can often be related to the stable isotopic composition of their diet (Gannes, 1997; Pearson *et al.*, 2003).

Over the past fifteen years stable isotope ratios of carbon and nitrogen have been increasingly used to elucidate patterns in food webs (Bearhop *et al.*, 2004). Their utility lies in the fact that stable isotope ratios in the proteins of heterotrophs reflect those of the proteins in their diet in a predictable manner (Hobson and Clark, 1992a). Stable isotope ratios are expressed in δ notation as parts per thousand ($^{0}/00$) according to the equation:

$$\delta X = (R_{sample}/R_{standard} - 1)\ \%\ 1000$$

Where $X = {}^{13}C$ or ${}^{15}N$ and $R={}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$

The ratio of ^{15}N to ^{14}N generally exhibits a stepwise enrichment (increase in the value of $\delta^{15}N$) at each trophic level and consequently the $\delta^{15}N$ values in the tissues of heterotrophs tend to be $2.5^0/_{00}$ to $5^0/_{00}$ greater than those of their diets (DeNiro and Epstein, 1981; Hobson and Clark, 1992b; Bearhop *et al.*, 2002).

Stable isotopes can be used to elucidate not only an animal's diet but also its body condition (Gannes, 1997). Protein in heterotrophs has a higher $^{15}N/^{14}N$ ratio than dietary protein (DeNiro and Epstein, 1981). This difference appears to be due to preferential removal of 'light' (^{14}N-containing) amine groups by the enzymes responsible for amino acid de-amination and trans-amination (Gannes, 1997). Excreted nitrogen contained in ammonia, urea, and uric acid is lighter than body and dietary protein (Steele and Daniel, 1978). Animals in neutral nitrogen balance typically show fractionations ranging from $+2^0/_{00}$ to $5^0/_{00}$ between dietary nitrogen and tissue nitrogen (DeNiro and Epstein, 1981; Hobson and Clark, 1992b; Bearhop *et al.*, 2002). Therefore because a heterotroph's nitrogen is heavier than its diet, nitrogen in the tissues of animals higher in the food chain tends to be heavier (i.e., to have more positive $\delta 15N$ values) than that of animals lower in the food chain (Minagawa and Wada, 1984; Hobson *et al.*, 1993).

The carbon and nitrogen isotopic composition of heterotroph tissues are therefore a function of: $\delta^{15}N$ and $\delta^{13}C$ of each prey species; the relative proportions of each prey species assimilated and the isotopic fractionation associated with converting prey tissue into heterotroph tissue (Bearhop *et al.*, 2004). The stable isotope signatures of tissue generally reflect the diet over the period during which the tissue was synthesised (Hobson and Clark, 1992b; Bearhop *et al.*, 2002). In studies of birds, feathers offer a non-destructive approach to the provision of isotopic information relating to the diet and trophic position of an individual (Thompson and Furness, 1995). Feathers are almost pure protein (mostly keratin), and therefore provide a reliable indicator of dietary protein (Mizutani *et al.*, 1992). Most bird species feed on a range of prey and therefore a range of isotopic inputs. The isotopic signature of a feather is thought to reflect that of the diet at the time of feather growth, therefore the isotopic signature of a feather sample potentially will be influenced by the choice of feather for analysis (Hobson and Clark, 1992a).

House Sparrow nestling feathers start to emerge and grow at approximately 4-5 days from hatching. A growing feather's isotopic value represents the diet ingested only during the period of growth (Mizutani *et al.*, 1992; Pearson *et al.*, 2003). Therefore in this investigation, a tertial wing feather was used to provide dietary intake information representing the period of the nestlings' development. Tertiary feathers appear at approximately 6-7 days from hatching, therefore the chick had to be at least 10 days old for the feather to be large enough to analyse.

Because $\delta^{15}N$ values concentrate up the food chain (i.e. are low in vegetable material, intermediate in the tissues of vegetarian animals, and highest in predators at the tops of food chains) they have the potential to reflect the relative proportions of invertebrate and vegetable material in ingested food (Hobson, 1999). Thus the feathers of House Sparrow chicks fed mainly peanuts and bread would be expected to have much lower $\delta^{15}N$ levels than those from chicks fed entirely invertebrates. Since a high proportion of vegetable material was associated with higher chick mortality (see section *4.3.2.2*), and lower chick condition (at 8-12 days, see section 6.3.2), I was interested to test whether $\delta^{15}N$ levels in chick feathers were related to subsequent chick survival or chick condition.

A calibration of key dietary components is needed to enable accurate interpretation of feather-isotope signatures when dietary preferences are to be inferred, the implicit assumption being that isotopic signatures of diets can be related to those of heterotroph in a predictable manner (Thompson and Furness, 1995; Bearhop *et al.*, 1999). In this case the most common prey groups being fed to House Sparrow nestlings were used in the calibration process to aid the interpretation of the feather analysis results.

Under conditions of fasting and nutritional stress, a greater proportion of nitrogenous compounds available for protein synthesis are derived from catabolism and, since this source of nitrogen has already been enriched in ^{15}N relative to diet, additional enrichment in the metabolic nitrogen pool must occur (Hobson *et al.*, 1993). A consequence of this process would be eventual enrichment in ^{15}N of all body tissues relative to periods without stress (Hobson *et al.*, 1993). Therefore studies using δ^{15}N analysis to infer diet must take account of the nutritional history of the individuals whose tissues are being examined

The main objectives behind this investigation were to firstly describe the stable isotope profiles of key dietary components of House Sparrows (in this case invertebrates and vegetable matter); secondly to test for relationships between δ^{15}N values in feathers and environmental factors and diet composition inferred from faecal samples; and thirdly to test for relationships between δ^{15}N values and chick survival and body condition.

7.2 Methods

7.2.1 Collection of invertebrate and feather samples

Isotopic profiles were obtained for six key invertebrate groups as well as artificial food in the form of seed, peanuts or bread. The invertebrate groups were spiders, ground beetles, weevils, ants, aphids and adult craneflies. These six groups were chosen due to their importance and predominance in the diets of nestling House Sparrows in suburban Leicester (Chapter 4). Invertebrate and artificial food samples were collected from five of my study sites, two in rural areas and three in suburban areas. No invertebrates were collected from urban sites, as no feathers were collected from urban chicks.

Single tertial feathers were collected from a single 10-day-old chick from 50 broods between April and August 2003. These broods were spread across a range of environmental conditions from suburban and rural landscapes. No feathers were collected from broods in urban areas as no chicks were available at the time feathers were being collected.

7.2.2 The preparation and isotope analysis of invertebrate prey and nestling feathers

Each tertial feather was removed from its sample vial and washed in 0.25M sodium hydroxide solution followed by two separate washes in purified water. The washed feathers were then returned to their sample vials. The clean feathers were then placed in a drying oven at 50°C overnight. The tertial feather samples were analysed with 20% duplication, where possible, using a sample size of 0.5mg. Each feather was cut to an appropriate size to reach a mass of approximately 0.5mg, taking the tip of each feather where there was more than 0.5 mg of material available. For duplicate analysis, a combination of feather vein and shaft was used for each analysis (Belanger, 2004)

The technique used for the analysis of nitrogen-15 and carbon-13 was elemental analyser combustion isotope ratio mass spectrometry (IRMS). Samples and reference materials were weighed into tin capsules, sealed, and then loaded into an automatic sampler on a Europa Scientific Roboprep-CN sample preparation module. Samples were then dropped into a furnace held at 1000^{o}C and combusted in the presence of oxygen. The combusted gases were swept in a helium stream over a combustion catalyst (Cr_2O_3), copper oxide wires (to oxidise hydrocarbons), and silver wool to remove sulphur and halides (Belanger, 2004).

The resultant gases (N_2, NO_x, H_2O, O_2, and CO_2) were swept through a reduction stage of pure copper wires maintained at 600°C. This treatment removed any oxygen and converted NO_x species to N_2. A magnesium perchlorate chemical trap removed water. Nitrogen and carbon dioxide were separated by a packed column gas chromatograph held at an isothermal temperature of 60°C. The resultant chromatographic peak entered the ion source of the Europa Scientific 20-20 IRMS where they were ionised and accelerated. Gas species of different mass were separated in a magnetic field then simultaneously measured on a Faraday cup universal collector array. For N_2, masses 28, 29, and 30 were monitored and for CO_2, masses 44, 45, and 46. Both references and samples were converted and analysed in this manner (Belanger, 2004). The analysis proceeds in a batch process, whereby a reference is analysed followed by a number of samples and then another reference (Belanger, 2004).

For the analysis of the feathers, the reference material used was NBS-1577A (powdered bovine liver) supplied by the National Bureau of Standards. NBS-1577A was used as it closely matches both the isotopic and elemental makeup of the feathers (Belanger, 2004). NBS-1577A has a δ-$^{15}N_{Air}$ value +7.25 ‰ and a δ-$^{13}C_{V\text{-}PDB}$ value of -21.68 ‰. This reference material has been calibrated against IAEA-N-1 Ammonium Sulphate (δ-$^{15}N_{AIR}$ = +0.4 ‰) for $\delta^{15}N$ and IAEA-CH-6 Sucrose (δ-$^{13}C_{V\text{-}PDB}$ = -10.43 ‰) for $\delta^{13}C$ (Belanger, 2004). The International Atomic Energy Agency (IAEA) distributes both of these materials as isotope reference standards (Belanger, 2004).

Samples of NBS-1577A, IAEA-N-1, IAEA-CH-6, IAEA-N-2 (Ammonium Sulphate, δ-$^{15}N_{AIR}$ = +20.3 ‰ for $\delta^{15}N$, distributed by the IAEA) and IA-R005 (Iso-Analytical sucrose, δ-$^{13}C_{V\text{-}PDB}$ – 26.03‰ for $\delta^{13}C$, calibrated against IAEA-CH-6) were analysed along with the feather samples as quality control checks (Belanger, 2004). The analysis of the seven prey groups followed the same methodology as the feather samples.

7.2.3 Statistical analysis and parameters investigated

7.2.3.1 The calibration process; Does $\delta^{15}N$ and $\delta^{13}C$ levels differ between prey groups

A one-way ANOVA test was used to determine if $\delta^{15}N$ and $\delta^{13}C$ levels differed between the seven prey groups (ants, beetles, spiders, aphids, cranefly, weevils and vegetable material). These prey groups were then aggregated into three groups according to their characteristics. For example ants, beetles and spiders were classed as carnivorous/mixed; the prey groups of aphids, cranefly and weevil were classed as vegetarian and the third group was vegetable material. A one-way ANOVA test was again used to determine if $\delta^{15}N$ and $\delta^{13}C$ levels differed between the three aggregated prey groups.

7.2.3.2 Factors affecting $\delta^{15}N$ levels

The possible environmental influences on stable-isotope ratios of carbon and nitrogen in sparrow nestling feathers were investigated. These were;
chick AGE (in days),
PERIOD (seasonality factor),
LANDSCAPE (three level factor: rural, suburban, urban),
NO2 (nitrogen dioxide levels around each box),
PRIN1 (continuous habitat variable),
PRIN2 (continuous habitat variable),

The composition of chick diet (spider, beetle, diptera, larvae, ant, homoptera and plant material) were also tested as possible biological influences on $\delta^{15}N$ and $\delta^{13}C$ levels in a separate analysis. Faecal sample results collected from the same chick that had a feather taken on the same day were used. Of the faecal samples collected from chicks that had feathers taken, all but 12 have faecal samples pertaining to them from an earlier age, however due to time constraints the priority was given to analysing the faecal samples collected on the same day as feather collection. General linear modelling (GLM), (with normal errors), was used to identify factors explaining significant variation in δ^{15}N levels, along with the inclusion of quadratic terms to test for curvilinear effects.

7.2.3.3 Determining whether δ^{15}N and δ^{13}C levels influence brood outcome, brood size at fledging, chick growth rate or chick condition

The level of δ^{15}N in each feather was tested to establish whether it predicts the number of young fledged from each brood using a Poisson general linear model. Due to the high number of feather samples that were taken from successfully fledging chicks compared to only one from a chick that subsequently died, there was no real power to test chick survival against δ^{15}N levels. However the outcome of the brood was tested to determine if δ^{15}N levels influenced partial loss within a brood.

Further analyses were undertaken using GLM (with normal errors) to determine whether δ^{15}N predicted brood size at fledging, chick mass growth rate and chick condition at day 10-11. The growth rate value was determined for each chick by calculating the daily increase in mass between two readings (mean grams gained per day), prior to the feather sample being taken. An expected mass for age day10-11, (based on a regression of chick mass on age) was calculated and then subtracted from the observed mass, giving a chick condition index. The δ^{15}N value for each feather was then tested as a predictor of both growth rate and chick condition.

7.3 Results

7.3.1 Variation in δ^{15}N and δ^{13}C levels between the seven prey groups

The invertebrate isotope ratios for each group type were determined to establish the food to feather fractionation (Figure 7.1). It can be seen from Figure 7.1 that certain invertebrates have higher δ^{15}N values than others. Spiders, beetles and ants generally have a higher δ^{15}N value than invertebrates such as aphids or artificial food such as seed, bread or peanuts. This is due to the invertebrate prey that the likes of carnivorous spiders and beetles eat, giving them a higher δ^{15}N value. It can be seen in Figure 7.1 that one of the four cranefly samples has a high δ^{15}N value (δ^{15}N = 13.45). This outlier reading is suspicious as craneflies are vegetarian invertebrates and therefore unlikely to have a high δ^{15}N value. This sample was therefore regarded as contaminated and excluded from the ANOVA analysis. The mean values of δ^{15}N and δ^{13}C for each of the seven prey groups can be seen in Table 7.1.

The values of δ^{15}N and δ^{13}C did significantly differ between the seven prey groups (δ^{13}C: P=0.036; n=31; δ^{15}N: P<0.0001; n=31). Once the seven groups were aggregated in to three groups, δ^{15}N was still significantly different between the carnivorous/mixed prey, the vegetarian prey and the vegetable material (δ^{15}N: P=<0.0001; n=31). However, δ^{13}C was not significantly different between the three aggregated prey groups (δ^{13}C: P=0.604; n=31). This significant difference indicates that stable isotopes, (in particular δ^{15}N), are a useful tool for measuring diet quality over a longer period than that usually covered by faecal samples.

Tertiary feathers appear at approximately 6 days from hatching, therefore the chick had to be at least 10 days old for the feather to be large enough to analyse. By that age most chicks were very likely to survive to fledging. The details of whether the chick was from a successful brood or whether partial failures occurred within the brood are presented in Figure 7.2.

Hobson and Clark (1992b) suggest $\delta^{15}N$ increases by between 1.1 and 3.5 units between diet and feather. Since the average feather score is 7.7 (80% of observations lie between 6.4 and 9.0) and it is assumed a mean fractionation of 3 units is representative, then chick diet must have average $\delta^{15}N$ scores of 4.7 (80% of chicks within 3.4 and 6.0) (Figure 7.2). This suggests the diet of many chicks must have been dominated by food items such as vegetable material and vegetarian invertebrates (i.e. aphids). The scores seen in Figure 7.2 suggest a fairly low level of nitrogen enrichment, therefore indicating a low quality diet amongst the broods whose feathers were taken.

7.3.2 Factors affecting $\delta^{15}N$ levels

There was a significant seasonal variation in the $\delta^{15}N$ values for each feather (Table 7.2) with the month of June recording the highest $\delta^{15}N$ values, followed by July with April and May showing the lowest $\delta^{15}N$ values (P=0.02; n=56). The low $\delta^{15}N$ values during the early part of the 2003 season (April/May) imply low quality diet (Figure 7.43). It should be noted that Chapter 5 highlighted relatively high chick starvation of first broods in 2003 (April/May), compared to the same period in 2002.

It can also been seen from Table 7.2 that the habitat variable PRIN2 (P<0.0001; n=56) and the proportion of spider remains within the diet (P=0.0016; n=50) were strong predictors of $\delta^{15}N$ values for each feather. The effect of PRIN2 (high proportion of concrete and evergreen, and low proportion of grass and arable, in home ranges) was negative (Figure 7.4). However the dataset was re-analysed without the four outlying results seen in Figure 7.4 and PRIN2 was found to be non-significant (P=0.59). Therefore the finding that the higher the proportion of concrete and evergreen vegetation surrounding a nest box, the lower the $\delta^{15}N$ values for each feather may need to be taken with slight caution.

The effect of the proportion of spider in brood faecal remains and the $\delta^{15}N$ value is a positive relationship (Figure 7.5). This might be expected as spiders are entirely carnivorous and therefore it could be anticipated this would cause an increase in $\delta^{15}N$ levels.

7.3.3 Determining whether $\delta^{15}N$ and $\delta^{13}C$ levels influence brood outcome, brood size at fledging, chick growth rate or chick condition

The value of $\delta^{15}N$ was found to be a non-significant predictor of the number of young fledged from each nest (brood size at fledging). It was still found to be non-significant after taking into account other significant predictors of the number of young fledged such as PERIOD and PRIN1 (taken from Table 5.9).

The score of $\delta^{15}N$ was a highly significant (P=0.007; n=56) predictor of chick growth rate (mean grams gained per day) (Table 7.2). The positive correlation between growth rate and $\delta^{15}N$ can be seen in Figure 7.6. As $\delta^{15}N$ has been confirmed to be a useful measure of diet quality, this positive relationship between growth rate and $\delta^{15}N$ implies that diet quality determines growth rate. Therefore when diet consists of high $\delta^{15}N$ prey items such as spiders, growth rate will also be greater.

The value of $\delta^{15}N$ was also a highly significant (P=0.008; n=56) predictor of chick condition at day10-11. The relationship between $\delta^{15}N$ and chick condition was positive (Figure 7.7) therefore the higher the $\delta^{15}N$ value the greater the chick condition index. This links high $\delta^{15}N$

levels and therefore good quality diet, to high chick condition levels. Good quality diet therefore implies greater growth rate and increased chick condition, ultimately improving nestling quality.

7.4 Discussion

Feathers reflect a bird's diet only through a particular temporal window. Factors that categorise this window include the turnover rate, biochemical composition, and the immediate organic source of the tissue as well as the animal's physiology (Mizutani *et al.*, 1992). A potential advantage of feathers as a dietary indicator is that feathers have a more narrowly defined window than other tissues, each feather reflecting the bird's diet during its formation (Mizutani *et al.*, 1992). Due to House Sparrow tertiary feathers forming at approximately 6 days, the dietary information gained will be from day 6 in the nest until the day of collection (approximately 10-11 days old).

7.4.1 The factors influencing stable-isotope ratios of carbon and nitrogen in sparrow nestling feathers

The seasonal variation in the $\delta^{15}N$ value suggests that there was in 2003 a variation in the availability of $\delta^{15}N$ high invertebrates such as spiders and beetles. This indicates that the availability of key invertebrates to the sparrow nestling's diet may be a problem across the season, especially during the early part of the season. This implication of low quality diet during the early part of the season in 2003 is highlighted in Chapter 5 with the relatively high chick starvation seen in the same period (Table 5.7 & 5.10).

It appears that the proportion of spider within nestling diet causes the $\delta^{15}N$ value to be higher. Habitat surrounding nest boxes that comprise of a high proportion of concrete and evergreen shrubs may give rise to lower $\delta^{15}N$ values, therefore suggesting nest boxes in these areas may have broods that are being fed fewer invertebrates that have high $\delta^{15}N$ values such as spiders.

7.4.2 Stable isotope ratios of nitrogen influence chick growth rate and chick condition

The positive relationship between $\delta^{15}N$ and growth rate and $\delta^{15}N$ and chick condition confirms that high $\delta^{15}N$ values represent high quality diet (such as spiders and beetles) and diet therefore determines growth rate and chick condition. Therefore high quality diet determines the health of the chick. In Chapter 6 it was shown that in areas with high nitrogen dioxide levels (urban/suburban areas), the brood mass at fledging was found to be significantly lower (Figure 6.10). This link between chicks in more urban/suburban areas being in poor condition and the implication that good quality diet influences the health of the chick suggests that the chicks in urban/suburban areas are ingesting a much poorer quality of diet. Hole (2001) showed that greater mass at fledging increased the probability of survival to independence. Therefore the suggestion that many chicks were being fed a poorer quality of diet (low $\delta^{15}N$ values; Figure 7.2) implies a reduction in the health of the chick at the time of fledging, which ultimately leads to a survival disadvantage between fledging and independence.

7.4.3 Conclusion

The variation in the $\delta^{15}N$ levels of invertebrates and artificial food (Figure 7.1) indicates that there is a potential use of $\delta^{15}N$ measurements to investigate the importance of plant versus invertebrate foods in general (Hobson, 1999). $\delta^{15}N$ values measured in chick tertial feathers probably provide a useful indicator of the quality of diet provided to chicks (in terms of the proportion of plant and vegetable material). In 2003, $\delta^{15}N$ values suggested that chick diet quality was lowest in home ranges with relatively large amounts of concrete and coniferous vegetation.

Table 7.1 The mean values of d15N and d13C for each of the seven prey groups and the three aggregated prey groups

Prey	Mean δ^{15}N value	Range of δ^{15}N values	Mean δ^{13}C value	Range of δ^{13}C values
1.Ants	7.68	7.24-8.26	–26.60	–25.56-–27.27
2.Beetles	7.28	6.42-7.83	–27.32	–26.47-–28.25
3.Spiders	7.06	5.28-8.85	–26.84	–26.07-–28.4
4.Weevils	6.41	4.36-9.39	–28.16	–26.55-–29.01
5.Cranefly	5.42	4.40-6.11	–27.14	–26.75-–27.69
Cranefly (including outlier value)	7.48	4.40-13.65	–27.96	–26.73-–30.4
6.Aphids	4.67	2.49-6.62	–25.57	–23.49-–28.28
7.Seed/bread/peanut	2.67	2.40-3.48	–26.39	–26.14-–26.9
1.Carnivorous/mixed	7.32	5.28-8.85	–26.94	–25.56-–28.4
2.Vegetarian	5.58	2.49-9.39	–27.04	–23.49-–29.01
Vegetarian (including cranefly outlier)	6.20	2.49-13.65	–27.30	–23.49-–30.4
3.Vegetable material	2.67	2.40-3.28	–26.39	–26.14-–26.9

Table 7.2 Summary of multivariate analyses of factors affecting the dN15 value of nestling sparrow feathers (n=56)

Dependent variables[1]	Independent Variables	Partial R^2 values	Direction & Magnitude of Effect
dN15 (n=56)	*PERIOD **PRIN2	12% 21%	middle>late>>early -VE
dN15 [diet] (n=50)	***PSPIDER	19%	+VE
Chick growth rate (n=56)	**N^{15}	11%	+VE
Chick condition (day10-11) (n=56)	**N^{15}	10%	+VE

[1] Significance levels: ****P*<0.001, ***P*<0.01, **P*<0.05, (*)*P*<0.08

Figure 7.1 The d15N and d13C values of key invertebrates and artificial food that are all important key components of nestling diet (n=32). Diets of invertebrate groups are described in parentheses.

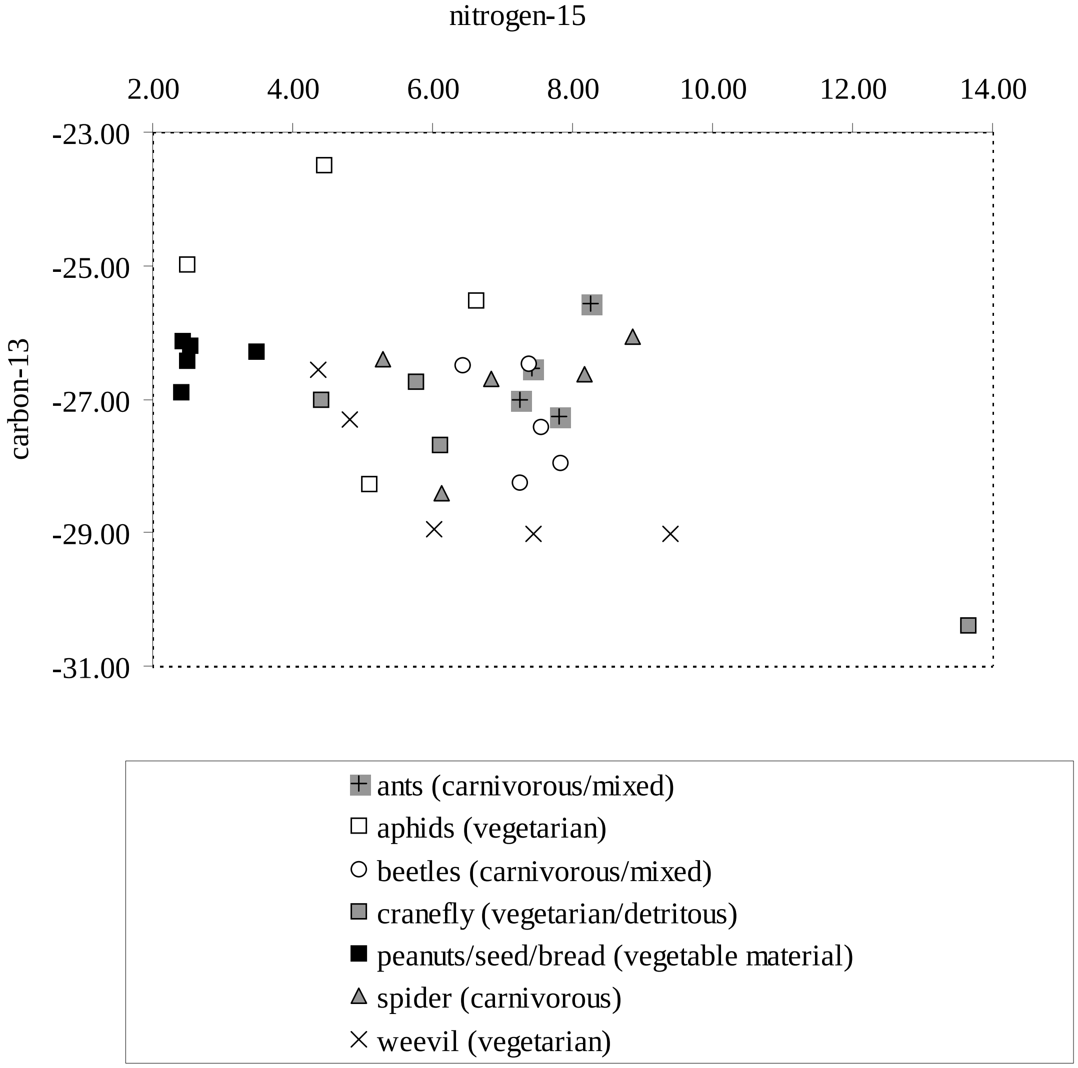


Figure 7.2 The d15N and d13C values from feathers taken from chicks within broods that all chicks successfully fledged or partially failed (n=56)

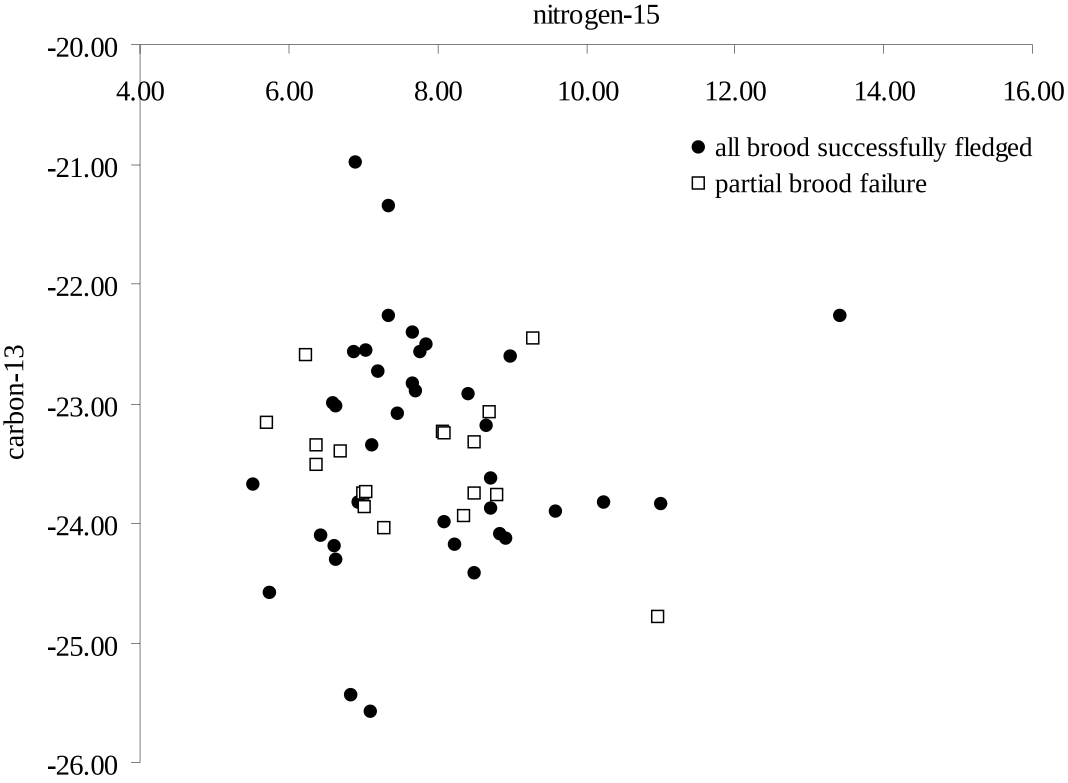


Figure 7.4 The relationship between d15N from nestling feathers and date [first egg date] (n=56)

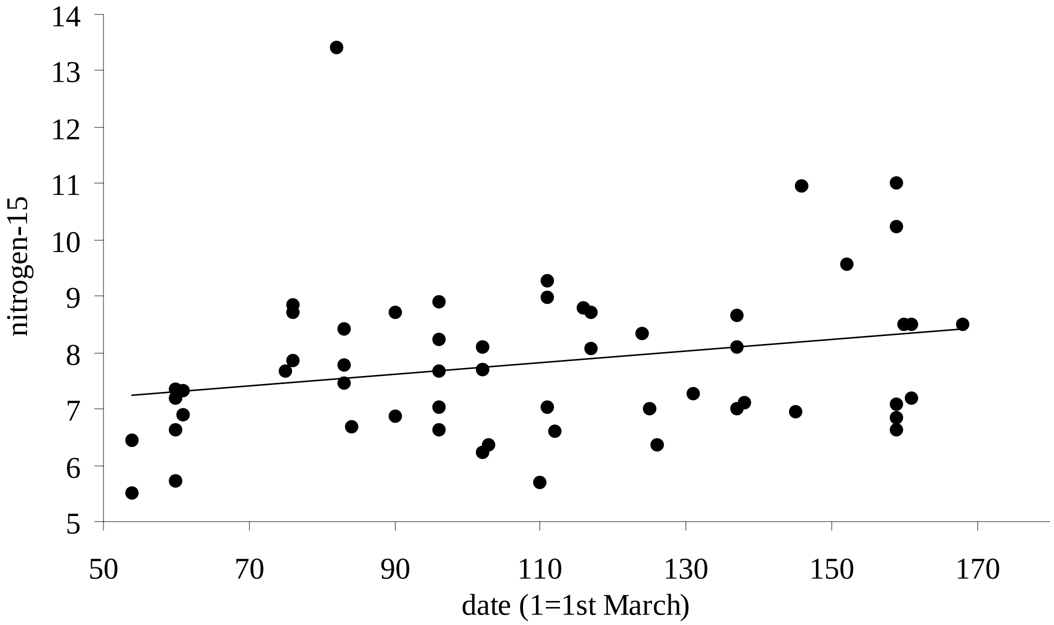


Figure 7.4 The relationship between d15N from nestling feathers and the habitat variable prin2 (n=56)

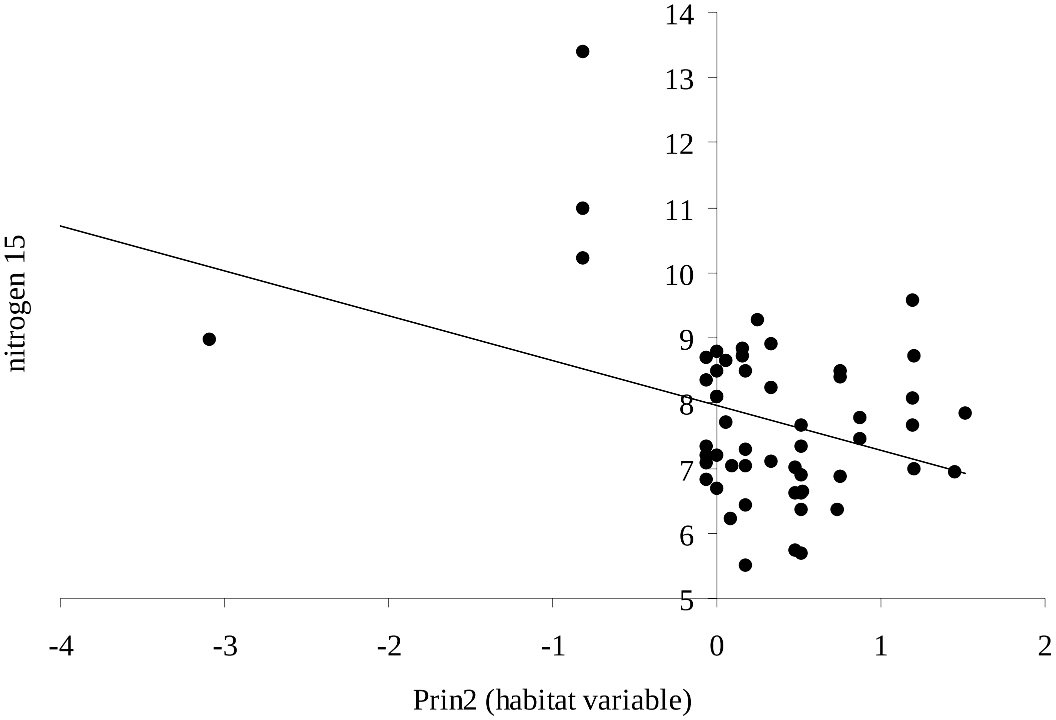


Figure 7.5 The relationship between the proportion of spider remains in faecal remains and d15N levels from nestling feathers (n=50)

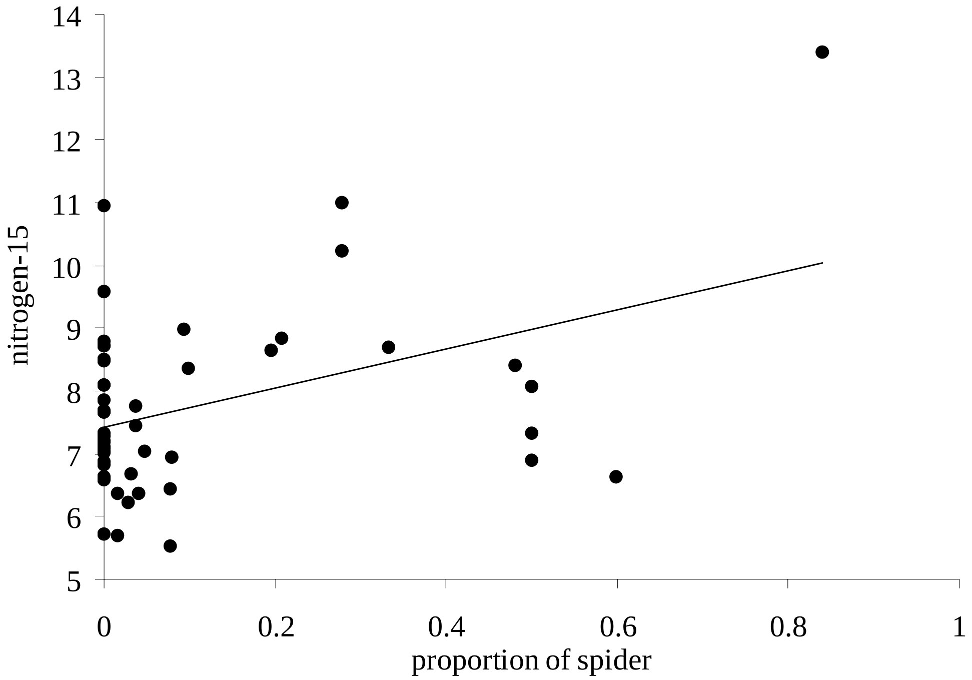


Figure 7.6 The relationship between d15N levels from nestling feathers and chick growth rate (mean grams gained per day) (n=56)

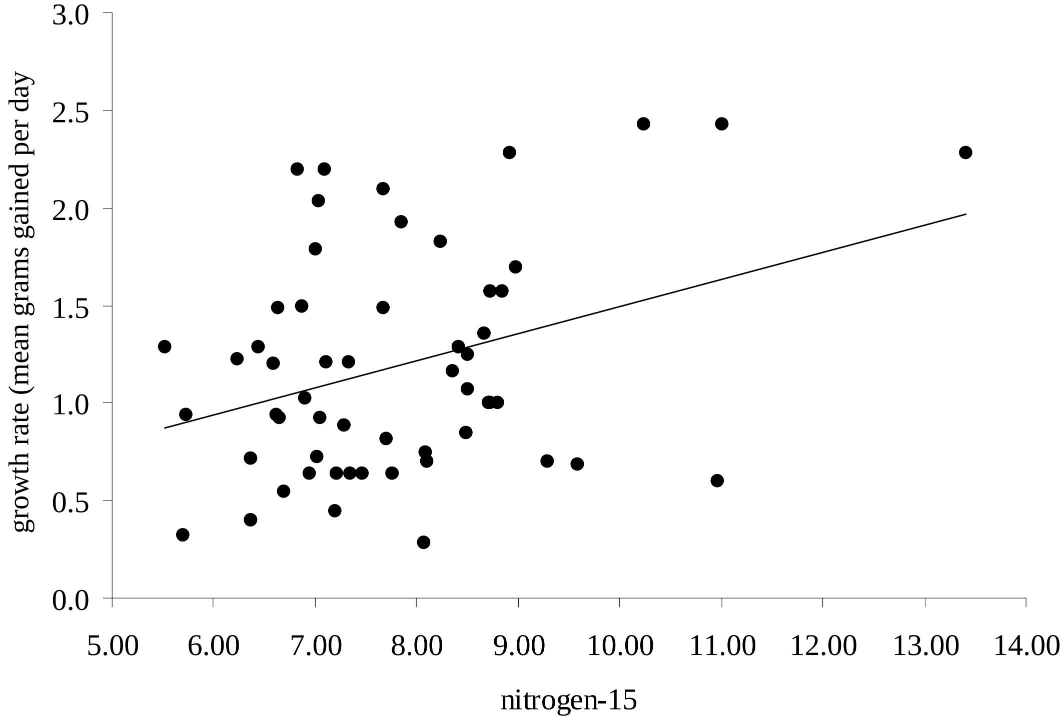
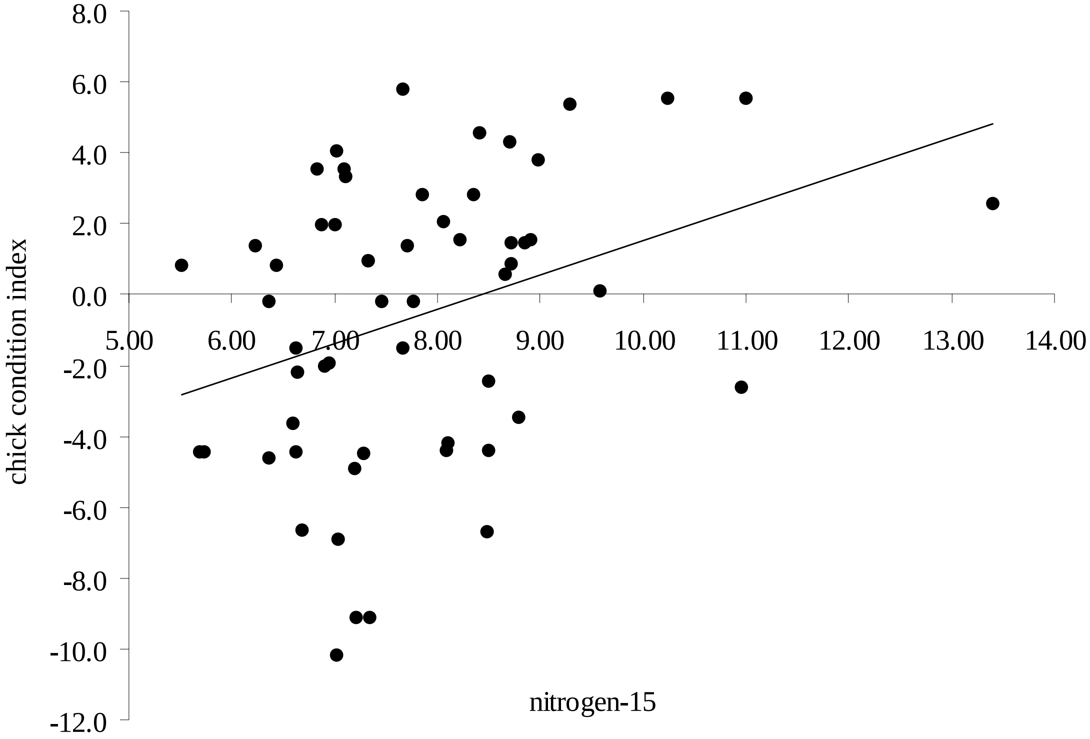


Figure 7.7 The relationship between the d15N levels from nestling feathers and chick condition at day10-11 (n=56)



CHAPTER 8

Habitat utilisation and selection by foraging fully-grown House Sparrows *Passer domesticus* throughout the breeding season

Abstract

The availability of suitable foraging habitat and the habitat composition within urban and suburban areas may have changed and it is not self-evident what the consequences of loss of suitable foraging habitat could be. Habitat use by House Sparrows searching for food to provision nestlings was compared across the season to determine whether foraging habits changed. Foraging observations along transect routes were recorded across the summer in 2002 and 2003. A total of 227 transects were completed during the two summers with 4555 foraging observations recorded. The most intensively used habitat in both years was deciduous shrub, with evergreen/ornamental shrubs being the least. Trees were most intensively used habitat in 2003, but one of the least intensively used in 2002. Tilled land, concrete and grass had an intermediate intensity of usage in both years. More subtle monthly effects were seen with grass being intensively used in May (2003) and less intensively used in July (2002), as well as trees being used less intensively in July (2003). This suggests that a key conservation prescription needed to increase the availability of invertebrates, and provide sparrows with a greater invertebrate food source, is the provision of a variation in deciduous native shrubs and trees within urban and suburban landscapes.

8.1 Introduction

The analysis of habitat selection and utilisation by birds is a complex subject (Aebischer and Robertson, 1992). However the loss or degradation of key habitats is a common cause of avian population declines, and understanding key habitat requirements is a common aim of many conservation biology studies. Knowledge of key, preferred and potentially limiting habitats can allow more to be provided in any conservation initiative. House Sparrow numbers have declined by about 60% in urban and suburban areas since the mid 1970s (Robinson *et al.*, 2005) and the habitat composition and quality in urban-suburban landscapes is likely to have changed over this period. It is not obvious what the consequences of loss of suitable foraging habitat could be. Habitat loss may have different consequences on the habitat use of a breeding bird, depending on the relative quality of alternative habitats (Bruun and Smith, 2003). Parents in impoverished landscapes may cover longer distances in order to utilise suitable habitats resulting in less food being delivered to offspring (Frey-Roos *et al.*, 1995). Alternatively, parents may search for food in less suitable habitats and therefore deliver food of lower quality to their offspring (Wright *et al.*, 1998).

House Sparrows are a mixed-diet species, granivorous for most of the year, with nestling diet largely composed of invertebrates (Summers-Smith, 1988). Nevertheless the information describing foraging habitat preferences of House Sparrows during the breeding season in urban and suburban areas are sparse. Therefore a comparison of habitat utilisation and selection through the breeding season was conducted. An important aim was to determine whether sparrows in urban-suburban landscapes were using habitats available to them randomly or whether there was selection of particular key foraging habitats. I was also interested if habitat usage (utilisation) or selection (usage in relation to availability) changed during the course of the breeding season.

8.2 Methods

8.2.1 Transect surveys

Usage of habitats by fully-grown foraging House Sparrows throughout the breeding season was determined during transect surveys. Line transects were established along the urbanisation gradient, with sixteen in rural locations, sixteen in suburban and twelve in urban areas. The lengths of each transect varied between 200m and 600m with a mean length of approximately 300m. The same sample of transects were surveyed in 2002 and 2003. Along each transect the percentage cover of 14 habitat categories (Table 2.2), 50 metres either side of the route was recorded, to determine the availability of habitat to foraging birds.

The recording of foraging sparrows was undertaken whilst walking along the fixed transect route once a month during May, June and July in 2002 and 2003. I undertook this fieldwork along with help from an assistant during 2002 and a different assistant during 2003. The number of fully grown foraging birds (including juveniles more than about 14 days after fledging) and the habitat category in which they were foraging in were recorded, as well as non-foraging (e.g. calling, bathing, loafing) birds. However only foraging birds were included in the analyses of habitat utilisation and selection described below. Where possible the species of vegetation the bird was feeding on was recorded, as well as the distance the bird was from the observer through the allocation of distance categories (e.g. 0-50m, >50m etc), the number of juveniles, the period of observation and the weather. Observations of all foraging activity were recorded for approximately 1.5 hours per transect. The time of day when the surveying took place was rotated between months so as to reduce the influence of any diurnal variation in foraging behaviour.

8.2.2 *Habitat utilisation*

The number of habitat categories used to record the percentage cover and foraging observations was initially thirteen but prior to analysis a number of categories were amalgamated to facilitate analysis. For example weedy patches, mown lawn, un-mown grass and grazed grass were amalgamated to form one category ‘all grass’. The habitat categories of woodland and individual trees were also amalgamated to form the category ‘trees’. Rare habitats that had no foraging observations were excluded from the analysis; these were water bodies and farm buildings. The category of arable farmland was included within the habitat utilisation analysis as foraging observations were recorded in this habitat but as it was a relatively rare habitat along the transects, it was excluded from the habitat selection compositional analyses.

Utilisation of habitat by foraging fully-grown birds was initially analysed using chi-square contingency test analysis (Fowler and Cohen, 1997). I tested whether the patterns of habitat utilisation differed between months (May, June and July) or between years or between landscapes (urban vs. suburban vs. rural).

8.2.3. Habitat selection

Habitat selection considers the utilisation of habitats in relation to its availability and can therefore be considered to reflect the relative intensity of usage of different habitats. The relative intensity of usage varied significantly between habitats during all three months in both years; in other words, habitat selection was significantly non-random (see results section; Table 8.3). Compositional analysis (Aebischer *et al.*, 1993) was used to describe habitat selection across the breeding season. The percentage cover of available habitat along each transect was derived from mapping surveys of all transect routes and the percentage of habitat used by foraging birds was calculated from the number of observations recorded within each habitat type. Only seven habitats were analysed due to the exclusion of the rare habitat of arable farmland (N.B. inclusion of the arable habitat caused the failure of the numerical procedure). The numerical analysis was performed using specialist software implemented in and provided by Microsoft Excel (Smith, 2003). This software implements the methods by Aebischer *et al*. (1993) and tests for non-random habitat selection using a randomisation test as recommended by Aebischer *et al*. (1993). This test overcomes problems arising when the distribution of log ratio differences is not multivariate normal.

When availability for some of the habitats was zero, the method recommended by Aebischer *et al*. (1993) was implemented, i.e. replacement of missing values in a particular residual log-ratio by the mean of all non-missing values for that log-ratio and then computation of a mean lambda by weighting each denominator-dependent value of lambda by the number of non-missing values involved in its calculation. Separate analyses were undertaken for each month (May, June and July) and one for combined observations in each year, giving a total of eight analyses.

8.3. Results

8.3.1 Habitat Utilisation

A grand total of 227 transects were completed during the two summers with 4555 foraging observations recorded (Table 8.1). The utilisation of habitat for foraging birds was significantly associated with year, month and landscape (Table 8.2). The percentage of observations recorded in each habitat for each month in 2002 and 2003 is shown in Figure 8.1. The main patterns that are evident are, during 2002 the greatest number of foraging observations were seen in grass habitats followed by concrete areas (buildings/roads/pavements), deciduous shrubs, and trees. Whereas during 2003, grass still had the greatest number of foraging observations but was followed by deciduous shrub, trees and then concrete. Therefore the usage of trees and deciduous shrubs increased in 2003.

These apparent differences in habitat usage between years were confirmed through the significant difference in the distribution of relative usage (Table 8.2). Therefore the use of habitat by foraging birds is dependent on year. Due to the statistically significant association between year and habitat usage, the monthly data for each year could not be pooled and each year had to be analysed separately. In 2002 and 2003, there is a significant association between months and habitat usage (Table 8.2 and Figure 8.1). It can be seen in Figure 8.1 that there is less variation in the foraging habitats utilised between months in 2002 than in 2003, with concrete, grass and deciduous shrubs playing an important part across the season in 2002.

The difference in habitat utilisation between landscapes in each month was shown to be statistically significant (Table 8.2). During May, urban transects recorded a greater proportion of foraging within concrete areas and trees. Whereas in the suburban landscape, grass habitat and deciduous shrub, played a more important role, with rural landscape showing grass and deciduous shrub to be important during this month also (Figure 8.2). In urban areas in June, concrete and trees were again both important foraging habitats, with suburban and rural areas showing grass and deciduous shrubs to be more important (Figure 8.3). Wheat and barley arable fields were being used during June in rural areas with birds taking unripe seed heads (Figure 8.3).

During July in urban areas, foraging in concrete areas accounted for nearly half of all observations (43.7%) followed by deciduous shrub (23.2%), however this was not the case in suburban areas with deciduous shrub (37.8%) and tilled and grass habitats being important (Figure 8.5). In rural areas in July deciduous shrub (34.6%) was the most important habitat followed by grass habitats like suburban areas but arable habitat (wheat and barley) were again being utilised (Figure 8.4).

Even though there was variation between months and landscapes, the three most important utilised habitats were deciduous shrub, concrete areas and grass, with trees becoming more important in 2003.

8.3.2 Habitat Selection

For each of the eight analyses the wilk's lambda value was highly significant therefore showing non-randomisation of habitat selection by foraging birds (Table 8.5). Evergreen and ornamental shrubs were avoided in both years (Table 8.4 & Table 8.), whereas deciduous shrub was preferred in both years. Trees were avoided in 2002 but strongly selected in 2003 (Table 8.4 & 8.5). The habitats of tilled land, concrete and grass were also selected in both years, though not as much as deciduous shrub and trees, especially in 2003.

There were generally fewer significant results through the season (Table 8.4 & 8.5) due to less data bringing less power to the analyses. However seasonal patterns were very similar to ALL, therefore suggesting few seasonal effects. Grass was less intensively used in July, compared to May and June in 2002, as was the case in 2003 (Table 8.4 & 8.5). Trees were intensively used during July in 2002 whereas they were much less intensively used during July in 2003. Tilled habitat (allotments and flowerbeds) was the most preferred habitat during June in 2002 and was used less intensively during May and July 2002. However it must be noted these seasonal monthly effects are not very pronounced.

Therefore it can be seen from both years that the key habitats across the season are deciduous shrub, tilled land, grassy areas and concrete, with trees being much more preferential in 2003 but importantly evergreen and ornamental are strongly avoided in all months and both years (Table 8.4 & 8.5).

8.4 Discussion

Deciduous shrubs (mainly hawthorn, blackthorn and dog rose), grassy areas and concrete were used in excess of their availability within foraging areas, with trees appearing to be extremely important in 2003. Ornamental, (non-native species) and evergreen shrubs were strongly avoided. The most important habitats regarding utilisation were grass and concrete in 2002 and deciduous shrub and trees in 2003. The high usage but intermediate selection of grass could suggest this is a very important habitat to foraging House Sparrows. Grass habitat is an important resource of invertebrates such as Tipulids and Diptera.

The high use of concrete areas as foraging habitat can be linked to the provision of artificial food such as seed and bread, due to the common occurrence of artificial food being available within this habitat. Ants are likely to be found on concrete and ants were commoner in the diet in 2002 (Chapter 4), as was the usage of concrete as a foraging habitat. It was shown in Chapter 4 that ants were associated with chick starvation and chick starvation was greatest when concrete usage was greatest in each year (i.e. July 2002 and May 2003) (Chapter 5).

It is well known that some trees and shrubs have many species of insects living upon them and others, recently introduced or non-native species, comparatively few (Southwood, 1961). Native deciduous shrubs such as hawthorn, blackthorn and apple and trees such as oak, willow and birch have a large number of insects attached to them (Southwood, 1961). Whereas evergreen species such as holly and fir have a relatively small number of insect species associated with them (Southwood, 1961). From undertaking feather isotope analysis (Chapter 7) it was shown that a high proportion of evergreen vegetation surrounding a nest box lowers the $\delta^{15}N$ value for each feather, therefore suggesting a lower availability of invertebrates with high $\delta^{15}N$ values such as spiders and beetles within this habitat. Therefore the low ranking of evergreen and ornamental shrub as a foraging habitat, probably reflects the relatively low density of suitable invertebrates available to foraging sparrows.

There were quite large differences in the utilisation of habitats between landscapes with grass usage greatest in rural habitats and least in urban habitats. This reflects the pattern of a greater number of Diptera found in faecal samples from rural areas than suburban and urban areas. Tree usage was greater in urban areas than rural areas except in July, while deciduous shrub was utilised more in rural areas. Therefore in urban areas there was heavy usage of concrete, where ants and artificial food are more common and trees, where Homoptera (aphids) are often found. Seel (1969) found that aphids were prominent in nestling diet and described adult sparrrows feeding in trees for aphids. Both ants and artificial food are associated with higher chick mortality (Chapter 4). In rural areas there was heavy usage of grass and deciduous shrub and relatively little use of concrete and tilled land.

The much greater consumption of Diptera in rural areas and the much lower consumption of Homoptera, seems to fit the general pattern of habitat usage/availability as it suggests Homoptera may be a ‘fall-back’ sub-optimal prey type only taken in large quantities (i.e. from trees) when better food is unavailable.

8.4.1 Conclusion

Urbanisation creates a heterogeneous mosaic of patches consisting of built-up areas, areas of construction, and remnants of indigenous habitat. The presence of high vegetative and structural diversity have been attributed to high arthropod diversity and abundance within suburban areas

(Owen and Owen, 1975), highlighting the need for a variation in deciduous native shrubs and trees within gardens.

Therefore it appears that sparrows prefer a varied vegetative structural diversity when foraging for invertebrates for nestlings, and deciduous shrubs, trees and grassy habitats appear to be the key habitats that provide that variation. However in areas where the availability of deciduous shrub and grassy habitats were low (e.g. urban areas), concrete areas and therefore the availability of artificial food became increasingly important. Evergreen and ornamental shrubs were rarely used by foraging House Sparrows even in areas lacking grass, trees or deciduous habitats.

Within Chapter 4 it has been shown that there is a problem with a lack of invertebrates within nestling diet causing high mortality and a low nesting success. Therefore if there is a lack of availability of habitat such as deciduous shrub which provides greater numbers of invertebrates to foraging sparrows, then this will have a secondary effect on the health of sparrow nestlings. Therefore the outcome of this investigation suggests that a key conservation prescription that needs to be implemented to increase the availability of invertebrates, and provide sparrows with a greater invertebrate food source, is the provision of native deciduous shrubs and trees within urban and suburban landscapes.

Table 8.1 The number of transects completed and the number of foraging observations recorded in each landscape, each month and each year (no. transect/no. observations)

	2002				2003			
	May	June	July	**Total**	May	June	July	**Total**
Urban	10/169	11/331	9/187	**30/687**	12/135	9/299	9/144	**30/578**
Suburban	17/268	15/311	15/478	**47/1057**	16/236	13/302	14/389	**43/927**
Rural	13/226	14/180	13/295	**40/701**	16/255	11/104	10/246	**37/605**
Total	**40/663**	**40/822**	**37/960**	**117/2445**	**44/626**	**33/705**	**33/779**	**110/2110**

Table 8.2 The significance of association resulting from chi-square testing between month (May vs June vs July) for each landscape in each year, between landscape (urban vs suburban vs rural) for each month in each year and between year (2002 vs 2003) for each month in each landscape

Factors testing for:	d.f.	χ^2	Probability (*P* value)
MONTH : (May vs June vs July)			
Urban 2002	12	65.53	<0.0001
Suburban 2002	14	65.53	<0.0001
Rural 2002	12	56.48	<0.0001
Urban 2003	12	126.68	<0.0001
Suburban 2003	12	21.62	0.042
Rural 2003	12	60.45	<0.0001
LANDSCAPE: (Urban vs Suburban vs Rural)			
May 2002	12	50.15	<0.0001
June 2002	14	45.39	<0.0001
July 2002	14	88.99	<0.0001
May 2003	12	54.97	<0.0001
June 2003	12	42.92	<0.0001
July 2003	12	85.51	<0.0001
YEAR: (2002 vs 2003)			
May Urban	6	59.24	<0.0001
June Urban	5	78.22	<0.0001
July Urban	5	54.52	<0.0001
May Suburban	6	19.27	0.0037
June Suburban	7	44.55	<0.0001
July Suburban	6	23.39	0.0007
May Rural	5	38.04	<0.0001
June Rural	7	34.59	<0.0001
July Rural	6	40.83	<0.0001

Table 8.5 Wilks lambda and randomisation probability values for habitat selection in 2002 and 2003 and across the season

Year & Month	Wilks Lambda	Randomization *P*
2002 May	0.40	0.001
2002 June	0.36	0.003
2002 July	0.32	0.001
2002 Combined	0.18	0.001
2003 May	0.15	0.001
2003 June	0.11	0.001
2003 July	0.17	0.01
2003 Combined	0.11	0.001

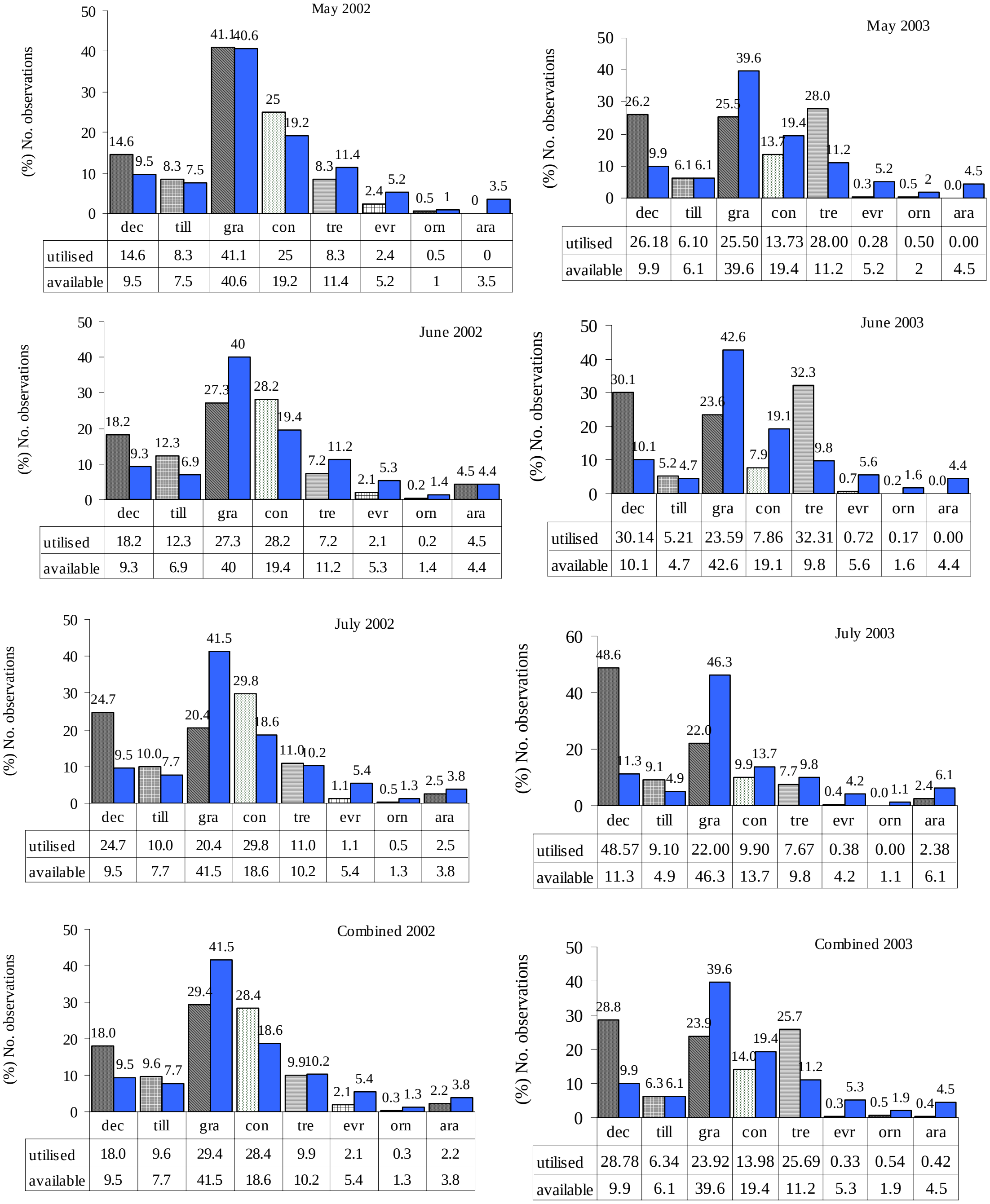
Table 8.4 Pairwise habitat preferences reflecting habitat selection at the level of month (ALL is the three months across the season combined) in 2002, as shown by compositional analysis. Signs indicate preferences for habitats down the left-side column relative to those running along the top row. Three +/- symbols represent statistically significant departures from random (at P < 0.05) while single symbols reflect non-significant preferences. Ranks indicate the most preferred (1) and most avoided (7) habitats in each month

		TILL	CONC	GRA	TREE	EVR	ORN	Rank
Deciduous (DEC)	MAY	+	+	+	+ + +	+ + +	+	1
	JUNE	–	+	+	+	+ + +	+	2
	JULY	+	+	+ + +	+	+ + +	+	1
	ALL	+	+	+	+ + +	+ + +	+ + +	1
Tilled (TILL)	MAY		–	+	+	+ + +	+	2
	JUNE		+	+	+	+ + +	+ + +	1
	JULY		+	+ + +	+	+ + +	+	2
	ALL		+	+	+	+ + +	+ + +	2
Concrete (CONC)	MAY			–	+	+ + +	+	2
	JUNE			–	+ + +	+ + +	+	4
	JULY			+	+	+ + +	+ + +	3
	ALL			+	+	+ + +	+ + +	3
All Grass (GRA)	MAY				+ + +	+ + +	+	2
	JUNE				+ + +	+ + +	+	3
	JULY				–	+	–	5
	ALL				+ + +	+ + +	+ + +	4
Trees (TREE)	MAY					+	–	6
	JUNE					+	–	6
	JULY					+	+	4
	ALL					+ + +	+	5
Evergreen (EVR)	MAY						–	7
	JUNE						–	7
	JULY						+	5
	ALL						+	6
Ornamental (ORN)	MAY							5
	JUNE							5
	JULY							5
	ALL							7

Table 8.5 Pairwise habitat preferences reflecting habitat selection at the level of month (ALL is the three months across the season combined) in 2003, as shown by compositional analysis. Signs indicate preferences for habitats down the left-side column relative to those running along the top row. Three +/- symbols represent statistically significant departures from random (at P < 0.05) while single symbols reflect non-significant preferences. Ranks indicate the most preferred (1) and most avoided (7) habitats in each month

		DEC	GRA	TILL	CONC	ORN	EVR	Rank
Trees (TREE)	MAY	+	+	+ + +	+ + +	+ + +	+ + +	1
	JUNE	+	+ + +	+	+ + +	+	+ + +	1
	JULY	– – –	+	+	+	+	+ + +	2
	ALL	+	+ + +	+ + +	+ + +	+ + +	+ + +	1
Deciduous (DEC)	MAY		+ + +	+	+ + +	+ + +	+ + +	2
	JUNE		+ + +	+	+ + +	+	+ + +	2
	JULY		+ + +	+	+ + +	+ + +	+ + +	1
	ALL		+ + +	+	+ + +	+ + +	+ + +	2
All Grass (GRA)	MAY			+	+	+	+ + +	3
	JUNE			–	+	–	+	5
	JULY			–	+	–	+	5
	ALL			+	+	+ + +	+ + +	3
Tilled (TILL)	MAY				+	+	+ + +	4
	JUNE				+	+	+ + +	3
	JULY				+	+	+	3
	ALL				+	+ + +	+ + +	4
Concrete (CONC)	MAY					+	+ + +	6
	JUNE					–	+	6
	JULY					–	+	6
	ALL					+ + +	+ + +	5
Ornamental (ORN)	MAY						+ + +	6
	JUNE						+	4
	JULY						+	4
	ALL						+	6
Evergreen (EVR)	MAY							7
	JUNE							7
	JULY							7
	ALL							7

Figure 8.1 Habitat utilisation by fully-grown foraging birds during May, June and July and combined (across the season) in 2002 and 2003. Available habitat is represented by blue bars. The habitat categories are as follows: dec=deciduous shrub; till=tilled land; gra=mown/unmown/grazed grass & weedy patches; con=concrete; tre=trees; evr=evergreen shrubs; orn=ornamental shrubs; ara=arable farmland



May 2002

	dec	till	gra	con	tre	evr	orn	ara
utilised	14.6	8.3	41.1	25	8.3	2.4	0.5	0
available	9.5	7.5	40.6	19.2	11.4	5.2	1	3.5

May 2003

	dec	till	gra	con	tre	evr	orn	ara
utilised	26.18	6.10	25.50	13.73	28.00	0.28	0.50	0.00
available	9.9	6.1	39.6	19.4	11.2	5.2	2	4.5

June 2002

	dec	till	gra	con	tre	evr	orn	ara
utilised	18.2	12.3	27.3	28.2	7.2	2.1	0.2	4.5
available	9.3	6.9	40	19.4	11.2	5.3	1.4	4.4

June 2003

	dec	till	gra	con	tre	evr	orn	ara
utilised	30.14	5.21	23.59	7.86	32.31	0.72	0.17	0.00
available	10.1	4.7	42.6	19.1	9.8	5.6	1.6	4.4

July 2002

	dec	till	gra	con	tre	evr	orn	ara
utilised	24.7	10.0	20.4	29.8	11.0	1.1	0.5	2.5
available	9.5	7.7	41.5	18.6	10.2	5.4	1.3	3.8

July 2003

	dec	till	gra	con	tre	evr	orn	ara
utilised	48.57	9.10	22.00	9.90	7.67	0.38	0.00	2.38
available	11.3	4.9	46.3	13.7	9.8	4.2	1.1	6.1

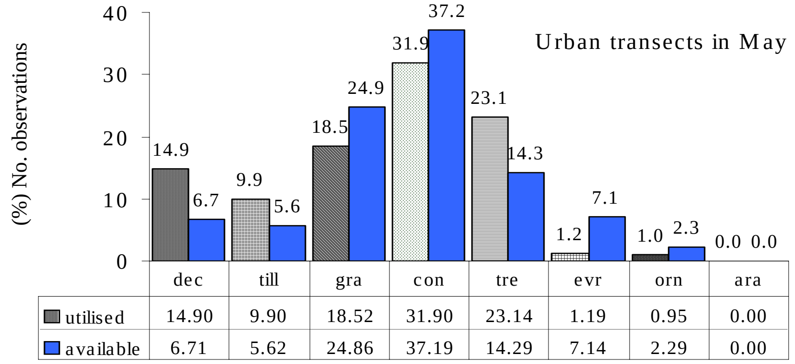
Combined 2002

	dec	till	gra	con	tre	evr	orn	ara
utilised	18.0	9.6	29.4	28.4	9.9	2.1	0.3	2.2
available	9.5	7.7	41.5	18.6	10.2	5.4	1.3	3.8

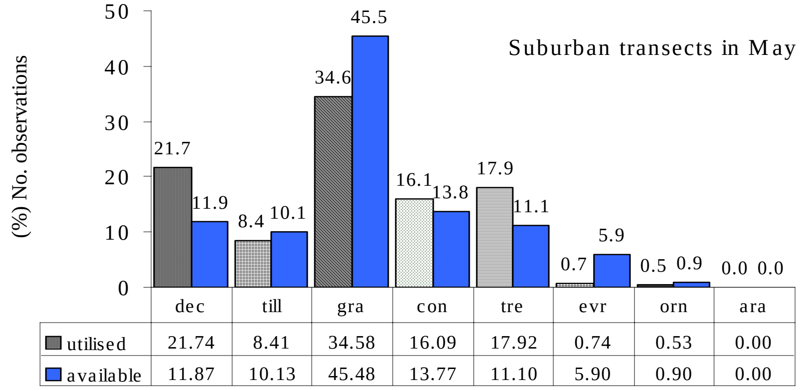
Combined 2003

	dec	till	gra	con	tre	evr	orn	ara
utilised	28.78	6.34	23.92	13.98	25.69	0.33	0.54	0.42
available	9.9	6.1	39.6	19.4	11.2	5.3	1.9	4.5

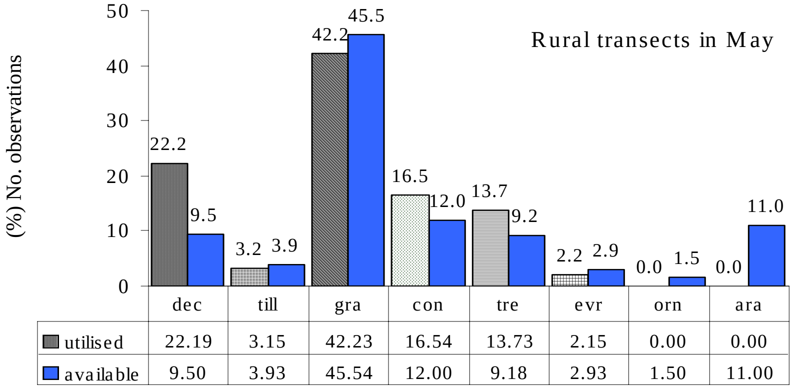
Figure 8.2 Habitat utilisation by fully grown foraging birds in May for urban, suburban and rural landscapes. The habitat categories are as follows: dec=deciduous shrub; till=tilled land; gra=mown/unmown/grazed grass & weedy patches; con=concrete; tre=trees; evr=evergreen shrubs; orn=ornamental shrubs; ara=arable farmland;



	dec	till	gra	con	tre	evr	orn	ara
▨ utilised	14.90	9.90	18.52	31.90	23.14	1.19	0.95	0.00
🟦 available	6.71	5.62	24.86	37.19	14.29	7.14	2.29	0.00

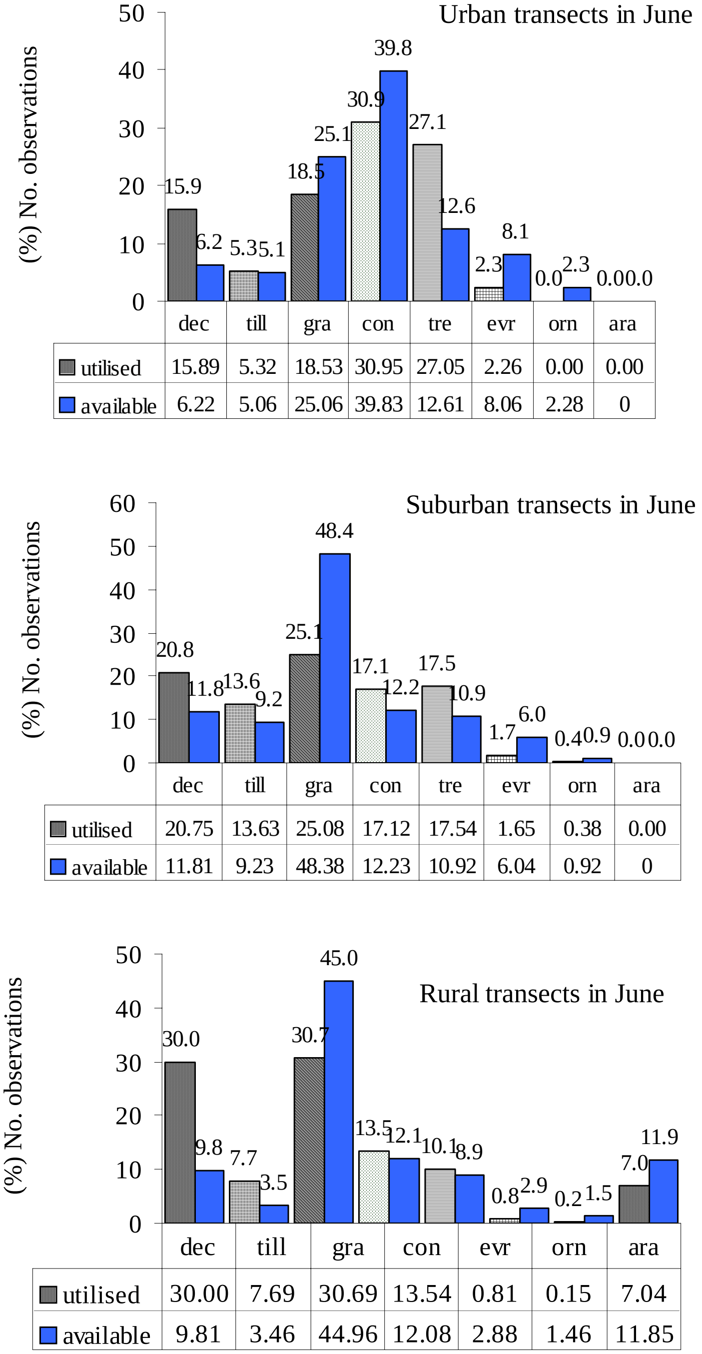


	dec	till	gra	con	tre	evr	orn	ara
▨ utilised	21.74	8.41	34.58	16.09	17.92	0.74	0.53	0.00
🟦 available	11.87	10.13	45.48	13.77	11.10	5.90	0.90	0.00



	dec	till	gra	con	tre	evr	orn	ara
▨ utilised	22.19	3.15	42.23	16.54	13.73	2.15	0.00	0.00
🟦 available	9.50	3.93	45.54	12.00	9.18	2.93	1.50	11.00

Figure 8.3 Habitat utilisation by fully grown foraging birds in June for urban, suburban and rural landscapes. The habitat categories are as follows: dec=deciduous shrub; till=tilled land; gra=mown/unmown/grazed grass & weedy patches; con=concrete; tre=trees; evr=evergreen shrubs; orn=ornamental shrubs; ara=arable farmland;

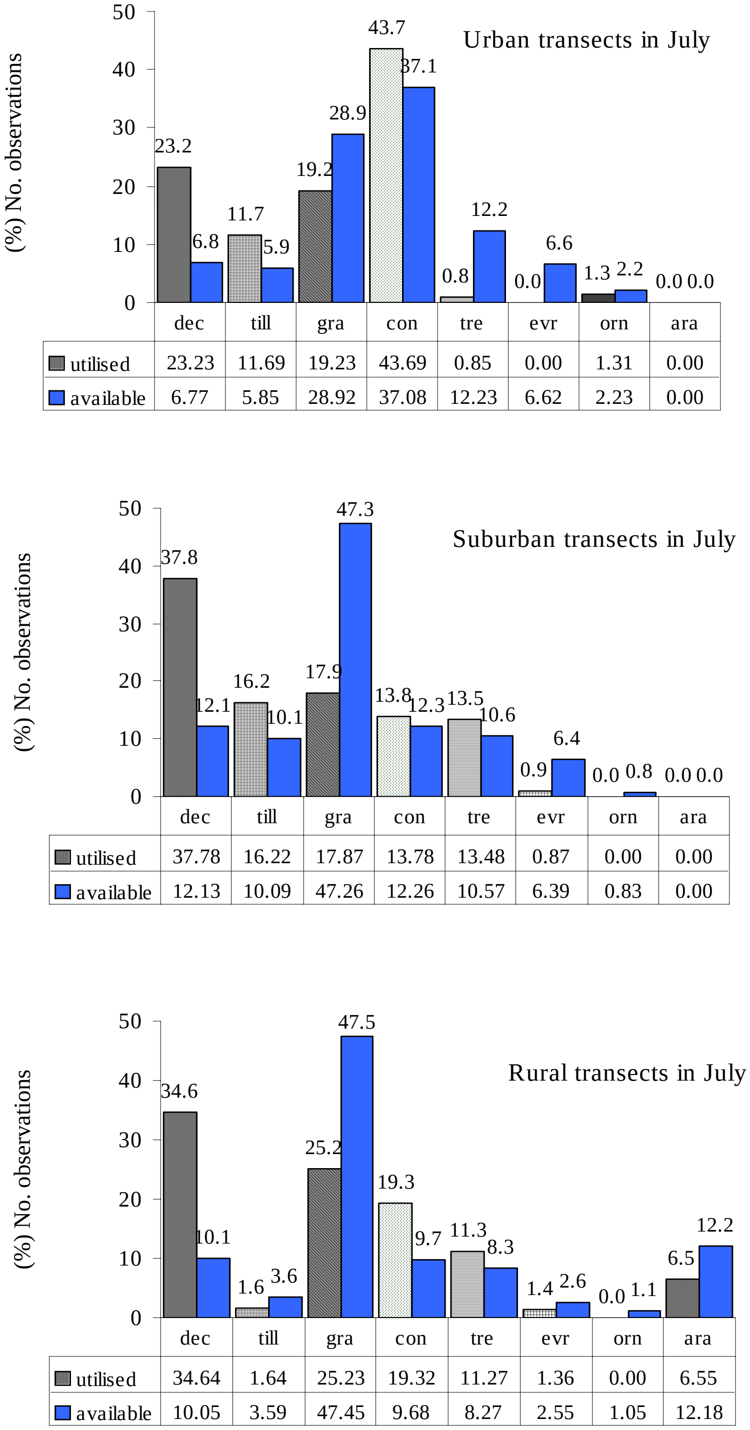


	dec	till	gra	con	tre	evr	orn	ara
utilised	15.89	5.32	18.53	30.95	27.05	2.26	0.00	0.00
available	6.22	5.06	25.06	39.83	12.61	8.06	2.28	0

	dec	till	gra	con	tre	evr	orn	ara
utilised	20.75	13.63	25.08	17.12	17.54	1.65	0.38	0.00
available	11.81	9.23	48.38	12.23	10.92	6.04	0.92	0

	dec	till	gra	con	evr	orn	ara
utilised	30.00	7.69	30.69	13.54	0.81	0.15	7.04
available	9.81	3.46	44.96	12.08	2.88	1.46	11.85

Figure 8.5 Habitat utilisation by fully-grown foraging birds in July for urban, suburban and rural landscapes. The habitat categories are as follows: dec=deciduous shrub; till=tilled land; gra=mown/unmown/grazed grass & weedy patches; con=concrete; tre=trees; evr=evergreen shrubs; orn=ornamental shrubs; ara=arable farmland



	dec	till	gra	con	tre	evr	orn	ara
▨ utilised	23.23	11.69	19.23	43.69	0.85	0.00	1.31	0.00
🟦 available	6.77	5.85	28.92	37.08	12.23	6.62	2.23	0.00

	dec	till	gra	con	tre	evr	orn	ara
▨ utilised	37.78	16.22	17.87	13.78	13.48	0.87	0.00	0.00
🟦 available	12.13	10.09	47.26	12.26	10.57	6.39	0.83	0.00

	dec	till	gra	con	tre	evr	orn	ara
▨ utilised	34.64	1.64	25.23	19.32	11.27	1.36	0.00	6.55
🟦 available	10.05	3.59	47.45	9.68	8.27	2.55	1.05	12.18

CHAPTER 9

Over-winter survival in the House Sparrow *Passer domesticus* within a suburban and rural habitat

Abstract

Over-winter survival was investigated using mark-resighting methodology at two study areas (one rural and one suburban) during the winter of 2002-2003. Ninety-four House Sparrows were trapped and colour-ringed between late August and early October. Surviving birds were then resighted at monthly intervals between November 2002 and March 2003. Resighting rates did not differ between months at each of the sites but differed between study sites, with the suburban site showing a higher re-sighting rate (28%) than the rural site (14%). Apparent survival was 100% during each month between November and March. There was no evidence that survival differed between adult and first-year sparrows or between study areas. The implausibly high monthly survival estimate between November and March (100%) was probably a consequence of the relatively small data sets and low precision.

9.1 Introduction

Populations of House Sparrows in rural areas have declined by 47% since the mid 1970’s, with populations in urban and suburban areas showing declines of about 60% (Robinson *et al.*, 2005). There is evidence that in rural areas, a reduction in over-winter survival is the demographic mechanism that may have driven population declines (Siriwardena *et al.*, 1999; Hole, 2001). However, very little is known about over-winter survival of House Sparrows in suburban habitats. I therefore investigated the survival of House Sparrows at a rural and a suburban location during the winter of 2002/03.

Food availability is often assumed to be crucial to the winter survival of birds (Lack, 1954), due to a decreasing food supply, short days and low ambient temperatures (Fretwell, 1972). Increased population levels of birds have been attained in some cases after addition of winter food (Krebs, 1971). Nevertheless, a critical test of the idea that winter food shortage is the underlying cause of winter mortality requires a simultaneous untreated control and also that survival and immigration can be separated (Jansson *et al.*, 1981). The strongest test of the ‘winter food limitation’ hypothesis so far is probably the evidence that low winter food supply may not always result in food shortage for the studied population (Pulliam and Parker, 1979). However in Oxfordshire it was found that the provision of supplementary seed food in winter increased over-winter survival within a farmland sparrow population (Hole, 2001; Hole *et al.*, 2002).

Estimating survival rates of wild populations of birds generally involves marking a representative sample of individuals from the population and then subsequently resampling them, usually by regularly recapturing or resighting birds that are still alive (Francis and Cooke, 1993). The quantitative analysis of survival studies and experiments must be based on capture-recapture or resighting models which consider recapture or resighting rates as well as survival rates (Lebreton *et al.*, 1992).

9.2 Methods

9.2.1 Field methodologies

9.2.1.1 Marking Procedure

Colour-ringing birds with combinations of metal and plastic colour rings is a common technique used by ornithologists to mark individuals (Milligan *et al.*, 2003). Through colour-ringing birds with coloured leg rings, it is possible to record their presence in a population or group using ‘sight recoveries’ without recapturing them (Kikkawa, 1997). Furthermore, there are few documented negative effects of coloured leg rings on behaviour or survival of birds (Weiss and Cristol, 1999; Bart *et al.*, 2001). Colour-ringing has many applications and is often used to estimate survival rates of birds (Rogers *et al.*, 1991).

House Sparrows were coloured-ringed at two of my nine study areas: the rural village of Keyham and the suburban area of Thurmaston. In both areas, individual birds were caught at various locations during intensive mist-netting sessions between late August and early October 2002. Birds were ringed with an aluminium ring and a unique combination of three coloured plastic rings. Colour rings were sealed using acetone.

The number of individuals caught and ringed at Thurmaston (suburban) was 51 birds, with 43 birds caught and ringed at Keyham (rural). Individuals were aged as adult or first-year using feather condition and stage of moult in relation to season (Svensson, 1992). Adult birds were sexed according to plumage characteristics and first-years were sexed according to plumage characteristics where possible, dependent on the state of moult (Svensson, 1992), or when they were first re-sighted.

9.2.1.2 Resighting methodology

The resighting area within the suburban site of Thurmaston covered approximately 6 hectares, of which 4.5 hectares was readily accessible to undertake observations. On each resighting occasion, ten suburban gardens were accessed within this area and feeders were checked, along with the surrounding vegetation for colour ringed birds. The rural site Keyham covered approximately 20 hectares, of which 14 hectares were readily accessible. This larger resighting area was due to the number of gardens accessible for the study being more spread out across the village. Within Keyham, twelve rural gardens were accessed and all feeders and surrounding vegetation were checked for colour ringed birds. At both resighting sites birds had access to artificial food via bird feeders; therefore both populations should be classed as supplementary fed.

Resighting was carried out once every four weeks between November 2002 and March 2003 (5 occasions). The same route was followed at each site with all accessible gardens being visited on each resighting occasion. A resighting period constituted two people observing for three hours (a total of six observer hours) usually starting between 08:00 and 09:00. Resighting observations were only undertaken during dry, fine conditions and not during wet weather. Each observer used binoculars to determine colour-ring combinations.

9.2.2 Survival analysis

For each study area, the dataset comprised of 5 resighting occasions. Each bird was classified as adult or first year. It is important to note that survival rates calculated from these datasets are *apparent* survival estimates, in that they contain an unknown component of emigration, which is a source of error inherent to all mark-recapture datasets (Lebreton *et al.*, 1992). The mark-resighting data were analysed using program MARK (version 4.2) (White and Burnham, 1999). Cormack-Jolly-Seber (CJS) type models were fitted to the data (Cormack, 1964; Jolly, 1965; Seber, 1965). With survival and resighting rates differing between time periods and the two age classes. Sex effects were not considered due to the sparseness of the data.

The CJS model has four basic assumptions: 1) every marked individual present in the population at time *t* has the same probability of recapture (P_{t+1}); 2) immediately after time *t* every marked animal in the population has the same probability of surviving to time $t + 1$; 3) leg rings are not lost or missed; 4) the capture recapture/resighting data are collected during a short period relative to the interval between occasion *t* and $t + 1$ (Lebreton *et al.*, 1992; Lebreton *et al.*, 1993).

Test 2 and 3 in programme RELEASE (Burnham *et al.*, 1987) were used to test whether the data met assumptions 1 and 2. These tests are computed as numerous component chi-squared tests, each being independent, so the component chi-squares are additive. RELEASE goodness-of-fit tests showed the suburban site (Thurmaston) to be non-significant ($\chi^2=1.83$; df=10; $P=0.99$) but the tests did not compute for the rural site due to the very small dataset. However when both datasets were combined (rural with suburban) the tests were non-significant ('all birds' dataset $\chi^2=5.59$; df=9; $P=0.78$). Thus, the assumptions of the CJS model are upheld at least when the datasets were combined which in this case was appropriate.

Initial survival modelling was carried out for each site separately. Models were initially fitted with month-specific survival and resighting rates for each of the two age classes of birds (adults and first-years). This starting model was then simplified, first by constraining resighting probability to be constant across months, and then to be constant across age classes. Survival was then simplified in the same way. Subsequent analyses involved combining the recapture data from the two study sites into a single multisite analysis, and simplifying survival and resighting in the same way. Akaike's information criterion (AIC), calculated as the deviance of the model plus twice the number of parameters, was used as the main guide to model selection and likelihood ratio tests (LRT) were used to test specific hypotheses (Lebreton *et al.*, 1992).

9.3 Results

9.3.1 Suburban site

Modelling was begun from the most saturated model that could be supported by the data, and that contained the minimum number of variables required for the investigation [i.e. model 16 Table 9.1- ϕt*g Pt*g]. This model included the interaction between time period (t) and age (g). The modelling indicated no significant age or time period effects (model 1 in Table 9.1). Between model 1 [ϕc Pc] and model 2 [ϕc Pg] there was only a delta AIC value of 0.37, the removal of age had no significant effect on the overall model (LRT: $\chi^2 = 1.9$; df=1; $P=0.18$). Under the preferred model, apparent survival was 1.0 across all months (standard error [s.e.] = 0 and resighting rate was 0.28 (s.e. = 0.047) across all months.

9.3.2. Rural site

A similar procedure was followed for the data collected in the rural study area (Table 9.2). Again there was no evidence that survival or resighting rate differed across months or between age classes. Between model 2 [ϕc Pc] and model 3 [ϕc Pg] there was a delta AIC value of 2.64, indicating evidence of age being significant. However the removal of age had no significant effect on the overall model (LRT: $\chi^2 =0.11$; df=1; $P=0.74$). Under the preferred model, apparent survival was 1.0 (s.e. = 0.245×10^{-7} and resighting rate was 0.14 (s.e. = 0.048 across all months.

9.3.3 The two sites combined

Since the site-specific modelling (above) indicated no age effects the two-site analysis considered only site and time period effects (Table 9.2). Including a site effect to the model (ϕc Psite) provided the most parsimonious description of the data (Table 9.3). Therefore the resighting rate is significantly different at the two sites, with the suburban site showing a higher resighting rate (0.28) than the rural site (0.14), with the survival rate at 1.0 (s.e. = 0.277×10^{-17}). This suggests the birds were harder to see in the rural habitat, possibly due to the denser, more established vegetation and less open feeding areas.

It can be seen in Table 9.4 that the survival rate for the suburban, rural and combined site was 1.0, whereas the resighting rate for the suburban site was 0.28, the rural site was 0.14 and the combined site was 0.23 (s.e. = 0.035). Fixing the implausibly high over-winter survival estimate to a more plausible 0.9 (Hole, 2001) had little effect on other parameter estimates (Table 9.4).

9.4 Discussion

The relative lack of information relating to over-winter survival rate of suburban House Sparrows encouraged me to attempt to study this aspect of House Sparrow ecology. However, the dataset I gathered was fairly small and allows only limited biological inference.

Between November and March, survival was estimated at 100%. Previous studies of House Sparrows in rural farmland have estimated monthly over-winter survival to be approximately 80-90% (Hole, 2001), and my high (boundary) estimate may simply reflect a combination of similarly high survival and low precision (due to modest sample sizes – see Table 9.5 for number birds ringed and re-sighted at each session). Fixing over-winter monthly survival at a more plausible 90% had little effect on the other parameters (Table 9.4), which supports the suggestion that the study lacked sufficient precision to estimate monthly survival.

Both study areas had several feeding stations and birds were regularly fed artificial food throughout the winter. November 2002 was mild, wet and dull and was the warmest November since 1997 and December 2002 was the wettest since 1989 and the warmest since 1997 (Mutton, 2002). January 2003 was the wettest January since 1999 and there was no lying snow throughout the month (Mutton, 2003). February 2003 was colder than January and was the coldest February since 1996, however it was dry and sunny, being the driest February since 1998 (Mutton, 2003). March 2003 was mild, dry and the sunniest March in Leicestershire since records began in 1896 (Mutton, 2003). Therefore the over-winter mortality rate is not expected to be high due to the favourable conditions and food supply not being a limiting factor.

9.4.1 Conclusions

Although there is evidence that changes in agricultural practice have led to a reduction in resource availability, particularly over-winter food for House Sparrows in rural habitats (Summers-Smith, 1988; Hole, 2001), this investigation has been unable to conclude and provide evidence that this is the case in suburban habitats. The relatively limited dataset generated in this study suggest that over-winter among supplementary fed suburban and rural House Sparrows remained high between November and March. Factors affecting survival of urban-suburban House Sparrows is a high priority topic for further research.

Table 9.1 Modelling resighting rate (P) and survival rate (ϕ) for House Sparrows in Thurmaston (suburban habitat). NP = number of parameters, DEV = deviance, AIC = Akaike's information criterion. The most parsimonious model is shown in bold. Models show variation in time period [month] (t), age [adults and first year] (g), interaction terms between time and age (t*g) and c representing a constant value.

Model	NP	DEV	AICc	Delta AICc	AICc Weight
1.{ϕc Pc}	**2**	**40.14**	**113.82**	**0.00**	**0.29**
2.{ϕc Pg}	3	38.22	114.18	0.37	0.24
3.{ϕg Pc}	3	40.08	116.03	2.22	0.10
4. {ϕg Pg}	4	38.23	116.56	2.74	0.07
5. {ϕc Pt}	5	39.94	120.75	6.94	0.01
6. {ϕt Pc}	5	39.96	120.77	6.95	0.01
7. {ϕt Pg)	6	38.09	121.51	7.69	0.01
8. {ϕg Pt}	6	39.93	123.34	9.53	0.00
9.{ϕt Pt}	7	39.92	126.07	12.25	0.00
10.{ϕc Pt*g}	9	35.93	127.96	14.15	0.00
11.{ϕt*g Pc}	9	36.71	128.75	14.93	0.00
12.{ϕg Pt*g}	10	35.93	131.14	17.32	0.00
13.{ϕt*g Pg}	10	36.06	131.26	17.45	0.00
14.{ϕt Pt*g}	11	35.61	134.16	20.35	0.00
15.{ϕt*g Pt}	11	35.87	134.42	20.61	0.00
16.{ϕt*g Pt*g}	14	35.07	144.84	31.02	0.00

Table 9.2 Modelling resighting rate (P) and survival rate (ϕ) for House Sparrows in Keyham (rural habitat). NP = number of parameters, DEV = deviance, AIC = Akaike's information criterion. The most parsimonious model is shown in bold. Models show variation in time [month] (t), age [adults and first year] (g), interaction terms between time and age (t*g) and c representing a constant value

Model	NP	DEV	AICc	Delta AICc	AICc Weight
[1. {ϕ0.9 Pc}	**1**	**26.02**	**43.82**	**0.00**	**0.56]**
2.{ϕc Pc}	2	25.22	45.46	1.65	0.25
3.{ϕc Pg}	3	25.10	48.10	4.28	0.07
4.{ϕg Pc}	3	25.21	48.21	4.39	0.06
5. {ϕc Pt}	5	20.36	49.95	6.13	0.03
6. {ϕg Pg}	4	25.10	51.19	7.37	0.01
7. {ϕt Pc}	5	21.99	51.58	7.77	0.01
8. {ϕg Pt}	6	20.36	53.95	10.13	0.00
9. {ϕt Pg}	6	21.79	55.38	11.57	0.00
10. {ϕt Pt}	7	18.58	56.79	12.97	0.00
11. {ϕc Pt*g}	9	15.77	65.72	21.91	0.00
12. {ϕt*g Pc}	9	20.41	70.36	26.54	0.00
13. {ϕg Pt*g}	10	15.74	73.33	29.52	0.00
14. {ϕt*g Pg}	10	20.38	77.97	34.15	0.00
15. {ϕt Pt*g}	11	13.72	80.64	36.83	0.00
16. {ϕt*g Pt}	11	16.19	83.11	39.30	0.00
17. {ϕt*g Pt*g}	13	12.67	106.26	62.45	0.00

Table 9.3 Modelling resighting rate (P) and survival rate (ϕ) for House Sparrows at both study sites. NP = number of parameters, DEV = deviance, AIC = Akaike's information criterion. The most parsimonious model is shown in bold. Models show variation in time [month] (t), site (site), interaction terms between time and site (t*site) and c representing a constant value

Model	NP	DEV	AICc	Delta AICc	AICc Weight
1.{ϕc Psite}	**3**	**41.77**	**156.71**	**0.00**	**0.38**
2.{ϕ0.9 Psite}	2	44.99	157.75	1.04	0.20
3.{ϕc Pc}	2	45.92	158.68	1.97	0.13
4. {ϕsite Psite}	4	41.77	158.96	2.25	0.11
5. {ϕ0.9 Pc}	1	48.40	159.04	2.32	0.11
6. {ϕsite Pc}	3	44.42	159.36	2.65	0.09
7. {ϕt Psite)	6	41.77	163.68	6.97	0.01
8. {ϕc Pt}	5	45.46	164.98	8.26	0.01
9.{ϕt Pc}	5	45.92	165.44	8.72	0.00
10.{ϕsite Pt}	6	43.78	165.69	8.98	0.00
11.{ϕc Psite*t}	9	36.73	166.31	9.60	0.00
12.{ϕsite*t Pc}	9	39.20	168.78	12.06	0.00
13.{ϕsite Psite*t}	10	36.73	169.04	12.32	0.00
14.{ϕt Pt}	7	45.46	169.85	13.13	0.00
15.{ϕsite*t Psite}	10	38.38	170.68	13.97	0.00
16. {ϕsite*t Pt}	11	38.49	173.62	16.91	0.00
17. {ϕsite*t Psite*t}	14	34.93	179.14	22.43	0.00

Table 9.4. Survival and resighting rates for all birds regardless of age in a suburban and rural habitat. [Values in brackets show 95% confidence limits where valid; where ϕ =1.0 the confidence limits are very small due to the small sample size]

Model	**ϕ (November to March)**	**P (November to March)**
ϕc Pc (combined)	1.0 ($\pm$ 0.277x10^{-17})	0.23 (± 0.035)
ϕc Pc (rural)	1.0 ($\pm$ 0.245x10^{-7})	0.14 (± 0.048)
ϕc Pc (suburban)	1.0 (± 0)	0.28 (± 0.047)
ϕ0.9 Pc (combined)	0.9	0.28 (± 0.045)

Table 9.5. The number of House Sparrows colour ringed and subsequently re-sighted during each session at each site

Site	Number birds ringed	Number of birds re-sighted at each session (1-5)				
		1	2	3	4	5
Keyham (rural)	43	6	5	5	5	9
Thurmaston (suburban)	51	14	9	15	11	8
Total	94	20	14	20	16	17

CHAPTER 10

General Discussion

10.1 Introduction

The aim of this thesis was to investigate the decline of the House Sparrow in suburban and urban landscapes, principally through the examination of the breeding biology. In this chapter, I summarise the key findings from each part of the study and review the evidence generated. Previous research on the breeding biology of House Sparrows in urban-suburban landscapes is limited and I suggest key aspects requiring further investigation.

10.2 Key findings from this study

- Counts of chirping males across 9 study areas in and around Leicester declined by 28% between 2001 and 2003. Annual rates of population change differed significantly between landscapes, averaging +3.7% in urban areas; –16.5% in suburban areas; and –24.6% in rural areas. .

- Nesting success of garden-nesting sparrows was studied mainly during 2002 and 2003. There were high rates of chick starvation in suburban and rural landscapes, especially during June and July. Such starvation was not recorded in recent studies of House Sparrows on farmland. Whole nest survival rate during the nestling stage was considerably lower in suburban areas (0.83) than those recorded for all habitats in Britain (0.96; (Baillie *et al.*, 2005)) and for Oxfordshire (0.87; (Hole, 2001)). This study showed a mean number of 1.98 young fledging per attempt in suburban areas and 2.37 within rural areas, compared to 2.6 in suburban and 2.9 in rural areas across the country (Baillie *et al.*, 2005), and 2.6 in Oxfordshire farmland (Hole, 2001). There were much lower brood sizes in successful nests (indicating high partial losses) within suburbia (2.65) compared to the BTO suburban nest record card scheme finding of 3.82 (Crick and Siriwardena, 2002). In suburban Leicester productivity (young/pair/year) was 4.21 whereas in rural areas productivity was 4.67 (Table 5.13). In comparison, Oxfordshire farmland recorded a productivity of 5.68 (Hole, 2001).

- The number of young successfully fledging per nesting attempt was greater in home ranges having relatively large areas of grass, deciduous shrubs and trees, and relatively little concrete, and, during late summer, in home ranges with relatively high densities of aphids.

- The diet of nestling House Sparrows was investigated through the analysis of faecal samples, and was found to be dominated by Dipteran flies and beetles during April to mid May, with Homopteran bugs being most prominent in June and ants being most abundant during July and August.

- Dipteran remains were proportionately commoner in the diet of nestlings in rural areas, while Homopterans (mainly aphids) were commoner in urban and suburban areas. This pattern may reflect lower availability of Dipterans in urban and suburban landscapes.

- Spiders constituted a higher proportion of invertebrate prey remains in faeces collected from chicks that successfully fledged, whereas ants constituted a higher proportion of invertebrate remains from faeces of chicks that subsequently died. The proportion of ant remains in faecal samples was highest in localities with high summer nitrogen dioxide levels.

- The amount of vegetable material (mainly supplementary food) in nestling faeces was greatest during July and August and was greater in faeces from chicks that subsequently died compared to those that went on to fledge successfully. Fewer young fledged from broods that were fed a plant-dominated diet. A high proportion of vegetable material in faecal samples probably reflects low availability of invertebrate prey within the home ranges of provisioning adults.

- Body condition of young chicks (2-6 days old) was correlated to recent weather conditions (temperature and rainfall), and was lower in localities with high summer nitrogen dioxide levels. Body condition of older chicks (8-12 days old) was positively correlated to the proportion of Coleopteran remains in faecal samples. Brood mass at fledging (a strong predictor of post-fledging survival) was negatively correlated to summer nitrogen dioxide levels, and this is likely to have resulted in much lower post-fledging survival rates among sparrows fledging in suburban localities than those fledging in rural localities. It has been shown that there is intercorrelation between NO2 and the habitat variable of PRIN1 (see chapter 2). However for the three models where either NO2 or PRIN1 was significant there were no confounding effects between the variables PRIN1 and NO2.

- Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were measured in a range of House Sparrow dietary items and in a sample of chick tertial feathers. $\delta^{15}N$ levels were low for artificial foods like bread and peanuts (mean=2.7), intermediate for vegetarian prey like aphids and craneflies (mean=5.6) and high for carnivorous prey like spiders and beetles (mean=7.3). $\delta^{15}N$ therefore provides an indirect measure of chick diet quality covering a longer time period than a single faecal sample. $\delta^{15}N$ in chick feathers varied through the breeding season (highest in June, lowest in April) and was positively related to the proportion of spider remains in faecal samples. $\delta^{15}N$ was also low in chicks reared in localities having a high proportion of concrete and evergreen shrubs, and lacking grassland and arable habitat. This suggests that broods in such localities were fed a diet with a lower average $\delta^{15}N$ level (i.e. more artificial plant material and fewer carnivorous invertebrates). $\delta^{15}N$ was positively related to chick growth rate and chick condition (at day 10-11).

- Key summer foraging habitats were deciduous shrubs, tilled land, grassy areas and concrete, with trees being more heavily used in 2003. Evergreen and ornamental vegetation was strongly avoided in all months and both years. More subtle monthly effects were seen with grass being intensively used in May (2003) and less intensively used in July (2002), as well as trees being used less intensively in July (2003). During July in urban areas, foraging in concrete areas accounted for nearly half of all observations, however in suburban areas, deciduous shrub, tilled and grass habitats were heavily used. In rural areas in July, deciduous shrubbery was the most important habitat followed by grass, with arable habitats (wheat and barley) also being utilised.

- A small-scale mark-resighting study suggested very low mortality among two populations of supplementary-fed House Sparrows between November 2002 and March 2003.

10.3 Are the observed productivity levels in suburban (4.21 young/pair/year) and rural (4.67) landscapes high enough to maintain population levels?

A direct effect of food limitation during the breeding season would be expected to result in a reduction in productivity, either through a reduction in the average number of breeding attempts, or through lower nesting success. In suburban Leicester, productivity (young/pair/year) was 4.21 whereas in rural areas productivity was 4.67 (Table 5.13). In comparison, Oxfordshire farmland recorded a productivity of 5.68 (Hole, 2001).

The question needs to be asked about the biological importance of the lower breeding productivity recorded in this study. The key question is whether the observed annual productivity rates in suburban and rural landscapes are high enough to maintain breeding population sizes given plausible adult, first year and post-fledging survival rates. A simple demographic model was used to predict the future population trend of a hypothetical closed population of 100 House Sparrows in suburban and rural Leicester, using the observed productivity levels from this study and recent estimates of typical House Sparrow survival.

Productivity and survival were assumed to remain constant over time and to be density independent, and productivity was assumed to not to vary with adult age. Immigration and emigration were assumed to cancel each other out and all surviving birds were assumed to breed at age one and in each subsequent year. The model leads to the following expression for population size at time *t*:

Demographic model; $N_t = (N_{t-1} \text{ x } P \text{ x } \phi^{\mathrm{PF}}_{t-1} \text{ x } \phi^{\mathrm{FY}}_{t-1}) + (N_{t-1} \text{ x } \phi^{\mathrm{AD}}_{t-1})$

Where N = population size; P = productivity per individual; ϕ_{t-1} = survival rate between year *t-1* and year *t*; PF denotes post-fledging survival, FY first year survival and AD adult survival.

Siriwardena *et al.* (1998) used national UK ring-recovery data to estimate annual survival of House Sparrows with respect to population trend on farmland between 1962-1994. Survival rates were estimated for two periods of consistent population trend (stable period = 1962-1975; declining period = 1976-94). The *stable* period annual adult survival rate was 0.582 while annual first-year survival was 0.526; equivalent rates during the *declining* period were 0.50 and 0.333 (Siriwardena *et al.*, 1998). Hole (2001) found that post-fledging survival (during the first ten days out of the nest) was 0.62 on Oxfordshire farmland.

Survival estimates from Siriwardena *et al.* (1998) and Hole (2001) were used to determine levels of annual productivity required to maintain stable breeding populations (i.e. where births balance deaths) and to predict expected annual rates of population change given the observed levels of productivity in rural and suburban Leicester. I also investigated the consequences for required productivity and predicted rates of population change of two lower levels of post-fledging survival (0.50 and 0.40). Finally, I calculated mean predicted post-fledging survival rate for sparrows in suburban and rural Leicester based on predicted body mass at fledging (Figure 6.11). For all suburban localities, the mean predicted post-fledging survival was 0.57, whereas in rural areas it was predicted to average 0.7.

It can be seen from Table 10.1 that observed productivity levels in suburban and rural gardens could maintain population size as long as adult and first year survival rates are at pre-population decline levels (i.e. 0.582 and 0.526) for all three levels of post-fledging survival. However, if adult and first-year survival in suburban and rural gardens are more typical of those suggested by national ring recovery data since 1976, (i.e. adult survival = 0.5; first-year survival = 0.333), then the observed levels of productivity in suburban and rural gardens are likely to lead to population declines even at high post-fledging survival rates (0.62). However, if post-fledging survival is lower than this (e.g. 0.57, which is plausible given observed nestling body mass shortly before fledging in suburban localities of Leicester; Figure 6.11) then population decline is expected to be rapid (e.g. ca. 10% per annum, Table 10.1). However, the higher observed productivity and predicted post-fledging survival for sparrows fledging in rural localities of Leicestershire (0.70), should be enough to maintain or increase breeding population size (Table 10.1).

The observed annual rates of population decline (Chapter 3) were of a similar magnitude to that predicted by the model for suburban study areas (-16.5% observed compared to -10% predicted). However, observed and predicted population changes were quite different for the rural study areas (-24.6% observed compared to +4% predicted) which suggests that actual survival rates were lower in rural areas, or that emigration exceeded immigration.

Hole's (2001) adult and first-year survival estimates for Oxford farmland populations (0.46 and 0.339 respectively) were not used in these calculations because they are derived from mark-recapture data which might underestimate true survival as a consequence of emigration or dispersal. Survival estimates derived from ring recovery data are not subject to this form of under-estimation bias. Therefore survival estimates from Siriwardena *et al.* (1998) are probably the best estimates of survival, and many of the birds involved will have been ringed in suburban and rural gardens.

10.4 Why have House Sparrows declined in suburban Leicester and surrounding villages? - A synopsis of the evidence

It must be noted that House sparrow numbers have slightly increased in urban areas (+3.7% per annum) and declined most in rural areas (–24.6% per annum) during the course of this study. However, the density of sparrows seen in the city centre was extremely low (Table 3.2) and there were just a few isolated pockets of urban birds in central Leicester (*pers, obs*). The density of House Sparrows in Leicester city centre is comparable to other cities like Edinburgh, Glasgow, London and Hamburg that have experienced population declines (Mitschke *et al.*, 1999; Sanderson, 1999; Dott and Brown, 2000; Summers-Smith, 2000) (Table 3.2). Therefore it is possible that the birds had already declined and had become stable in small isolated pockets in the centre of Leicester and therefore I was surveying a post-decline population. This scenario appears to have happened in London (Peach, 2005) and Bristol (Bland, 1998).

The main finding of this thesis is that declining House Sparrow populations in suburban Leicester probably raise too few young through to independence, to sustain local breeding populations. High rates of chick starvation (especially during June and July) coupled with low fledging body mass (and therefore low post-fledging survival) are the main demographic causes of this low productivity. More chicks were raised in better body condition from home ranges that provided (i) more deciduous shrubs, trees and grassland (PRIN1), (ii) relatively small areas of concrete and evergreen vegetation (PRIN2), and (iii) had relatively low levels of (NO2) air pollution during summer.

Although habitat descriptors PRIN1 and PRIN2 are, by definition, uncorrelated, a strong negative correlation between PRIN1 and summer NO2 levels (r=-0.5, Table 2.5) reflects that these variables are to a large extent different measures of the same urbanisation gradient. Localities having relatively large areas of deciduous shrubs, trees and grassland tend to have low levels of air pollution and vice versa, and sparrow productivity appears to be quite strongly dependent on this urbanisation gradient (e.g. Table 5.9, Figure 5.4, Table 6.4, Figures. 6.2, 6.7, 6.10 & 6.11). For all models where either NO2 or PRIN1 was significant (Chapters 5, 6 & 7), the addition of the opposing variable was added to the final MAM to test for confounding effects between these variables. However, there were no confounding effects found between the variables PRIN1 and NO2 in any models, suggesting these variables are not interchangeable and it is possible to disentangle the two for interpretation purposes.

The mechanism for this relationship appears to be lack of suitable invertebrate prey in highly urbanised localities. Evidence supporting this includes (i) direct positive relationships between the number of young fledged per attempt (during late summer) and aphid density (Figure 5.9), (ii) positive relationships between chick survival probability and diet quality in terms of the proportion of vegetable material (mainly supplementary food; Table 4.4, Figure 4.7) and low quality invertebrates such as ants (Table 4.3, Figure 4.3), and (iii) negative relationships between chick body condition and diet quality as measured by δn15 stable isotopes (Figure 7.7).

Chicks were less likely to starve if their diet contained a high proportion of spiders. Spiders are more likely to be found in deciduous shrub and grassland habitats (Owen, 1991). Aggregate chick biomass was greater in areas of deciduous shrubbery, trees, grass and relatively little concrete, as well as chick body condition being greater from home ranges that provided more deciduous shrubs, trees and grassland. Data presented in Chapter 8 showed that House Sparrows utilised several key habitats when foraging during the summer months. Key selected habitats were deciduous shrubbery, grassland and tilled soil (Chapter 8), presumably because these provide relatively high densities of invertebrate and seed prey.

The invertebrate prey most likely to be found in deciduous shrubbery, trees, grassland and tilled soil are aphids, spiders, Diptera, and beetles (Owen, 1991; Baines, 2000). Whereas low quality prey items such as ants and supplementary food (Chapter 4) are more likely to be found on concrete. One possibility is that in built up areas, important habitats such as deciduous shrubs, grassland and trees are becoming less available due to increasing brown-field development within city centre areas (Robinson et al., 2005) as well as becoming less common in urban-suburban gardens. Therefore invertebrate abundance in suburban areas is probably determined by the availability of suitable habitat.

Therefore, observed low productivity and poor nestling body condition in the suburban landscape can be linked to poor chick diet, probably caused by lack of invertebrate prey in the home range. This lack of high quality invertebrate prey is possibly caused by habitat factors, such as the possible lack of deciduous shrubbery and grassland in urban-suburban Leicester. These findings lead to the conclusion that invertebrate availability during summer is probably limiting the annual productivity of suburban House Sparrows in and around Leicester.

10.5 Likely causes of House Sparrow decline in urban-suburban environments

CBC data suggest House Sparrows have declined by 53% in Britain since 1976 (Siriwardena *et al.*, 2002). The Breeding Bird Survey (BBS) monitors bird population trends in most UK habitats and regions. BBS data indicate that House Sparrow numbers have continued declining, at least in south eastern Britain, between 1994 and 2000, and especially in suburban and urban landscapes (Crick *et al.*, 2002). Regional variations in population changes are highlighted in Table 1.1. The steepest declines have occurred in northeast England, East Anglia and southeast England, where House Sparrow numbers are greatest. Combining House Sparrow CBC and BBS data for the period 1976 until 2002, indicates a national population decline of 69% (Baillie *et al.*, 2005).

In the centre of Edinburgh, House Sparrow numbers declined by 90% over the last 15 years, while numbers of other bird species in the same area have not changed (Dott and Brown, 2000). Local surveys in cities such as Manchester and Glasgow have documented House Sparrow declines on the scale of 80-95% (Summers-Smith, 1999). Since 1994, House Sparrow numbers in London have declined by 60% (Raven *et al.*, 2005). In the German city of Hamburg, sparrow numbers have declined by more than 50% in the last 30 years (Mitschke *et al.*, 1999). In Paris, a city thought to have a relatively high density of House Sparrows, numbers of sparrows have declined by 36% over the last forty years (Galinet, 2003).

In UK garden habitats, during winter months, sparrow numbers have declined by 58% since 1970 (Robinson *et al.*, 2005). Numbers in gardens were largely stable until 1983, with a continuous decline since then. Sparrow populations in rural gardens have declined to a lesser extent (48%) than those in suburban gardens (60%) (Robinson *et al.*, 2005). Over the last twenty years there has been a marked increase in both the prevalence of garden bird feeding and the quantity and range of foodstuffs provided (Cannon, 2000). However, numbers of House

Sparrows using gardens did not increase in response to this (Robinson *et al.*, 2005). It is possible that a greater decline in sparrow numbers would have been recorded had these additional resources not been available.

10.5.1 Availability of invertebrate prey in summer

I have shown that invertebrate availability during summer is probably limiting the annual productivity of suburban House Sparrows in and around Leicester, and the magnitude of effect is large enough to have led to population decline. However, for invertebrate availability to have caused the long-term population declines of sparrows in suburban Britain, evidence is needed to show invertebrate densities have declined over the same period (i.e. mid-1980s to 2000). There is good evidence that agricultural intensification has adversely affected invertebrate availability on farmland (Donald, 1998; Wilson *et al.*, 1999; Benton *et al.*, 2002). This is consistent with the view that agricultural change has influenced bird numbers through changes in food quality or quantity. However, as far as I am aware, there is no equivalent evidence showing declining invertebrate availability in urban-suburban habitats.

The widespread declines of invertebrates seen mainly in farmland (Donald, 1998; Wilson *et al.*, 1999; Benton *et al.*, 2002), propounds the idea that invertebrate prey could have declined in gardens, as it has in the wider countryside. The causes behind a possible decline in gardens may well be different to the wider countryside, with changes in gardening practices, or even climate change, being feasible contenders.

Studies at various locations in Europe have shown that nest-box populations of tits in urban habitats produce fewer eggs and fledglings than birds in rural habitats (Cowie and Hinsley, 1987; Solonen, 2001). Cowie and Hinsley (1987) found that suburban tits reared half as many young as populations in woodland. Despite the additional supply of supplementary seed food in suburban gardens, nestling mortality through starvation was very high (Cowie and Hinsley, 1987). Solonen (2001) found that urban tit populations laid fewer eggs and had lower fledgling production than their rural counterparts. Therefore breeding conditions for tits were generally less suitable in urban areas (Cowie and Hinsley, 1987; Horak, 1993; Solonen, 2001). These findings suggest that suburbia may be an invertebrate-poor habitat for birds generally.

Invertebrate availability during the summer appears to be a factor that limits reproductive success in suburban House Sparrows.My findings make this environmental factor a much more likely potential cause of the population decline. However, there may be other potential environmental factors that need to considered.

10.5.2 Lack of seed food in summer/winter

Lack of seed food in summer/winter may well be limiting House Sparrows in suburbia and might have caused the decline. Hole *et al.* (2002) identified the key limiting factor for House Sparrows on farmland to be winter seed and suggested that lack of seed during the winter was the main cause of the population decline. Therefore on this evidence, lack of seed (in summer or winter) may be a limiting factor or a cause of the population decline for suburban House Sparrows. Undertaking mark-resighting analysis (Chapter 9) at two supplementary fed sites (one suburban and one rural) provided evidence of high over-winter survival, although this is based on very small sample sizes which may give unreliable estimates. However, lack of seed food, especially in late summer when feeding in gardens is less, could still be a problem for the large numbers of House Sparrows that are around at that time.

10.5.3 Lack of nest sites

The number of nest boxes that were occupied after three years in this study was only approximately 10%. Therefore this low uptake of nest boxes suggests nest sites may not be limiting in my study areas in Leicester. However, from a national survey investigating the use of houses for nesting birds, Wotton *et al.* (2002) found that a lower percentage of modern or newly renovated buildings were occupied. This suggests that nest site availability may influence the distribution of nesting House Sparrows.

10.5.4 Predators

The Mammal Society found that 28 percent of prey, taken by cats, were House Sparrows (Woods *et al.*, 2003) and cats therefore are a possible source of mortality amongst adult House Sparrows (Mead, 1982; Woods *et al.*, 2003). Sparrowhawks are another possible predator of adult House Sparrows (Barnard, 1979; Newton, 1986; Newton and Perrins, 1997). However, Thomson *et al.* (1998) examined whether Sparrowhawks could have depressed the rates of year to year population change in 23 songbird species. The results indicated that Sparrowhawks are unlikely to have caused the declines because patterns of year to year population change did not differ between sites with and without the presence of this predator (Thomson *et al.*, 1998).

There is little information on predation of House Sparrows in natural nesting sites. However, most House Sparrow nests in natural cavities in roof spaces and nest boxes will be inaccessible to predators such as Magpies and cats, but may be accessible to mammals such as Grey Squirrels and weasels. Nevertheless, there were no cases of nest predation or cases of adults disappearing from active nests throughout this study (Chapter 5), which suggests predation during the nesting period is not a limiting factor.

10.5.5 Competition

The Collared Dove and Wood Pigeon are both granivorous species and would be the two most likely species to compete with House Sparrows for food (Snow and Perrins, 1998). There could possibly be depletion competition for food between these species as they all have a granivorous diet. There are now thought to be five million Wood Pigeons in Britain, a doubling of numbers since 1970 and the Collared Dove population is now thought to stand at half a million birds, an eight fold increase since 1970 (Crick *et al.*, 2004). However, even though both the Wood Pigeon and Collared Dove have increased in numbers during the last twenty years, there is still no evidence to suggest these two species are causing House Sparrow decline due to competition for seed food.

10.5.6 Air Pollution

Air pollution may have both direct and indirect effects on avian reproduction (Furness and Greenwood, 1993). It has been shown that there is intercorrelation between NO2 and the habitat variable of PRIN1 (see chapter 2). However were no confounding effects between the variables PRIN1 and NO2 within any models (see Chapter 5 and 6). Therefore although these variables are intercorrelated, it is possible to disentangle the two when interpreting the results of each model. I have shown in this study that brood mass at fledging (a strong predictor of post-fledging survival) was negatively related to summer nitrogen dioxide levels. This ultimately could result in much lower post-fledging survival rates among sparrows fledging in suburban localities than those fledging in rural localities (Chapter 6).

In Poland, Kaminski (1995a) found that in unpolluted areas Tree Sparrow nestlings attained maximum body weight quicker and achieved a higher rate of biomass increase than nestlings in the polluted area. Therefore, the unpolluted area provided better conditions for the development and reproduction of the Tree Sparrow than the polluted area (Kaminski, 1995a). Consequently, the degree of pollution in urban-suburban habitats could be a possible demographic factor affecting the condition and health of nestlings, which in turn effects House Sparrow productivity.

Eeva *et al.* (1997) found a positive correlation between pollution reduced food supply and breeding performance in Great Tits (Eeva *et al.*, 1997). Great Tit nestlings grew well in the beginning, but suffered increasing mortality later in the nestling stage, i.e. at the time of highest food demand (Eeva *et al.*, 1997). This pattern would be expected if the available food for nestlings were limited. Currently, there is no evidence that pollution is affecting invertebrate densities in urban-suburban areas in the UK and therefore an indirect effect on House Sparrow numbers from air pollution causing invertebrate decline cannot be validated.

10.6 Proposed management prescriptions

Given that summer invertebrate food appears to be limiting House Sparrows in suburban areas, the management and creation of key habitat is important. Key selected habitats were deciduous shrubbery, grassland and tilled soil (Chapter 8). Native deciduous shrubs such as hawthorn, blackthorn and apple and trees such as oak, willow and birch have a large number of insects attached to them (Southwood, 1961), whereas recently introduced or non-native species, have comparatively few (Southwood, 1961). Sycamore is often rich in aphids (a known invertebrate prey of sparrows; Chapter 4) and Seel (1969) found that this species of tree was heavily used by sparrows as an invertebrate food source. Invertebrate rich deciduous species such as hawthorn, apple, elder, wild rose and buddleia were all used frequently as a source of foraging by sparrows (*pers.obs*). Owen (1991) recorded the larvae of eighteen moth species on one buddleia plant in her suburban Leicester garden. Therefore, to increase invertebrate densities in gardens, the planting of deciduous shrub species and native trees needs to be encouraged (Baines, 2000).

Invertebrate prey species that accounted for 80% of all items found in nestling faecal samples were spiders, aphids, Diptera and beetles (Chapter 4). These prey types are likely to be found in the most intensively used foraging habitat (Chapter 8) e.g. aphids and spiders in deciduous shrubs and trees, Diptera and spiders within grassland and beetles on tilled soil (Owen, 1991). Consequently, these are the key habitats that need to be encouraged within a suburban landscape.

Householders should be encouraged to allow small grassy areas to grow tall in their gardens, as invertebrates (such as Diptera and spiders) thrive in long grass throughout the summer (Owen, 1991; Baines, 2000). Patches of structural diversity are more beneficial than uniform homogenous areas (Ryrie, 2003), therefore, when planting flowerbeds (tilled soil), structural variation is important. However, more importantly native plants and shrubs should be chosen, as evergreen and ornamental shrubs were strongly avoided by foraging sparrows.

It was shown that aphids are an important sparrow prey (Chapter 4) and therefore the use of pesticides to destroy aphids should be discouraged (Owen, 1991; Ryrie, 2003). As well as wiping out a food source, the input of pesticides affects the balance within the invertebrate food chain (Ryrie, 2003). Owen (1991) never used pesticides in her suburban garden (0.07 hectares) and recorded over 2000 species of invertebrates.

Private gardens in Britain cover an area in excess of 400,000 hectares or 1 million acres (Ryrie, 2003). This is a huge resource which needs to be given more attention (Owen and Owen, 1975). By designing and suggesting key management practices, honed specifically to encourage invertebrate availability in urban and suburban gardens, the summer invertebrate food source for House Sparrows can be improved.

10.7 Future areas of research in suburban and urban populations

No other study has investigated the ecology of suburban House Sparrows in detail; therefore this thesis provides several new insights into House Sparrow ecology. The use of certain methodologies such as nestling diet analysis, feather analysis using stable isotopes, habitat selection by foraging adult sparrows and over-winter survival have never been undertaken before in a suburban environment. This study has investigated the possible environmental factors that may be limiting House Sparrow nesting success and through gaining knowledge of these limiting factors, management prescriptions can then be devised that might increase nesting success and ultimately population levels.

The conclusion that summer invertebrate food supply may be the principal limiting factor on survival in suburban House Sparrow populations warrants further investigation. Investigating whether providing supplementary invertebrate food during the breeding season over successive summers would be worthwhile. An experimental approach is needed to establish if this would help adults provide enough food for nestlings and therefore increase productivity across the season. Work currently being undertaken on summer food supply for House Sparrows in London is welcomed to further establish and corroborate the findings resulting from this study.

Winter diet and House Sparrow over-winter survival in suburbia are both factors that are currently unknown in the context of House Sparrow ecology. Further studies would be advantageous to illuminate the complex issue of the decline in an urban-suburban environment. Nest sites may well be a limiting factor in areas where modern housing developments are prevalent. Further study is needed to provide more nesting sites in these areas and to clarify if nest sites may be limiting.

Predation may be a key limiting factor to the decline of House Sparrows. A source of mortality amongst adult House Sparrows are cats (Mead, 1982; Woods *et al.*, 2003) and Sparrowhawks (Barnard, 1979). However, there is no evidence to suggest these two predators have caused suburban House Sparrow decline. Further study on predation in suburban areas is warranted.

By undertaking detailed analyses of population trend data (such as BBS data), the current status of sparrow populations in different habitats can be assessed, especially in suburban and urban habitats. Although there is evidence that House Sparrow numbers have declined markedly especially in South and East Britain and in several towns and cities, a detailed nation-wide picture is unavailable. Further analyses of population trend data in different cities and conurbations are definitely needed in order to gain a clearer picture of local and regional declines.

Ecological research into the suburban and urban habitat in this country has received relatively little attention. New policy initiatives are needed to encourage a change in mentality with regard to the importance of our suburban environment in providing a habitat for many species of flora and fauna. Many people’s only interaction with wildlife is within a suburban environment. In order to turn this interaction into a positive one and encourage conservation, an accumulation of detailed knowledge of urban and suburban habitats needs to be given priority at every level of environmental research.

Table 10.1 The predicted annual population changes (%) calculated from the demographic model equation (see text) given the observed suburban and rural productivity levels. As well as the productivity levels needed to maintain a stable population for various survival rates. The observed post-fledging survival rates were the mean rates for suburban and rural birds taken from Figure 6.11

Adult survival %	First-year survival %	Predicted Post-fledge survival %	Productivity needed to maintain stable population	Predicted annual popt changes (%) given Suburban level (4.21)	Predicted annual popt changes (%) given Rural level (4.67)
Stable Period					
58.2	**52.6**	**62.0**	**2.56**	**+26.8**	**+34.3**
58.2	**52.6**	**50.0**	**3.18**	**+13.6**	**+19.6**
58.2	**52.6**	**40.0**	**3.97**	**+2.5**	**+7.3**
Decline Period					
50.0	**33.3**	**62.0**	**4.84**	**−7.0**	**−1.8**
50.0	**33.3**	**50.0**	**6.00**	**−15.3**	**−11.1**
50.0	**33.3**	**40.0**	**7.51**	**−22.2**	**−19.2**

Adult survival %	First-year survival %	Observed Post-fledge survival % (data from Fig; 6.11)	Productivity needed to maintain stable population	Predicted annual popt changes (%) given Suburban (4.21)	Predicted annual popt changes (%) given Rural (4.67)
Stable Period					
58.2	**52.6**	**57.0 (suburb)**	**2.78**	**+21.3**	**N/A**
58.2	**52.6**	**70.0 (rural)**	**2.25**	**N/A**	**+44.2**
Decline Period					
50.0	**33.3**	**57.0 (suburb)**	**5.36**	**−10.0**	**N/A**
50.0	**33.3**	**70.0 (rural)**	**4.29**	**N/A**	**+4.43**

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APPENDIX

Relationships between diet composition inferred from faecal sample composition and provisioning watch data

Introduction

Studies of the diet of nestlings have traditionally been based on indirect or direct methods, corresponding to diet assessment before ingestion such as provisioning observations or after ingestion such as the analysis of faeces. Direct observation is not usually a reliable method, as accurate identification of the food items can be difficult. Therefore quantitative estimates of the composition of the diet of birds are often made, by counting prey remains in faeces. However in order to establish the validity of faecal analysis for estimating the composition of diet, the relationship between the overall composition of invertebrate prey remains in faecal samples and the composition of invertebrates from provisioning watches was assessed.

Methods

A total of 55 provisioning watches were undertaken at nest-boxes during the summer of 2003, of which 9 were conducted in the urban landscape, 12 in the rural and 34 in suburban areas (see section *2.2.5*). During these watches the food brought back to the nestlings was assessed through direct observation and recorded. Provisioned food was categorised into six groups: Coleoptera (beetles), Arachnida (spiders), Homoptera (aphids/froghoppers), Diptera (flies/craneflies), artificial food (bread/seed/peanuts), and unknown.

After each provisioning watch was completed, the nest site was vacated, before returning between two and three hours later to collect biometric data and faecal samples from the nestlings. This delay in collecting faecal samples was intended to allow the observed provisioned food to pass through the gut and therefore be present in the faeces (Moreby and Stoate, 2000). I tested for relationships between provisioned prey composition and the subsequent invertebrate and vegetable composition of faecal samples.

Faecal invertebrate log ratios were treated as dependent variables with provisioning watch log-ratios as independent variables in a MANOVA (Tabachnick and Fidell, 2001). All faecal prey groups were tested as dependent variables against each of the provisioning watch prey groups in turn. I also tested for relationships between individual faecal prey groups and the corresponding prey group from provisioning watches using linear regression. Relationships between the proportion of vegetable material in faecal samples and the proportion of artificial food ingested during provisioning watches were also tested using simple linear regression.

Results

There was no significant relationship between the overall composition of invertebrate prey remains in faecal samples and the composition of invertebrates from provisioning watches. Similarly the proportions of individual prey groups in faecal samples were unrelated to those in provisioning watches (Table 1).

The proportion of artificial food brought to nestlings during provisioning watches was significantly and positively related to proportion of vegetable material in faeces (b=0.815; $P<0.05$; n=19; $R^2=0.185$) (Figure 1). This suggests the proportion of vegetable material recorded from faeces was probably a reasonable indicator of the importance of artificial food provisioned to nestlings during the previous three hours. One possible reason for the relatively weak relationship is that House Sparrows eat a wide range of vegetable material (e.g. cereal grain and seeds) and not just the artificial food that was scored during provisioning watches.

Discussion

It may be that the 2-3 hour period allowed for the passage of the invertebrates through the nestling gut was too short, or that passage rates vary between invertebrate groups (Green and Tyler, 1989). However as digestion in nestling passerines is relatively rapid, resulting in a short transit time of food through the gut, this time period was deemed acceptable (Moreby and Stoate, 2000). This absence of relationships could also be due to different biases affecting the two sampling techniques. Faecal analysis tends to under-represent small soft-bodied invertebrates like Homopterans (Moreby and Stoate, 2000). The technique of recording food types brought back to the nest is subject to human recording error which may be more pronounced for smaller prey groups. These biases therefore may have contributed to no relationship appearing between the two observational techniques.

As mentioned previously there was no relationship between ingested invertebrate prey and the amount found within faeces. This could be due to the fact that the amount of time needed for vegetable material to pass through the nestling gut fully is less than that for invertebrate prey. Many invertebrate prey groups contain hard chitinous structures and therefore passage rates may be slower than those of vegetable material. Green and Tyler (1989), reported longer passage times for hard chitinous body parts which could be retained in the digestive tract for some time (between several hours to days), to help mechanical breakdown of other food items (Jenni *et al.*, 1989).

This secondary analysis of whether faecal analysis provides a reliable estimate of food intake during the preceding 2-3 hours highlights that the reconstruction of the true diet of the House

Sparrow is still not fully possible. Further research is needed to gain information on the relative passage rates and detectability in faecal remains of the various prey items from ingestion to defecation.

Table 1. The non-significant covariates when testing for relationships between the composition of invertebrate prey in faecal samples and the composition of invertebrates observed from provisioning watches

Covariates	Wilks Lambda value	Significance *P* value
Spiders in provisioning watch	0.76	0.85
Beetles in provisioning watch	0.64	0.64
Diptera in provisioning watch	0.51	0.36
Ants in provisioning watch	0.72	0.78
Homoptera in provisioning watch	0.63	0.60

Figure 1. The relationship between the proportion of vegetable material observed in provisioning watches against the relative proportion of vegetable material found in nestling faecal samples