A CURATE’S EGG: FEEDING BIRDS DURING REPRODUCTION IS ‘GOOD IN PARTS’. A STUDY OF BLUE TITS *CYANISTES CAERULEUS* AND GREAT TITS *PARUS MAJOR*

by

TIMOTHY JAMES EDWARD HARRISON

A thesis submitted to

The University of Birmingham

for the degree of

DOCTOR OF PHILOSOPHY

Centre for Ornithology

School of Biosciences

The University of Birmingham

February 2010

ABSTRACT

Food supplementation of birds in gardens is widespread and UK householders have recently been advised to supplement birds throughout the spring and summer. This coincides with reproduction of many avian species and supplementation with specific foods (e.g. live invertebrates) is encouraged to support breeding attempts in gardens. To investigate this further I mimicked food supplementation in gardens by providing two commercial bird foods (peanut cake and mealworms *Tenebrio molitor*) to blue tits *Cyanistes caeruleus* and great tits *Parus major* breeding in woodland in central England from 2006 to 2008. Supplementation advanced laying and reduced the number of young fledged significantly in both species, but provisioning with mealworms during the nestling phase increased apparent survival of fledglings. Intriguingly, however, stable isotope analysis revealed that supplement use was insubstantial and similar between birds on supplemented and non-supplemented territories. Analyses of data from the British Trust for Ornithology’s Nest Record Scheme demonstrated strong parallels between findings of my field study and patterns of reproduction of blue and great tits in urban habitats across the UK. I discuss the implications of my findings, including the use of food supplementation in avian conservation and in pure scientific research, and I outline exciting future directions.

Dedication

Tits, blue and great

Harrison family, especially Mum

All of my friends

Nephews, Toby and Joseph

Kingston family, especially Lizzie

Yoc

Ornithology in the garden

University of Birmingham

With love
Tim

ACKNOWLEDGEMENTS

My research was funded by the Natural Environment Research Council (NERC), including a CASE Studentship with the British Trust for Ornithology (BTO) as the CASE partner, and through a Life Sciences Mass Spectrometry Facility (LSMSF) grant for the stable isotope work. I am extremely grateful to CJ Wildlife Ltd. (especially Peter Deans and Chris Whittles) for providing equipment, consumables, and financial support, and for always being at hand to help when needed. The Worcestershire Wildlife Trust generously allowed the use of Chaddesley Woods National Nature Reserve and special thanks to Mervyn and Rose Needham for their kindness, good humour, and barbequing during my project. Volunteers of the Worcestershire Wildlife Trust collected valuable data regarding caterpillar availability and also cut mist-net rides. Their commitment was impressive and jollity very much appreciated.

Ringing activities were made possible through generous commitments made by Bert Coleman and, especially, Leigh and Tony Kelly. I am also grateful to other ringers that assisted periodically with my research, especially Michael Barstow, Stefan Bodnar, Steve Dodd, Phil Ireland, Jane Moody, Andy and Karen Moss, and Dan Potter. The time afforded to my research by volunteer ringers, who often travelled considerable distances for starts at dawn, was exceptional. Thanks also to John Hodson for an emergency bail-out with rings in 2006 and to the BTO Ringing Unit for organising personal and Birmingham University Ringing Group permits so efficiently.

Numerous people provided considerable help with field, laboratory, and office work, particularly Munhazaya Battsengel, Ivana Budinski, Lena Farruggio, Gisela Helfer, Chan Heu, Elizabeth Kingston, Ewa Kos, Louise Leigh, Marija Majer, Vladimir Rakić, and Laine Wallace. I would like to extend special thanks to Nardie Hanson for her industrious help and good company during my research. Data from the BTO’s Nest Record Scheme (NRS) that was analysed as part of my study were collected by volunteer nest recorders throughout the UK. I am very grateful to the BTO for financing the input of these data and to Mark Grantham for producing the NRS maps that are provided in Appendix Six.

I gained considerable insight, technical assistance, and enjoyment through working with external collaborators during my project. Rona McGill and Jason Newton were very accommodating in helping me to get to grips with stable isotope analysis techniques, and collaboration with Stuart Bearhop and Richard Inger was also fundamental in this regard. Richard Bevan was very helpful in enabling me to extract lipid from egg yolks using Soxhlet Apparatus and came up with numerous clever D.I.Y solutions to keep the system working. As part of the Supplementary Feeding Group, I have enjoyed many lively discussions with Stuart Bearhop, Jon Blount, Nick Carter, Dan Chamberlain, Dave Leech, Kate Plummer, and Gill Robb regarding ways in which I could develop my research. In particularly, however, I would like to thank Dan and Dave for their supervisory work throughout my study. Their feedback and commitment to my research was always appreciated, and I feel that my work with the BTO enriched my study greatly. Aongais, Damian, and Ross – thank you for putting me up at the drop of a hat while on my travels, very generous indeed. Phillip Cassey and Kate Lessells provided me with useful statistical advice, and I would also like to thank Simon Harold for keeping me on the straight and narrow in this regard. The Home Office and Natural England granted licences to enable my work, and I am grateful to all of those who facilitated these processes. Thanks also to Chris du Feu for providing information regarding the best ways in which to establish a successful nestbox-scheme.

My colleagues at the University of Birmingham, particularly Jen Smith and Simone Webber, provided considerable assistance, kindness, and good cheer during my research. Jen

also baked me some amazing birthday cakes in the middle of different field seasons, each a sterling, and tasty, effort! Lastly, I would like to thank my supervisors, Jim Reynolds and Graham Martin, for their enthusiasm, support, and unwavering commitment to my research.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter Two

Chapter Three

Chapter Four

<u>Chapter Five</u>

Chapter Six

Chapter Seven

Appendix One

Appendix Two

Appendix Five

Appendix Six

LIST OF TABLES

Chapter Two

Chapter Three

Chapter Four

Chapter Five

Chapter Six

Chapter Seven

Appendix One

Appendix Six

GLOSSARY

BLC: Broadleaved land cover

BTO: British Trust for Ornithology

NNR: National Nature Reserve

NRS: Nest Record Scheme

PC: Peanut cake-supplemented

PCMW: Peanut cake and mealworm-supplemented

RSPB: The Royal Society for the Protection of Birds

SIA: Stable isotope analysis

Supplementation: when ‘supplementation’ is referred to in this thesis without direct reference as to what is being supplemented, please assume that the entity provided is food unless stated otherwise.

ULC: Urban land cover

UN: United Nations

Chapter One

GENERAL INTRODUCTION

1.1. Feeding wild birds: a common activity

Providing food for free-living birds is a common activity across the world (Jones & Reynolds 2008; Robb *et al.* 2008a). This provisioning of food is often termed ‘food supplementation’ and is characterised by the provision of types and/or quantities of food that are not available naturally. Food supplementation has multiple significant effects on avian populations including those on reproduction and survival during non-breeding periods (reviewed in Robb *et al*. 2008a). Food supplementation of birds occurs in a wide range of situations that can be divided into two broad categories: (i) intentional feeding – for example to encourage closer interaction between humans and birds (e.g. in gardens), to promote conservation of endangered species (e.g. Florida scrub jay *Aphelocoma coerulescens* – Schoech *et al.* 2008), and in scientific investigations (e.g. reviewed in Boutin 1990); and (ii) unintentional feeding – for example at landfill sites (e.g. Smith & Carlile 1993) and on discards from fisheries (e.g. Spaans 1971). The scale of such food supplementation is vast owing largely to the ‘benevolence’ and wastefulness of humans, and to the plasticity of avian foraging strategies that have enabled multiple anthropogenic food sources to be exploited.

1.1.1. Food supplementation in gardens

1.1.1.1. Scale and importance

On a national and international scale, the most common form of intentional food supplementation occurs in gardens or backyards (hereafter ‘gardens’ in this thesis). Across the Western world, billions of pounds are spent on food and associated feeding equipment each year (Jones & Reynolds 2008). In the UK, this amounts to *c.* £200 million (British Trust for Ornithology [BTO] 2006b) with *c.* 50-60 thousand tonnes of food provided for birds annually (BTO 2006b; Glue 2006). Around 40-50% of UK households provide food for birds in gardens, corresponding to a mean feeder density of *c.* 100 km^{-2}, or one feeder for every nine individual birds that could utilise this resource (Davies *et al.* 2009; Fuller *et al.* In press). Around half of all households in the Western world provide food for birds at some time during the year (Jones & Reynolds 2008). It is also notable that this proliferation in supplementation (see note on ‘supplementation’ in Glossary) in gardens has occurred only in the last few decades (Chamberlain *et al.* 2005; Jones & Reynolds 2008). Indeed, the global market for bird seed is now so large and expanding so fast (*c.* 4% per annum) that the United Nations (UN) has promoted speciality seed as a cash-crop in developing nations (Lin 2005).

The human population is becoming increasingly urbanised (UN 2008) with a concomitant expansion of urban land cover (European Environment Agency 2006; Elvidge *et al.* 2007). In response, many avian species have adapted to exploit urban habitats successfully (Evans *et al.* 2009). Such habitats include gardens that comprise a land area of over 400,000 ha in the UK alone (an area larger than the county of Suffolk, England – Davies *et al.* 2009). Of the numerous species that breed in urban habitats in the UK, some are of conservation concern (e.g. song thrush *Turdus philomelos*, common starling *Sturnus vulgaris*, house sparrow *Passer domesticus* – Gregory & Baillie 1998; Mason 2000; Bland *et al.* 2004; Shaw *et al.* 2008). Other species that use gardens include ‘pest’ species of economic importance (e.g. Eurasian collared dove *Streptopelia decaocto*, carrion crow *Corvus corone* – Cannon *et al.* 2005). Food supplementation usually increases the abundance and diversity of birds visiting individual gardens (Savard *et al.* 2000; Chamberlain *et al.* 2005; Daniels & Kirkpatrick 2006) and it can also increase avian diversity in adjacent green spaces such as parks (Chamberlain *et al.* 2007). Indeed, food supplementation is currently endorsed by the UK government as a form of ‘wildlife gardening’ (i.e. management practices that are designed to encourage wildlife in gardens – Department for Environment, Food and Rural Affairs 2008).

1.1.1.2. Food supplementation during reproduction

A key attitudinal change with respect to feeding birds in gardens in the UK has been the endorsement of year-round supplementation. Historically, supplementation by householders in temperate latitudes was restricted to winter to ‘help’ diurnal birds survive this ‘harsh’ period (Jones & Reynolds 2008). It was also considered that natural foods were usually abundant outside of winter and that supplementation could cause more harm than good, for example through the provision of unsuitable supplements to nestlings (e.g. Wood 1985). However, it is now thought that shortages of food can occur at any time of the year (The Royal Society for the Protection of Birds [RSPB] 2006) and that food can be limiting during the spring and summer due to high nutritional demands of breeding adults and young (Toms & Sterry 2008). The subsequent recommendation to feed birds throughout the spring and summer has been made relatively recently, and communicated widely (e.g. RSPB 2006; Toms & Sterry 2008; BTO 2009). Indeed, a common mantra now exists with respect to supplementation in gardens: ‘once you start, you can’t stop’ (Jones 2008).

Despite this recommendation there are concerns regarding year-round food supplementation of birds in gardens. For example, in temperate latitudes the provision of seed during winter might encourage passerines to remain in gardens to breed in the following spring, when alternative habitats would otherwise be sought. Since the abundance of invertebrates with which to feed young is often lower in urban, compared with rural, habitats

(Perrins 1979; comparisons of the availability of other food types are less common in the literature and are also less pertinent since passerines rely typically on invertebrate food to rear young successfully), over-winter provision of seed could inflate avian perception of habitat quality regarding reproduction in the spring, thereby creating an ecological trap (also discussed in Robb *et al.* 2008a). Under such circumstances, year-round supplementation of seed might not provide sufficient nutrients to prevent a nutritional shortfall from occurring. In some species, this problem might be ameliorated through supplementation with invertebrate foods (e.g. mealworms *Tenebrio molitor*) in gardens during the nestling phase, as is currently recommended in the UK (e.g. CJ Wildlife 2009). However, empirical data regarding the effects of such provision in gardens on avian breeding performance are, currently, lacking.

1.1.2. Food supplementation during reproduction: use in conservation initiatives

Food supplementation is often used to enhance breeding productivity (e.g. larger clutches, more young fledged and recruited into the breeding population) of endangered species of birds. The range of species for which food supplementation is used for these purposes is considerable, and include Spanish imperial eagle *Aquila adalberti* (Blanco 2006), kakapo *Strigops habroptila* (Clout *et al.* 2002), stitchbird *Notiomystis cincta* (Castro *et al.* 2003), San Clemente loggerhead shrike *Lanius ludovicianus mearnsi* (Heath *et al.* 2008), Florida scrub jay (Schoech *et al.* 2008), and Seychelles magpie-robin *Copsychus sechellarum* (Komdeur 1996). Enhanced breeding productivity as a result of food supplementation has been found in numerous studies (e.g. Castro *et al.* 2003; Houston *et al.* 2007; Heath *et al.* 2008; Schoech *et al.* 2008) and sometimes the effects can be dramatic. For example, recruitment of juvenile Seychelles magpie-robins into the breeding population increased five times over as a result of food supplementation (Komdeur 1996).

The extent to which food supplementation increases population growth can vary according to the nutrients provided. For example, supplements that are rich in fat and protein may enhance aspects of breeding performance more than supplements rich only in fats (e.g. increased egg weight – Reynolds *et al.* 2003b). Kakapos supplemented with a specially formulated diet that was rich in essential nutrients such as amino acids laid larger clutches than conspecifics provided with a supplement with a higher energy, but lower essential nutrient, content (Houston *et al.* 2007). Supplementation of other micronutrients (e.g. carotenoids) can enhance nestling growth in endangered species (stitchbird – Ewen *et al.* 2008). Therefore, while demonstrating obvious benefits of food supplementation, these studies also highlight the difficulty of selection of suitable food supplements.

In recent years, other concerns regarding food supplementation of endangered species have emerged. For example, supplementation might enhance survival rates of poor quality individuals (Blanco 2006) and, thereby, reduce the reproductive potential of breeding populations. Extinction risk might also be increased because of male-biased sex ratios of young as a consequence of supplementation (e.g. kakapo – Clout *et al.* 2002; Robertson *et al.* 2006; see also interaction between supplementation and laying sequence on brood sex ratio of lesser black-backed gull *Larus fuscus* in Nager *et al.* 1999). Chronic supplementation over an extended period could lead to the dilution of fitness benefits (Schoech *et al.* 2008), and supplementation can only enhance population recovery to a threshold before other factors (e.g. the availability of nest sites, mortality caused by other factors – Komdeur 1996; Armstrong *et al.* 2007) become limiting.

1.1.3. Food supplementation during reproduction: use in pure scientific research

Food supplementation is often used in scientific research to isolate the role of food within different biological processes, commonly during reproduction. In one of the earliest food supplementation studies to examine the role of food during reproduction of free-living birds, Källander (1974) investigated Perrins' (1965) proposal that great tits *Parus major* initiated clutches later in the breeding season than appeared optimal (measured by subsequent breeding productivity) because egg production was constrained by low food availability early in the breeding season (the constraint hypothesis). Källander (1974) found that great tits that were supplemented mealworms pre-laying initiated clutches earlier than non-supplemented conspecifics, appearing to corroborate Perrins' hypothesis.

This study by Källander (1974), and other early studies that employed food supplementation during avian reproduction (e.g. Yom-Tov 1974; Crossner 1977), have now burgeoned into an array of food supplementation research that has set out to answer a wide range of questions in reproductive biology (e.g. reviewed in Boutin 1990; Meijer & Drent 1999; Robb *et al.* 2008a). For example, the importance of specific nutrients has been investigated (e.g. Eldridge & Krapu 1988; Bolton *et al.* 1992; Tilgar *et al.* 1999) as has the role of food availability during distinct reproductive phases (e.g. Nilsson & Smith 1988; Nilsson & Svensson 1993b; Nilsson 1994). The role of food supply in determining density-dependent effects on reproduction (e.g. a negative association between breeding density and clutch size) has been explored using food supplementation (e.g. Arcese & Smith 1988), as has the importance of food abundance in determining prey selectivity by parents feeding nestlings (Grieco 2002). Food supplementation has also revealed that food availability can have carry-over effects between seasons (e.g. Grieco *et al.* 2002; Brommer *et al.* 2004; Robb *et al.* 2008b). In summary, food supplementation is a valuable tool in order to manipulate food availability to address a wide range of questions in reproductive biology – the utility of which is evidenced by a large, and growing, body of research (e.g. see Robb *et al.* 2008a).

1.1.4. Food supplementation during reproduction: unintentional feeding

Humans often provide food for breeding birds unintentionally. For example, at landfill sites large aggregates of birds feed on refuse, including (grouped by order due to large number) Ciconiiformes (e.g. Ciconiidae – Tortosa *et al.* 2002), Falconiformes (e.g. Accipitridae – Elliott *et al.* 2006; De Giacomo & Guerrieri 2008), Charadriiformes (primarily Laridae – Blanco & Marchamalo 1999; Nelson *et al.* 2008), and Passeriformes (primarily Corvidae – Baxter & Robinson 2007; Olea & Baglione 2008). In some species, use of food from landfill becomes increasingly pronounced throughout the breeding period (e.g. yellow-legged gull *Larus cachinnans* – Duhem *et al.* 2003) and is the only food source used by some individuals (silver gull *Larus novaehollandiae* – Smith & Carlile 1993). Indeed, attempts to reduce landfill waste (e.g. landfill tax and increased recycling) could cause reduced fecundity in nearby populations of birds (Pons 1992; Kilpi & Ost 1998).

Numerous species of birds are also supplemented with food unintentionally through discards from fisheries, including (grouped by order due to large number) Procellariiformes (e.g. Diomedeidae; Procellariidae – Thompson 1992; Louzao *et al.* 2006), Pelecaniformes (e.g. Sulidae – Furness *et al.* 1992; Garthe *et al.* 1996), and Charadriiformes (e.g. Laridae; Stercorariidae – Oro & Ruiz 1997; Arcos *et al.* 2002). Fisheries' discards can form a substantial component of the diet of some seabird species, including the diet of nestlings (e.g. herring gull *Larus argentatus* – Spaans 1971; Furness *et al.* 1992). Indeed, without alternative resources, policies to reduce discards from fisheries can result in extremely low breeding productivity in nearby gull colonies (e.g. Audouin's gull *Larus audouinii* – Oro *et al.* 1996) perhaps due to decreased rates of provisioning nestlings (Oro *et al.* 1997).

1.2. Effects of food supplementation during reproduction

Food supplementation during reproduction can have considerable effects on breeding parameters of birds. In numerous reviews on this topic (e.g. Martin 1987; Arcese & Smith 1988; Boutin 1990; Meijer & Drent 1999; Christians 2002; Nager 2006; Robb *et al.* 2008a) a wide range of significant effects of food supplementation on avian reproduction have been reported. In Sections 1.2.1-1.2.7 I introduce many of these effects with an emphasis on breeding parameters that I have examined with respect to food supplementation in my study, and on previous supplementation studies of the focal species in my research: blue tits *Cyanistes caeruleus* and great tits (e.g. Källander 1974; Clamens & Isenmann 1989; Nilsson 1994; Nager *et al.* 1997; Grieco 2003; Robb *et al.* 2008b; see also Table 2.2). A full outline of my aims and methods is provided in Section 1.3.

1.2.1. Clutch initiation date

The most common effect of food supplementation on avian reproduction is advanced clutch initiation (e.g. common kestrel *Falco tinnunculus* – Dijkstra *et al.* 1982; American coot *Fulica americana* – Arnold 1994; boreal owl *Aegolius funereus* – Korpimäki 1989; belted kingfisher *Megaceryle alcyon* – Kelly & Van Horne 1997; great tit – Nager *et al.* 1997). The mechanisms behind advanced clutch initiation as a result of food supplementation are difficult to establish, but explanations have included an alleviation of early season nutritional constraints and/or supplementation acting as a cue that peak food abundance later in the season (e.g. during the nestling period) is advanced (see discussion in Ramsay & Houston

1997). Timing of breeding can have substantial fitness consequences in many avian species. Therefore, in this respect, food supplementation might have a pronounced influence on reproductive success. For example, the survival rate of blue and great tits both pre and post-fledging tends to decrease throughout the breeding season in the UK (Perrins 1965). Therefore, in these species, advanced breeding as a consequence of supplementation is likely to have a broadly positive influence on breeding productivity (but see Nilsson 1994).

1.2.2. Clutch size

Clutch size is an important determinant of breeding productivity (Lack 1954), especially in species that are short-lived and usually single-brooded in each year (e.g. blue and great tits breeding in the UK – Perrins 1979). Clutch size can be constrained by food availability, as evidenced through a positive influence of food supplementation on clutch size in numerous previous studies (e.g. common kestrel – Aparicio 1994; lesser black-backed gull – Hiom *et al.* 1991; blue tit – Ramsay & Houston 1998; western jackdaw *Corvus monedula* – Soler & Soler 1996; song sparrow *Melospiza melodia* – Arcese & Smith 1988). However, supplementation has a stronger positive influence on clutch size when clutches of non-supplemented birds are smaller than average (i.e. in less favourable years – reviewed in Nager *et al.* 1997). Indeed, a smaller proportion of supplementation studies have reported an increase of clutch size as a result of supplementation than those that have found an advancement of clutch initiation (e.g. see review in Robb *et al.* 2008a).

1.2.3. Incubation period

Further to clutch initiation date, another determinant of breeding phenology is incubation period. Incubation can cause nutritional stress, not least because time available for foraging is restricted in incubating adults (Eikenaar *et al.* 2003). In income-breeding species (i.e. those that rely on exogenous rather than endogenous nutrients during reproduction, such as blue and great tits – see Meijer & Drent 1999), a trade-off between time needed for incubation and time needed to forage might be especially pronounced. Food supplementation is likely to enhance the foraging efficiency of incubating adults. Therefore, an increase in incubation intensity (e.g. Australian reed warbler *Acrocephalus australis* – Eikenaar *et al.* 2003) and a reduction of incubation period (e.g. blue tit – Nilsson & Smith 1988; European pied flycatcher *Ficedula hypoleuca* – Sanz 1996) as a consequence of food supplementation can occur.

1.2.4. Hatching success

Hatching success can be influenced by factors such as incubation behaviour (e.g. a positive association with incubation attendance – e.g. Lyon & Montgomerie 1985) and egg size (a positive relationship – e.g. Saino *et al.* 2004) (see also Sections 1.2.3 & 1.2.5). Nilsson & Smith (1988) found that supplemented blue tits experienced higher hatching success than non-supplemented conspecifics, and the same has been found in other species (e.g. black-legged kittiwake *Rissa tridactyla* – Gill & Hatch 2002; Eurasian magpie *Pica pica* – Högstedt 1981). However, the proportion of studies that have found no significant effect of food supplementation on hatching success is approximately equal to that of studies that have found a positive association (reviewed in Robb *et al.* 2008a).

1.2.5. Egg size and composition

In addition to clutch size, nutritional constraint on egg production could occur through reduced egg size. Food supplementation has been found to increase egg size in a number of species (e.g. American coot – Hill 1988; lesser black-backed gull – Hiom *et al.* 1991; blue tit

– Ramsay & Houston 1997; Florida scrub jay – Reynolds *et al.* 2003b; zebra finch *Taeniopygia guttata* – Williams 1996), despite egg size being relatively inflexible within individuals (reviewed in Christians 2002). Hatchlings from large eggs are heavier and can have faster rates of growth than conspecifics hatched from small eggs (e.g. great tits – Schifferli 1973). Since egg size is usually an accurate proxy for the quantity of nutrients therein (Christians 2002) it is usually a reliable indicator of egg ‘quality’. However, supplementation can alter egg composition independently of egg size (e.g. Arnold *et al.* 1991). For example, increased lipid in the egg as a result of supplementation (Arnold *et al.* 1991) might serve as an important food reserve in the yolk sac of nestlings early in the nestling phase (Schifferli 1973). Alternatively, other important egg nutrients (e.g. protein – Nisbet 1978) might also increase as a consequence of food supplementation.

1.2.6. Nestling growth and survival

The nestling phase involves the rapid growth of young (e.g. Perrins 1979) and, in altricial species, substantial energetic expenditure in breeding adults (reviewed in Drent & Daan 1980). Therefore, perhaps unsurprisingly, food supplementation has been found to enhance nestling growth in many species (e.g. black-legged kittiwake – Gill *et al.* 2002; European crested tit *Lophophanes cristatus* – von Brömssen & Jansson 1980; great tit – Rytkönen & Orell 2001; common starling – Crossner 1977; song sparrow – Arcese & Smith 1988). More developed young are at lower risk of starvation than less developed contemporaries (e.g. due to a competitive advantage in the nest – Perrins 1979). Therefore, as might be expected, food supplementation has been found to increase fledging success in the majority of studies in which it has been recorded (see review in Robb *et al.* 2008a).

1.2.7. Post-fledging survival

One of the most important effects that food supplementation can have on avian reproduction is on survival rates of fledglings. Food requirements of young can peak after fledging (reviewed in Martin 1987) and in some species, such as blue and great tits, mortality rate post-fledging is considerable (Perrins 1979) and important in regulating population size (reviewed in Payevsky 2006). It is predicted, therefore, that food supplementation during reproduction should impact positively on post-fledging survival. Few studies have examined this possibility but in those that have enhanced survival rates of fledglings (e.g. northern goshawk *Accipiter gentilis* – Dewey & Kennedy 2001) and/or increased production of independent young (e.g. Florida scrub jay – Schoech *et al.* 2008) as a consequence of supplementation has been found. However, there remains a paucity of evidence regarding the influence of food supplementation during the breeding period on the survival of fledglings.

1.3. Summary of aims and methods

The primary aim of this study was to investigate the recent recommendation that birds in gardens should be provided with food supplements throughout the spring and summer, rather than only in winter as has been advised historically (Section 1.1.1.2). To date, this recommendation has been made without sufficient empirical data to support it. It is important to establish the effects of such food supplementation particularly because many species of birds use gardens during the spring and summer as habitats in which to breed (Bland *et al.* 2004). To investigate this problem, I examined the reproduction of two passerine species, blue and great tits, exposed to different food supplementation manipulations in a rural (woodland) site at a local scale, as well as considering the potential effects of food provision across an urban gradient at a broader (national) scale (see details below). In addition to food supplementation in gardens, my study has broader implications in terms of other situations in which birds are exposed to supplementation during reproduction, particularly the controlled, intentional food supplementation that occurs as part of conservation initiatives (Section 1.1.2) and in pure scientific research (Section 1.1.3).

To investigate the influence of food supplementation during the spring and summer on birds in gardens I have used two approaches. First, I conducted a field study in central England, UK, from 2006-2008. In this study, two commercial garden bird foods were supplemented during the spring and summer to blue and great tits, species that commonly breed in UK gardens (Bland *et al.* 2004). One supplement (‘peanut cake’ – beef tallow and peanuts) was provided in a diffuse manner, between adjacent breeding territories, to mimic the availability of food supplements in individual gardens. Peanut cake was provided from pre-laying to post-fledging of both species. The other supplement (mealworms) was provided more directly to focal nests during the nestling period to mimic the recommendation for live invertebrates to be supplemented during chick-rearing in gardens (e.g. CJ Wildlife 2009). The effects of supplementation were examined in multiple breeding parameters pertaining primarily to breeding phenology (e.g. clutch initiation date and incubation period) and productivity (e.g. clutch size, fledging success, and apparent survival of fledglings) (see Section 1.2).

Many food supplementation studies have preceded my own (e.g. see Section 1.2) but few have examined the influence of protracted food supplementation across the breeding period (e.g. see Meijer & Drent 1999 and references therein). Such a schedule is likely to be important in order to ascertain the influence of food supplementation throughout reproduction (e.g. as recommended in UK gardens). In this respect, and indeed in others (outlined later in this thesis), my field study builds and improves upon previous food supplementation research.

Ideally, my field study would have been conducted in an urban setting (e.g. gardens), but this presented considerable logistical difficulties (e.g. access to private property, controlling the amount and the type of foods provided, human-disturbance of food and/or nests, and ensuring sufficient sample sizes). Consequently, the study took place in a rural woodland which eliminated almost all of these difficulties.

The second approach that I undertook was an examination of patterns in breeding parameters of blue and great tits in urban and non-urban habitats across the UK, using data from the BTO's Nest Record Scheme (NRS). Although exact patterns of food supplementation were unknown, supplementation is widespread in UK gardens (see Section 1.1.1.1) and, therefore, it was reasonable to assume that it might have detectable effects on reproduction of the focal species in urban habitats. As with the field-based components of my research, I examined breeding parameters pertaining to breeding phenology and productivity. To this end, I hoped that the results of my field study would be informative as to patterns in breeding parameters expected in urban habitats if supplementation was influential.

1.4. Thesis structure

In **Chapter Two** I examined the influence of food supplementation on measures of breeding phenology (clutch initiation date and incubation period) and productivity (clutch size, hatching success, and brood size) of blue and great tits breeding in a rural woodland. In **Chapter Three** I investigated the influence of food supplementation in a rural woodland on egg size and composition, and the subsequent growth of nestling blue and great tits. In **Chapter Four** I explored the influence of food supplementation on longer-term measures of breeding success (e.g. fledging success and the apparent survival of young several months post-fledging) of blue and great tits in a rural woodland. In **Chapter Five** I examined the consumption of food supplements by blue and great tits in a rural woodland using stable isotope analysis. In **Chapter Six** I used NRS data to compare the breeding phenology and productivity of blue and great tits across an urban gradient throughout the UK. In **Chapter Seven** I used NRS data to partition the influence of urbanisation on breeding phenology and productivity of blue and great tits into proximate and landscape-scale effects. Finally, in **Chapter Eight** I discuss my findings within the context of previous studies and provide directions for future research.

Chapter Two

DOES FOOD SUPPLEMENTATION ENHANCE PRODUCTIVITY OF BREEDING BIRDS?

2.1. Abstract

Food availability influences multiple stages of the breeding cycle of birds, and supplementary feeding has helped in its understanding. Most supplementation studies have caused advancements of laying, while others, albeit less numerous, have also demonstrated fitness benefits such as larger clutches, shorter incubation periods and greater hatching success. Relatively few studies, however, have investigated the effects of supplementary feeding for protracted periods across multiple stages of the breeding cycle. These effects are important to understand since long-term supplementation of birds is recommended in urban habitats and as a tool to increase reproductive output in endangered species. Here, I compare the breeding phenology and productivity of blue tits and great tits breeding in food-supplemented and non-supplemented blocks in a rural woodland in central England over three seasons, between 2006 and 2008 inclusive. Supplementation was provided continuously from several weeks pre-laying until hatching, and had multiple significant effects. Most notably, supplementation reduced brood size significantly in both species, by half a chick or more at hatching. Reduced brood sizes of supplemented pairs were driven by significantly smaller clutches of both species and, in blue tits, significantly lower hatching success. These are novel and concerning findings of food supplementation. As expected, supplementary feeding advanced laying and shortened incubation periods significantly in both species. I discuss the striking parallels between my findings and patterns in blue and great tit reproduction in urban habitats, and conclude that supplementary feeding may not always enhance productivity of breeding birds.

2.2. Introduction

In recent years supplementary feeding studies of birds have addressed numerous questions including topics in the fields of evolutionary biology (e.g. de Neve *et al.* 2007), behavioural ecology (e.g. Grieco *et al.* 2002), animal physiology (e.g. Schoech *et al.* 2007), and applied ecology (e.g. Robb *et al.* 2008b). In many studies, particularly of small passerines (e.g. Källander & Karlsson 1993; Nager *et al.* 1997; Ramsay & Houston 1997), supplements have been provided for relatively short periods, sometimes to examine the importance of food during distinct reproductive phases (e.g. Nilsson & Smith 1988; Nilsson 1994). Little is known about the effects of continuous food supplementation across multiple stages of the breeding cycle, and this is important because protracted supplementation of birds is advocated in urban habitats (i.e. year-round – RSPB 2006; Toms & Sterry 2008) and to increase reproductive productivity of endangered species (e.g. stitchbird – Castro *et al.* 2003; Florida scrub jay – Schoech *et al.* 2008).

Although the design of food supplementation studies has varied widely, there have been some consistent results. Principally, supplementation usually advances reproduction (reviewed in Martin 1987; Meijer & Drent 1999; Robb *et al.* 2008a). In blue and great tits breeding in temperate seasonal latitudes, breeding early in the spring usually enhances reproductive success (Nilsson 2000). For example, early-hatched nestlings tend to grow more rapidly (Perrins & McCleery 1989) and show greater long-term survival than those that fledge later in the same breeding season (Norris 1993).

Incubation period also determines breeding phenology, and can be influenced by food availability, particularly if food is limited and/or energetic costs are high during incubation (Eikenaar *et al.* 2003). Shorter incubation periods are likely to be beneficial due to earlier hatching (Perrins 1965) and because incubating adults experience reduced foraging time

(Eikenaar *et al.* 2003). Therefore, food supplementation is expected to shorten incubation periods (e.g. Nilsson & Smith 1988; Sanz 1996) although some studies have found no significant effect (e.g. Nilsson 1994; Nager *et al.* 1997).

In addition to breeding phenology, food supplementation may influence breeding productivity. Two fundamental determinants of productivity are clutch size and hatching success, parameters that cumulatively determine brood size at hatching (hereafter ‘brood size’). Clutch size can be limited by food availability both during egg production (e.g. nutritional constraint – Williams 1996; Ramsay & Houston 1998) and after laying (e.g. by the number of young that a pair can rear successfully – Lack 1954; Pettifor *et al.* 1988). Despite the importance of food availability, food supplementation studies have produced mixed results (e.g. reviewed in Martin 1987; Boutin 1990), with significant positive associations between clutch size and supplementation found in some (e.g. Nilsson 1991; Soler & Soler 1996) but not in others (e.g. Davies & Lundberg 1985; Svensson & Nilsson 1995). Similarly, hatching success has sometimes increased as a result of food supplementation (e.g. Nilsson & Smith 1988) but most studies show no significant effect (e.g. Ewald & Rohwer 1982; Arcese & Smith 1988). As a corollary, food supplementation has resulted in either increased brood size, or in no significant effect.

Here, I report the influence of continuous food supplementation from several weeks pre-laying through to hatching on the breeding phenology and productivity of blue and great tits in three successive years. Blue and great tits are ideal focal species because they are quick to explore novel objects (e.g. feeders) and take readily to nestboxes (Perrins 1979), enabling breeding parameters to be recorded easily. I hypothesised that supplementary feeding would: (i) advance clutch initiation; (ii) enlarge clutch size; (iii) shorten incubation period; (iv) enhance hatching success; and (v) enlarge brood size.

2.3. Materials and methods

2.3.1. Study site and experimental design

The study was conducted over three breeding seasons (2006-2008) at Chaddesley Woods National Nature Reserve (NNR), a 101-hectare woodland in Worcestershire, UK (UK Ordnance Survey Grid Reference: SO914736, 52.36 N, -2.14 E) (Appendix One). The study area consisted of three treatment blocks, each containing 96 nestboxes arranged on a square grid at *c.* 40 m spacing (*c.* 6.25 nestboxes ha^{-1}) (Appendix One). This nestbox density is comparable to that of other established nestbox studies of tits in similar habitats (e.g. Minot & Perrins 1986; Mänd *et al.* 2005). In food-supplemented blocks there were 24 feeders, with one feeder placed centrally in the quincunx formed by each set of four nestboxes and a feeder so that each nestbox was *c.* 28 m from a feeder. In the control treatment block no food supplements and no feeders were present. The habitat in each treatment block was similar, consisting of broadleaved, deciduous woodland, predominantly oak *Quercus* spp. There was a buffer strip of *c.* 90 m width between nestboxes on the perimeter of one treatment block and the closest feeders in an adjacent block (Appendix One). Although some ‘crossing-over’ between treatments may have occurred (see Wilkin *et al.* 2009 for details of parid foraging ranges), blue and great tits are territorial from January, becoming increasingly so as spring approaches (Gosler 1993). Therefore, access to feeders is likely to have been markedly lower in control, compared with supplemented, birds. Nestboxes were tree mounted *c.* 2 m above the ground and the 32 mm entrance holes faced NE (away from the prevailing SW winds).

2.3.2. Food supplementation

In each year of the study one treatment block received no supplementary food (hereafter ‘control’) and two treatment blocks received peanut cake (comprising 50% ground peanuts and 50% beef tallow; hereafter ‘supplemented’). Peanut cake is an energy-rich commercial bird food (CJ Wildlife Ltd., Upton Magna, UK). Both species were observed feeding on this supplement throughout the study (TJEH pers. obs.). Peanut cake was provided from early March (*c.* 4-5 weeks pre-laying) to the end of July (*c.* 6-8 weeks post-fledging) in each year. Hatching usually occurred in early to mid-May, at which point an additional food supplement was added in one of the two supplemented treatment blocks. This Chapter summarises effects of supplementation prior to initiation of this third treatment. Feeders were checked regularly (*c.* twice a week – each peanut cake weighed 500 g and usually lasted over a week) and were replenished upon marked depletion so that peanut cake was provided *ad libitum.* Occasional heavy utilisation (e.g. by grey squirrels *Sciurus carolinensis*) disrupted this supply, but such interruptions were brief (*c.* 1-2 days). Peanut cake was stored in an outdoor shed at cool temperatures, so incidents of mould were rare. Dietary treatments were rotated over the three study years so that each treatment block was supplemented twice and was the control once.

2.3.3. Breeding parameters

Clutch initiation dates were determined by visiting nestboxes at least twice a week and noting on what day the first egg was laid or by back-counting eggs (assuming one egg laid per day – Perrins 1979) when two or more eggs were already present. Visits to nestboxes were made after 0800 hours GMT since blue and great tits usually lay at around 0600 hours GMT in the UK (Perrins 1979). Clutch size and clutch completion date were recorded by monitoring nestboxes in which eggs had been laid every 1-2 days until laying ceased. Incubation period was defined as the number of days between clutch completion date (day 0 of incubation) and hatching date of the first egg (Cresswell & McCleery 2003). A mean incubation period of *c.* 12-13 days was expected (Perrins 1979; Cresswell & McCleery 2003), so hatching checks were carried out on a daily basis from 10 days after clutch completion until the first egg hatched. Blue and great tits do not remove un-hatched eggs from their nests (Kempenaers *et al.* 1998; TJEH pers. obs.) so un-hatched eggs were counted *c.* 20 days after hatching (when fledging checks were conducted). Hatching success was defined as the proportion of a clutch that hatched. Brood size was calculated as the clutch size minus any un-hatched eggs (i.e. the maximum possible brood size), to eliminate the influence of early nestling phase mortality.

2.3.4. Filtering data

In all analyses, only first clutches were considered (second brood attempts were extremely rare, consistent with the literature – e.g. Perrins 1979). Clutch initiation date analyses included all first clutches. Clutch size analyses excluded clutches that were abandoned prior to clutch completion. Clutches with laying breaks > 2 days, and one clutch where the duration of a laying break was unknown, were excluded from clutch size, hatching success, and brood size analyses. Two clutches that were apparently abandoned prior to the eventual onset of incubation were excluded from incubation period, hatching success, and brood size analyses. Hatching success and brood size analyses only included nests in which hatching occurred.

2.3.5. Statistical analysis

All statistical analyses were carried out using PROC GLIMMIX in SAS (SAS Institute Inc. 2008) or Minitab 15 (Minitab 2007). Combined-year analyses were conducted unless the influence of supplementation differed significantly between years (year × dietary treatment: $P \leq 0.05$), in which case within-year analyses were conducted. Nestbox nested in treatment block was specified as a random factor in combined-year analyses due to repeated measures on nestboxes and blocks, and the spatial nesting of nestboxes within blocks. In within-year analyses, treatment block was specified as a random factor. Clutch initiation date was square-root transformed (to improve the normality of the distribution of these data and to reduce over-dispersion) with subsequent analyses fitted with normal errors after examination of model fit (Generalised Chi-Square / DF = *c.* 1). Similarly, analyses of incubation period were fitted with a normal error structure after examination of model fit. Poisson errors were fitted in clutch and brood size analyses, whereas binomial errors were specified in hatching success analyses (binomial logistic regression).

Year was included as a fixed factor in all combined-year analyses (to account for annual variation in breeding conditions – Nager *et al.* 1997). In analyses of clutch size, clutch initiation date was specified as a covariate (due to a seasonal decline in clutch size – Perrins & McCleery 1989). Incubation period analyses included clutch completion date and clutch size (that can both influence incubation period – Perrins 1979; Gosler 1993; Deeming 2002) as covariates. Hatching success and brood size analyses included hatching date as a covariate (due to a seasonal decline in brood size and hatching success – Perrins 1979). Covariate × dietary treatment interactions were tested to examine if covariate effects were consistent between treatments. I had no *a priori* expectation that these interactions would be significant, so these terms were not included in all models but, instead, were tested for significance independently of one another. If more than one interaction was significant, all were included in the final model provided that each remained significant. Non-significant interactions ($P >$ 0.05) were removed if there was no significant change in model deviance where applicable.

Full results for each model are provided in Table 2.1. The Figures were plotted as means ± 1 SE from statistical estimates (illustrating the effect of treatment while accounting for other predictors in each final model – see Table 2.1). For models with non-normal error structures (see above), standard errors were calculated using the delta method (SAS Institute

Table 2.1. Models of reproductive parameters (*F* and associated *P* values) of blue (BT) and great (GT) tits at Chaddesley Woods National Nature Reserve in 2006-2008. Combined-year analyses except BT and GT incubation period (significant year × dietary treatment interactions: $P \leq 0.05$). Fixed factors specified in each model are given with significant *P* values in bold text. Directions of significant effects are given: '-' denotes a significant negative relationship and 'NS' denotes non-significance ($P > 0.05$). Dietary treatments: C = control (non-supplemented); PC = peanut cake. See text for details.

Breeding parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Clutch initiation date	BT	2006-08	Dietary treatment	$F_{1,187} = 11.06$	**P = 0.001**	C = later; PC = earlier
			Year	$F_{2,187} = 101.16$	**P < 0.001**	2006 = latest; 2007 = earliest
	GT	2006-08	Dietary treatment	$F_{1,86} = 22.51$	**P < 0.001**	C = later; PC = earlier
			Year	$F_{2,86} = 54.89$	**P < 0.001**	2006 = latest; 2007 = earliest
Clutch size	BT	2006-08	Dietary treatment	$F_{1,151} = 7.65$	**P = 0.006**	C = larger; PC = smaller
			Year	$F_{2,151} = 82.81$	**P < 0.001**	2006 = largest; 2007 = smallest
			Clutch initiation date	$F_{1,151} = 141.66$	**P < 0.001**	-
	GT	2006-08	Dietary treatment	$F_{1,80} = 9.45$	**P = 0.003**	C = larger; PC = smaller
			Year	$F_{2,80} = 14.58$	**P < 0.001**	2006 = largest; 2008 = smallest
			Clutch initiation date	$F_{1,80} = 19.90$	**P < 0.001**	-
Incubation period	BT	2006	Dietary treatment	$F_{1,125} = 9.44$	**P = 0.003**	C = longer; PC = shorter
			Clutch completion date	$F_{1,125} = 22.70$	**P < 0.001**	-
			Clutch size	$F_{1,125} = 7.64$	**P = 0.007**	-
		2007	Dietary treatment	$F_{1,139} = 0.32$	P = 0.57	NS
			Clutch completion date	$F_{1,139} = 19.86$	**P < 0.001**	-
			Clutch size	$F_{1,139} = 30.85$	**P < 0.001**	-
		2008	Dietary treatment	$F_{1,98} = 17.98$	**P < 0.001**	C = longer; PC = shorter
			Clutch completion date	$F_{1,98} = 110.54$	**P < 0.001**	-
			Clutch size	$F_{1,98} = 0.00$	P = 0.95	NS
			Clutch completion date × dietary treatment	$F_{1,98} = 11.05$	**P = 0.001**	C = pronounced seasonal shortening; PC = less pronounced
	GT	2006	Dietary treatment	$F_{1,59} = 20.87$	**P < 0.001**	C = longer; PC = shorter
			Clutch completion date	$F_{1,59} = 0.33$	P = 0.57	NS
			Clutch size	$F_{1,59} = 0.02$	P = 0.88	NS
			Clutch completion date × dietary treatment	$F_{1,59} = 3.91$	**P = 0.05**	C = seasonal shortening; PC = the opposite
			Clutch size × dietary treatment	$F_{1,59} = 7.35$	**P = 0.009**	C = shorter with larger clutches; PC = the opposite
		2007	Dietary treatment	$F_{1,71} = 6.88$	**P = 0.01**	C = longer; PC = shorter
			Clutch completion date	$F_{1,71} = 13.69$	**P < 0.001**	-
			Clutch size	$F_{1,71} = 15.80$	**P < 0.001**	-

Table 2.1. continued

Breeding parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Incubation period	GT	2008	Dietary treatment	$F_{1,100} = 4.32$	**$P = 0.04$**	C = longer; PC = shorter
			Clutch completion date	$F_{1,100} = 58.27$	**$P < 0.001$**	-
			Clutch size	$F_{1,100} = 7.65$	**$P = 0.007$**	-
Hatching success	BT	2006-08	Dietary treatment	$F_{1,132} = 8.10$	**$P = 0.005$**	C = higher; PC = lower
			Year	$F_{2,132} = 1.02$	$P = 0.36$	NS
			Hatch date	$F_{1,132} = 0.26$	$P = 0.61$	NS
			Hatch date × dietary treatment	$F_{1,132} = 6.65$	**$P = 0.01$**	C = seasonal decrease; PC = the opposite
	GT	2006-08	Dietary treatment	$F_{1,70} = 0.30$	$P = 0.58$	NS
			Year	$F_{2,70} = 7.20$	**$P = 0.001$**	2006 = highest; 2008 = lowest
			Hatch date	$F_{1,70} = 0.07$	$P = 0.80$	NS
Brood size	BT	2006-08	Dietary treatment	$F_{1,129} = 8.28$	**$P = 0.005$**	C = larger; PC = smaller
			Year	$F_{2,129} = 23.46$	**$P < 0.001$**	2006 = largest; 2007 = smallest
			Hatch date	$F_{1,129} = 19.34$	**$P < 0.001$**	-
	GT	2006-08	Dietary treatment	$F_{1,69} = 5.51$	**$P = 0.02$**	C = larger; PC = smaller
			Year	$F_{2,69} = 2.89$	$P = 0.06$	NS
			Hatch date	$F_{1,69} = 0.01$	$P = 0.93$	NS
			Hatch date × dietary treatment	$F_{1,69} = 4.42$	**$P = 0.04$**	C = seasonal decrease; PC = the opposite

Inc. 2008). Hatching success was analysed as a proportion (see Section 2.3.3) but is presented as a percentage in the Results. The magnitudes of the effects of supplementation presented in this Chapter are described by comparing the means presented in the Figures.

2.4. Results

Supplementation advanced clutch initiation date significantly in both species (mean advancement in blue tits: 2.0 days; $F_{1,187} = 11.06$, $P = 0.001$; great tits: 3.0 days; $F_{1,86} = 22.51$, $P < 0.001$) (Fig. 2.1). Clutch size of both species reduced significantly as a result of supplementation (mean reduction in blue tits: 0.4 eggs; $F_{1,151} = 7.65$, $P = 0.006$; great tits: 0.6 eggs; $F_{1,80} = 9.45$, $P = 0.003$) (Fig. 2.2).

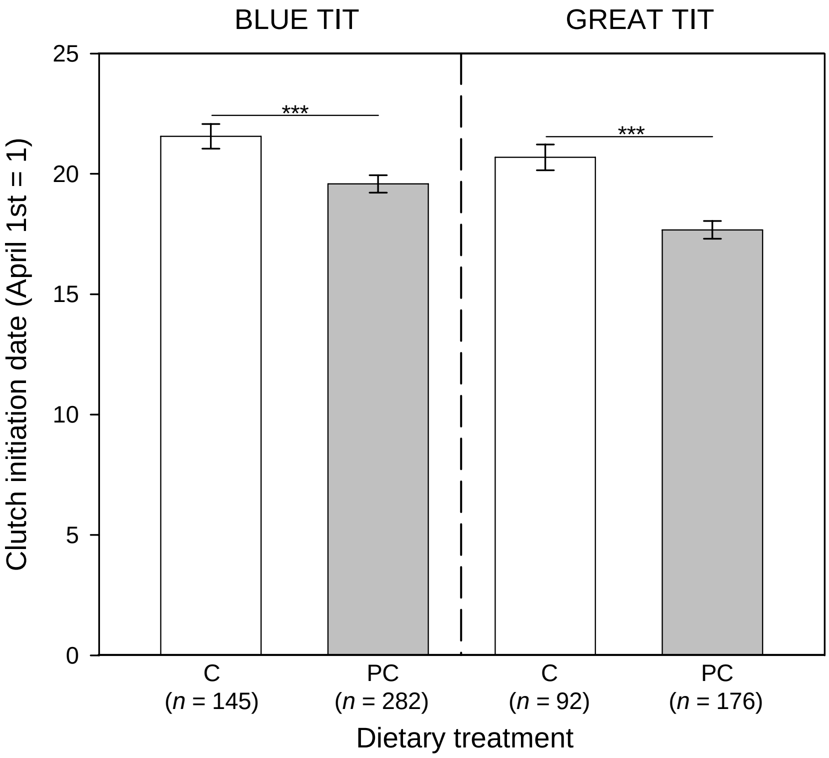

Figure 2.1. Clutch initiation date (mean ± 1 SE from statistical estimates) of blue and great tits at Chaddesley Woods National Nature Reserve in 2006-2008. Dietary treatments: C = control (non-supplemented); PC = peanut cake. *** = $P \leq 0.001$. Number of clutches is in parentheses below dietary treatments. See Table 2.1 for statistical findings and see text for details.

The effect of supplementation on incubation period duration varied significantly between years (year × dietary treatment in blue tits: $F_{2,149} = 8.44$, $P < 0.001$; great tits: $F_{2,69} = 7.14$, $P = 0.002$) (Fig. 2.3). Supplementation shortened incubation periods of blue tits significantly in 2006 (mean reduction: 0.6 days; $F_{1,125} = 9.44$, $P = 0.003$) and 2008 (mean reduction: 1.2 days; $F_{1,98} = 17.98$, $P < 0.001$), but had no significant effect in 2007 ($F_{1,139} = 0.32$, $P = 0.57$) (Fig. 2.3). However, in great tits, incubation periods were shortened significantly by supplementation in each year (mean reduction in 2006: 1.3 days; $F_{1,59} = 20.87$, $P < 0.001$; 2007: 0.5 days; $F_{1,71} = 6.88$, $P = 0.01$; 2008: 0.4 days; $F_{1,100} = 4.32$, $P = 0.04$) (Fig. 2.3). The influence of clutch completion date and clutch size on incubation period showed some differences between treatments (see interactions in Table 2.1) but these differences were not consistent between years or species.

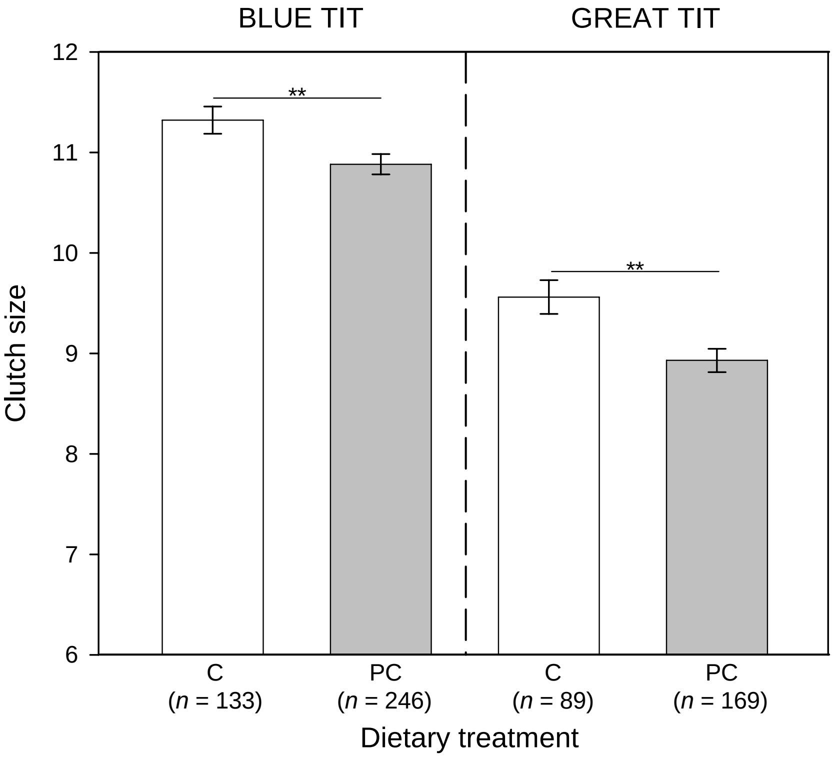

Figure 2.2. Clutch size (mean ± 1 SE from statistical estimates) of blue and great tits at Chaddesley Woods National Nature Reserve in 2006-2008. See Figure 2.1 for explanations of dietary treatments and sample sizes. ** = $P \leq 0.01$. See Table 2.1 for statistical findings and see text for details.

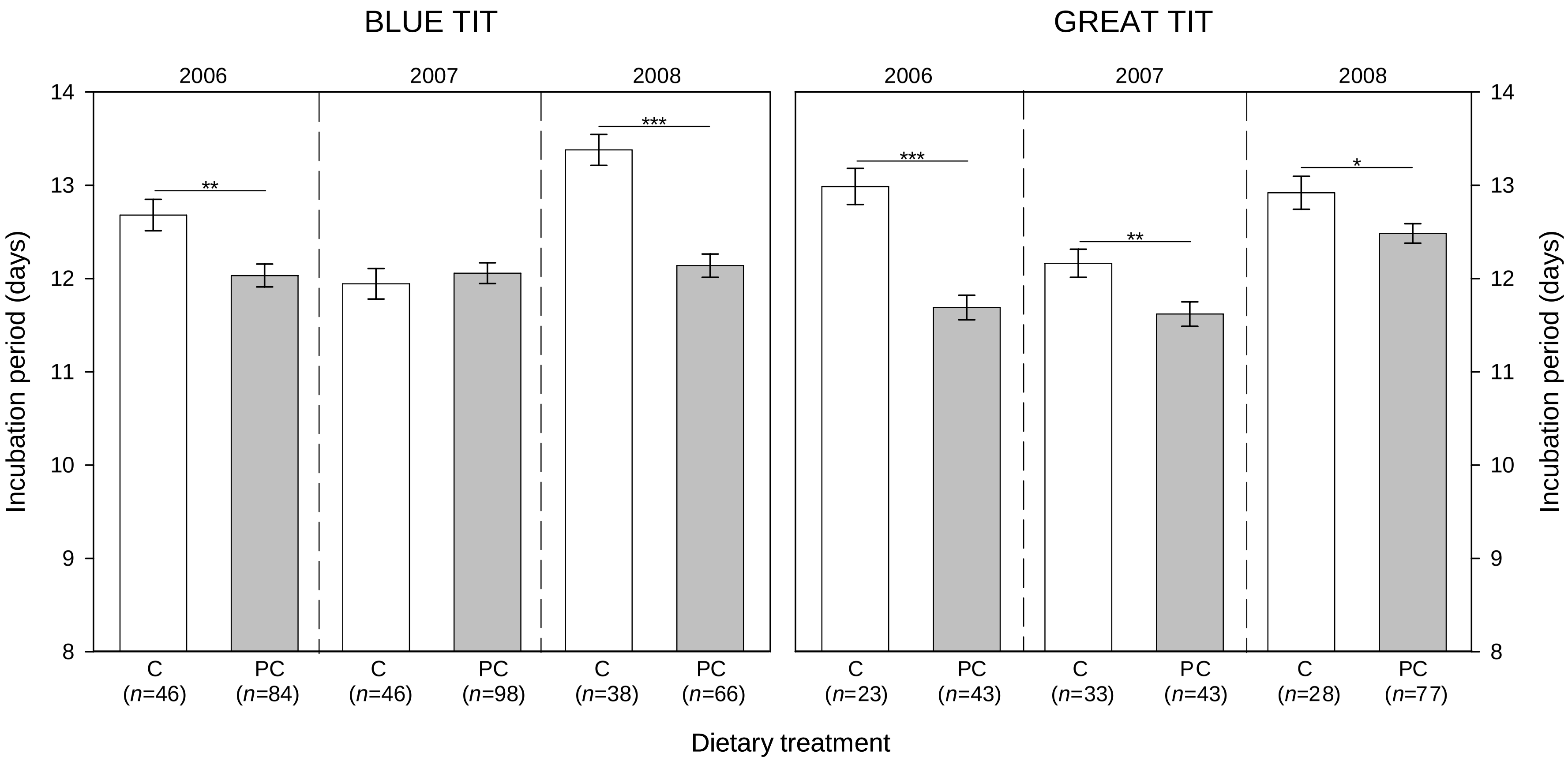

Figure 2.3. Incubation period duration (mean ± 1 SE from statistical estimates) of blue and great tits at Chaddesley Woods National Nature Reserve in 2006-2008. Separate years are presented because of a significant year × dietary treatment interaction in blue ($P < 0.001$) and great ($P = 0.002$) tits. See Figure 2.1 for explanations of dietary treatments and sample sizes. * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$. See Table 2.1 for statistical findings and see text for details.

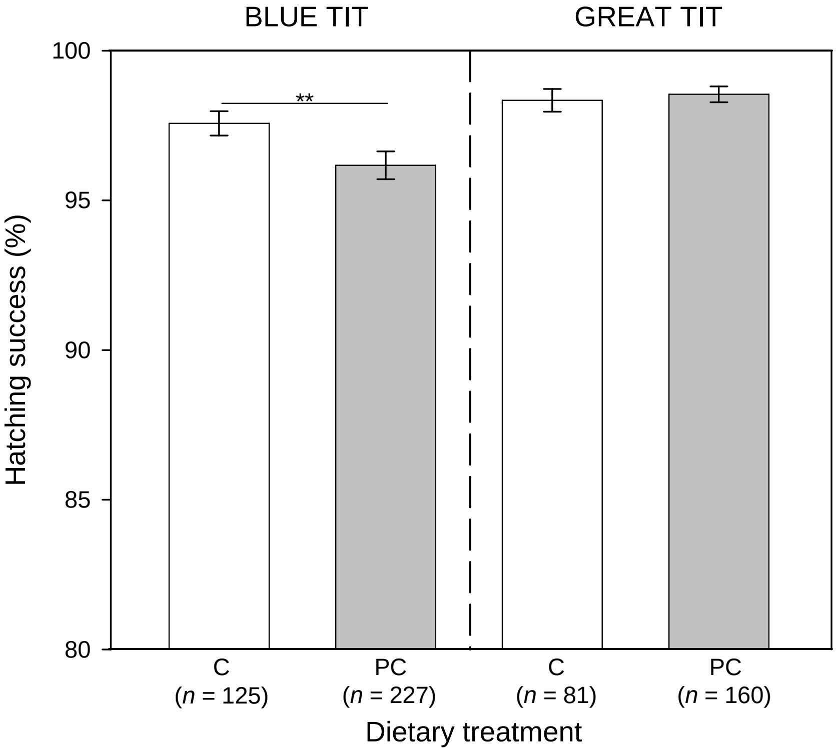

Figure 2.4. Hatching success (mean ± 1 SE from statistical estimates) of blue and great tits at Chaddesley Woods National Nature Reserve in 2006-2008. See Figure 2.1 for explanations of dietary treatments and sample sizes. ** = $P \leq 0.01$. See Table 2.1 for statistical findings and see text for details.

Hatching success was significantly lower in supplemented, compared with control, blue tits (mean reduction: 1.4%; $F_{1,132} = 8.10$, $P = 0.005$) (Fig. 2.4), but great tits showed no significant differences between treatments ($F_{1,70} = 0.30$, $P = 0.58$) (Fig. 2.4). Hatching success of supplemented blue tits increased throughout the breeding season, but the opposite was found in control conspecifics (hatching date × dietary treatment: $F_{1,132} = 6.65$, $P = 0.01$).

Brood size of both species declined significantly as a result of supplementation (mean reduction in blue tits: 0.6 chicks; $F_{1,129} = 8.28$, $P = 0.005$; great tits: 0.5 chicks; $F_{1,69} = 5.51$, $P = 0.02$) (Fig. 2.5). In great tits, brood size increased with later hatching in supplemented pairs, but the opposite was found in controls (hatching date × dietary treatment: $F_{1,69} = 4.42$, $P = 0.04$).

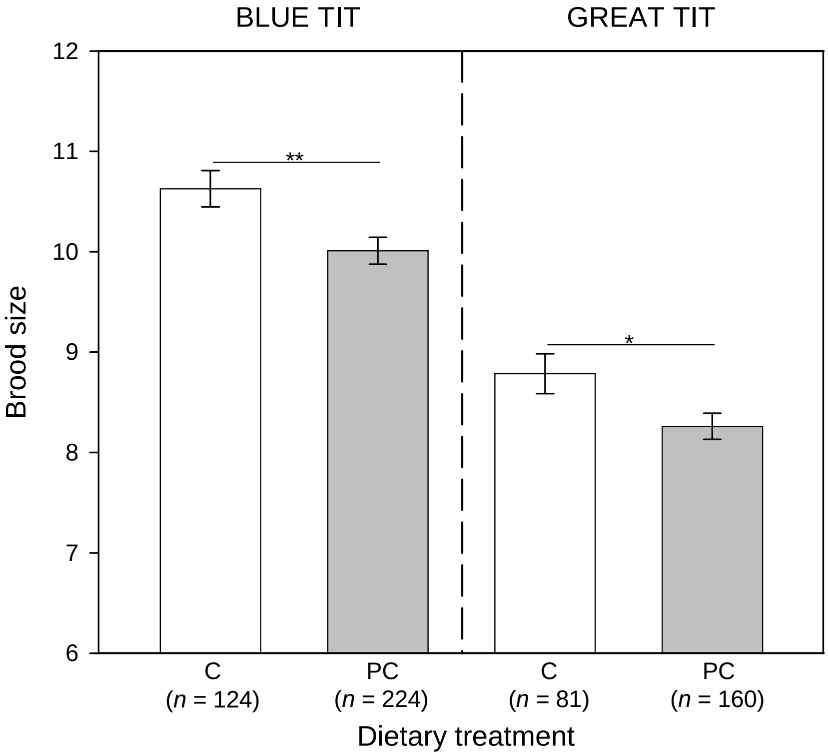

Figure 2.5. Brood size (mean ± 1 SE from statistical estimates) of blue and great tits at Chaddesley Woods National Nature Reserve in 2006-2008. See Figure 2.1 for explanations of dietary treatments and sample sizes. * = $P \leq 0.05$; ** = $P \leq 0.01$. See Table 2.1 for statistical findings and see text for details.

2.5. Discussion

Continuous food supplementation throughout multiple stages of the breeding cycle had pronounced effects on breeding phenology and productivity of blue and great tits. As hypothesised, food supplementation advanced clutch initiation (Fig. 2.1) and shortened incubation periods (except of blue tits in 2007) significantly in both species (Fig. 2.3). Advanced laying is consistent with most previous supplementation studies, although shorter incubation periods have been reported less widely (Table 2.2). Contrary to my hypotheses, clutch (Fig. 2.2) and brood (Fig. 2.5) sizes of both species were reduced significantly by supplementation. Furthermore, hatching success was significantly lower in supplemented blue, but not great, tits (Fig. 2.4). To my knowledge, smaller clutches as a result of supplementation is a novel finding in passerines (reported in one previous study of birds:

Table 2.2. Summary of food supplementation studies of blue (BT) and great (GT) tits. The bottom row summarizes the findings of Robb *et al.* (2008a), the most recent review of supplementation studies across multiple species of birds (number of studies cited given in parentheses). Comparisons are between supplemented and non-supplemented (control) birds except Ramsay & Houston (1998) where the influence of two supplements is distinguished with superscript letters. Clutch initiation date: ‘+’ = later, ‘-’ = earlier; clutch size: ‘+’ = larger, ‘-’ = smaller; incubation period: ‘+’ = longer, ‘-’ = shorter; hatching success: ‘+’ = higher, ‘-’ = lower. Non-significant effects are denoted by ‘NS’. Empty cells represent non-published variables. ‘N/A’ = not applicable (e.g. because of the timing of supplementation).

Sp.	**Food supplement(s)**	**Clutch initiation date**	**Clutch size**	**Incubation period**	**Hatching success**	**Brood size**	**Reference**
BT	Mealworms	N/A	N/A	-	+		Nilsson & Smith (1988)
BT	Sunflower seeds, margarine, dried insects, mealworms, and tineas	-	NS			NS	Clamens & Isenmann (1989)
BT	Mealworms	-	NS				Nilsson & Svensson (1993)
BT	Mealworms	-	NS	NS	NS	NS	Nilsson (1994)
BT	(i) Mealworms; (ii) Mealworms and boiled chicken egg	-	NS				Svensson & Nilsson (1995)
BT	(i) Lard; (ii) boiled chicken egg, lard and oatmeal	-	NS	NS	NS		Ramsay & Houston (1997)
BT	(i) Peanuts enriched with essential amino acids ^{a}; (ii) peanuts not enriched with essential amino acids ^{b}.	NS	+ $^{a\ vs.\ b\ \mathrm{or\ control}}$ NS $^{b\ vs.\ \mathrm{control}}$	NS	NS	NS	Ramsay & Houston (1998)
BT	Peanuts	-	NS				Robb *et al.* (2008b)
GT	Mealworms	-					Källander (1974)
GT	Sunflower seeds, margarine, dried insects, mealworms, and tineas	NS	NS			NS	Clamens & Isenmann (1989)
GT	(i) Sunflower seeds in coconut fat; (ii) mealworms in coconut fat	-	+	NS	NS		Nager *et al.* (1997)
Review of supplementation studies of birds		- (34) + (1) NS (24)	- (1) + (28) NS (34)	- (2) + (0) NS (7)	- (0) + (9) NS (11)		Robb *et al.* (2008a)

American coot – Hill 1988) (Table 2.2). Reduced hatching success and brood size are, to my knowledge, novel findings (Table 2.2), although Pierotti and Annett (1991) found that herring gulls that specialised in foraging on refuse (that was provided unintentionally and, therefore, in a less controlled manner than supplements in 'intentional' food supplementation research) rather than natural foods also experienced reduced hatching success and brood size. In Sections 2.5.1-2.5.5, I consider the fitness consequences and possible mechanisms underlying these results. I finish by discussing the applied importance of my findings (Section 2.5.6).

2.5.1. Clutch initiation date

In seasonal environments, initiating clutches early in the breeding season may bring fitness gains to parents and young. Among blue and great tits, early-laid clutches hatch nestlings that tend to grow rapidly due to the close synchronisation of nestling peak food demand with a peak in the abundance of caterpillars, the preferred food of nestlings (Perrins & McCleery 1989; Cresswell & McCleery 2003). Furthermore, the probability of recruitment into the breeding population declines with later fledging (Verhulst & Tinbergen 1991). However, there are fitness costs associated with breeding too early, including reduced survival of juveniles and breeding females (Norris 1993; Nilsson 1994). The effects of breeding phenology on later stages of reproduction are discussed in Chapters Three and Four.

The mechanisms with which food supplementation promotes early laying are difficult to elucidate. Early laying may be constrained in seasonal environments due to the substantial nutritional requirements of egg formation (the constraint hypothesis: Perrins 1965; Lack 1966). Were this to apply to my study, supplementation may have advanced laying by facilitating the earlier attainment of nutritional thresholds and/or the sequestration of other, potentially limiting, nutrients (e.g. calcium: Reynolds *et al.* 2004; protein: Schoech *et al.*

2004). Alternatively, rather than influencing a nutritional constraint, it is possible that increased food availability early in the breeding season acts as a cue that richer foraging conditions at a key point later in the breeding cycle, for example during chick rearing, are relatively advanced (the cue/anticipation hypothesis: Lack 1954; Perrins 1965). Supplementation may have acted directly or indirectly as a predictive cue: directly, if perceived as a resource that was suitable to feed young; indirectly, if peanut cake enabled more time and/or greater success in foraging for natural food items that, in turn, acted as a cue to clutch initiation. Indeed, supplementation may have acted directly or indirectly throughout the breeding cycle. A third possibility is that supplementation advanced settlement on to breeding territories (Kelly & Van Horne 1997), perhaps because birds that settled in the control treatment competed initially for a supplemented territory.

Not all breeding adults were caught in this study, so some predictors of clutch initiation date are difficult to investigate. For example, there may be carry-over effects of dietary treatment from the previous year (Grieco *et al.* 2002). However, advanced laying as a result of supplementation was recorded in all three years of the study in both species, including the first year in the absence of such carry-over effects. Laying tends to be earlier in resident and older tits (Nager & van Noordwijk 1995) and the ratio of resident to immigrant birds and/or the age structure of the breeding population may have differed between treatments. The latter seems unlikely, however, since older females usually lay larger clutches (Perrins 1979), but this was not found in the supplemented treatment (Fig. 2.2).

2.5.2. Clutch size

The optimisation of clutch size has been studied widely (individual optimisation hypothesis: Lack 1954; Lack 1966; Charnov & Krebs 1974; Perrins & Moss 1975; Gustafsson &

Sutherland 1988; Pettifor *et al.* 1988). For short-lived species such as blue and great tits, clutch size is likely to be optimised within each breeding season to maximise the number of young recruited into the breeding population – mediated on an individual basis by the rearing capacity of each pair. Evidence has been found in support of such optimisation (e.g. Pettifor *et al.* 1988) but other studies have found a mis-match, usually biased towards clutch sizes that are sub-optimally small (reviewed in Lessells 1986; but see Rytkönen & Orell 2001). If future conditions are unpredictable at the point of laying, conservative clutch sizes may, in evolutionary terms, be most productive (Charnov & Krebs 1974; Perrins & Moss 1975). In my study, supplementation, presumably, reduced nutritional constraints on egg production and 'insulated' blue and great tits against unpredictable future conditions (e.g. reduced food availability – Schoech *et al.* 2008). In these respects, and since larger clutches usually produce a greater number of recruits into the breeding population (Boyce & Perrins 1987), a reduction of clutch size as a result of food supplementation is difficult to interpret.

The availability of protein – or perhaps, more specifically, essential amino acids (Ramsay & Houston 1998) – may limit egg production (Jones & Ward 1976; Williams 1996; but see Nager *et al.* 1997) and peanut cake may have influenced smaller clutch sizes because it is fat-rich and protein-poor. A comparison of peanut cake with other common food supplements for birds (as % fat and protein, respectively) reveals peanut cake to contain 70.5% and 17.1% compared with 44.5% and 28.7% (peanuts), 44.4% and 18.0% (black sunflowers) and 58.0% and 21.4% (sunflower hearts) (CJ Wildlife pers. comm.). Significant consumption of peanut cake might have reduced clutch size through insufficient sequestration of protein (or other limiting nutrients). Low protein intake at the point of laying may also act as a predictive cue for low protein availability later in the season (Drent & Daan 1980). A substantial amount of protein-rich food is required to rear chicks successfully (Gosler 1993) and this could drive clutch size. Supplement use is investigated in detail in Chapter Five.

Smaller clutches enable earlier hatching within the season, and this often has fitness benefits (see above). Therefore, supplemented birds may have reduced clutch size to facilitate earlier hatching. However, in Wytham Woods (Oxfordshire, UK), the fitness gains of earlier hatching (more young recruited into the breeding population) fail to explain satisfactorily the small clutch sizes of great tits, since larger clutches almost always produce more recruits (Perrins & McCleery 1989). If blue and great tits in the population that I have studied also lay clutch sizes that are conservative, it is likely that a further reduction (i.e. as a consequence of food supplementation) will reduce the number of recruits per brood.

Rather than being a poor quality supplement, peanut cake might be of high quality with respect to adult maintenance (albeit not reproduction) and thereby enhance adult survival (e.g. Jansson *et al.* 1981). Smaller clutches (Fig. 2.2) represent a smaller investment in current reproduction (in absolute terms) and this could increase adult survival. However, there is little evidence that smaller clutches enhance survival (e.g. Pettifor *et al.* 1988) but such findings have not been made in the context of supplementary feeding. Despite this, both species are relatively short-lived and future reproduction may be of secondary importance in shaping life-history traits compared with current reproduction (Blondel *et al.* 1998).

Finally, increased breeding density reduces clutch size of both species (e.g. Perrins 1965; Perrins & McCleery 1989; Wilkin *et al.* 2006) and this might explain the treatment differences in my study. However, in blue tits, nestbox occupancy (recorded when laying occurred – see Appendix One), which may be a surrogate for minimum breeding density (I do not have data for the occurrence and, hence, density of natural cavities), did not differ significantly between treatments (combined years: $F_{1,573} = 0.17$, $P = 0.68$). In great tits, the influence of supplementation on occupancy differed significantly between years (year × dietary treatment: $F_{2,571} = 3.41$, $P = 0.03$), but was only significant in 2007 when occupancy on control territories was significantly higher (control = 38.5%, supplemented = 24.0%; $F_{1,286} = 6.48$, $P = 0.01$). Total occupancy (blue and great tits combined) tended to be greater in the control treatment (combined years: control = 87.9%, supplemented = 84.2%; $F_{1,573} = 3.41$, $P = 0.07$). Therefore, the smaller clutch size of supplemented birds is even more remarkable. Moreover, clutch size decreased with later laying of both species, so advanced laying of supplemented birds (Fig. 2.1) should have promoted larger, rather than smaller, clutches.

2.5.3. Incubation period

Shorter incubation periods are likely to be adaptive. For example, there are direct fitness benefits because the foraging time of incubating adults is restricted and because eggs and nestlings are more vulnerable to predation than are fledged young (i.e. truncation of these formative stages is likely to be beneficial – Bosque & Bosque 1995). There are also indirect fitness benefits because shorter incubation advances hatching and, usually therefore, fledging that enhances the probability of recruitment into the breeding population (Verhulst & Tinbergen 1991).

Supplementation may have shortened incubation periods through greater incubation attendance (Eikenaar *et al.* 2003), perhaps driven by increased foraging efficiency of females and/or increased courtship feeding of females by their mates (Nilsson & Smith 1988). Furthermore, supplemented females may have commenced incubation with enhanced body condition compared with controls and, as a result, foraged less during incubation (Wiebe & Martin 2000). However, rather than influencing incubation efficiency, supplementation may advance incubation onset relative to the laying sequence, perhaps to maintain perceived synchrony with natural food resources (e.g. caterpillars – Cresswell & McCleery 2003). Nilsson (1994) found that blue tits that were food-supplemented throughout egg-laying until incubation initiated incubation earlier relative to clutch completion date compared with conspecifics that had supplements removed at the onset of laying or non-supplemented controls. Although advanced hatching can have fitness benefits, achieving this via advanced onset of incubation relative to the laying sequence might cause greater hatching asynchrony (Cresswell & McCleery 2003; Eikenaar *et al.* 2003) and subsequent brood reduction and/or lower hatching success (Perrins 1979; Nilsson 1993). The influence of supplementation on incubation period was not consistent in all years (Fig. 2.3), and this is difficult to explain. Furthermore, the influence of clutch completion date and clutch size on incubation period showed some differences between treatments, but these effects were not consistent (see interactions in Table 2.1).

2.5.4. Hatching success

Hatching success determines the efficiency with which investment in egg production is carried forward into the nestling phase. Reduced hatching success is likely to be deleterious since egg production is energetically/nutritionally expensive (Robbins 1981; Walsberg 1983) and more investment (e.g. heat – Wiebe & Martin 2000) may be required to incubate larger clutches.

Differences in incubation behaviour between treatments might explain differences in hatching success (Perrins 1979; Lyon & Montgomerie 1985). If shorter incubation periods of supplemented compared with control blue tits (2006 and 2008) and great tits (2006-2008) (Fig. 2.3) were caused by greater incubation attendance (e.g. Eikenaar *et al.* 2003), then *ceteris paribus* enhanced, not reduced, hatching success would be expected (Lyon & Montgomerie 1985; Nilsson & Smith 1988). If, however, shorter incubation periods resulted from supplemented females initiating incubation earlier in the laying sequence, hatching asynchrony might have occurred (Cresswell & McCleery 2003), reducing hatching success as a result (Perrins 1979). However, reduction of hatching success of supplemented, compared with control, blue tits was greatest in 2007 when incubation period did not differ significantly between treatments (Fig. 2.3). Furthermore, hatching success of great tits showed the least difference between treatments in 2006 when incubation periods were shortened most significantly by supplementation (Fig. 2.3). Interestingly, hatching success of supplemented blue tits increased throughout the breeding season, but the opposite was found in control nests (hatching date × dietary treatment – Table 2.1). This indicates further subtle effects of food supplementation that are, currently, difficult to interpret.

2.5.5. Brood size

Unless broods are very large (e.g. > *c.* 10 in great tits), increased brood size normally results in a greater number of surviving young (Perrins & Moss 1975). Since mean brood sizes were not especially large in the population that I studied (Fig. 2.5), it is probable that larger broods were more productive. However, the survival probability of individual fledglings decreases with increased brood size (Gustafsson & Sutherland 1988; Naef-Daenzer *et al.* 2001), often as a result of decreased nestling growth (Perrins 1965; Nur 1984) and/or later hatching (Perrins & McCleery 1989). It is possible, therefore, that the smaller broods of supplemented birds represented a fine-tuning of reproductive investment. The influence of brood size on downstream measures of reproductive success between treatments is investigated in Chapters Three and Four.

Smaller brood sizes of supplemented pairs were driven by significantly smaller clutch sizes (Fig. 2.2) and, in blue tits, significantly lower hatching success (Fig. 2.4). Clutch size may have been reduced strategically in supplemented birds, but an adaptive reduction of hatching success in blue tits seems implausible due to the nutritional costs and time-delay caused by unnecessary egg production. As expected, brood size decreased throughout the breeding season in blue tits and in non-supplemented great tits (Table 2.1). However, brood size of supplemented great tits increased throughout the breeding season (hatching date × dietary treatment interaction in Table 2.1), perhaps due to a relative ‘under-performance’ of early-breeding pairs and/or because later-breeding pairs were ‘insulated’ from declining peaks of natural foods. Therefore, normal seasonal patterns in brood size of great, but not blue, tits appear to be disrupted by protracted food supplementation during the breeding season.

2.5.6. Applied importance

Many of my results of food supplementation are unexpected (i.e. smaller clutch and brood sizes of both species and lower hatching success of blue tits). However, there are striking similarities between the patterns in reproduction of blue and great tits that I report and those of conspecifics in urban habitats where food supplementation is common (Jones & Reynolds 2008; Robb *et al.* 2008a). For example, in urban habitats both species initiate clutches earlier than in non-urban ones and lay smaller clutches (reviewed in Chamberlain *et al.* 2009). Moreover, blue, but not great, tits might experience lower hatching success with increased urbanisation (TJEH *unpubl. data*).

The applicability of my findings to urban areas should, however, be treated with caution due to marked habitat differences. Furthermore, other factors in addition to supplementary feeding may influence reproductive parameters of birds in urban habitats (e.g.

temperature – Visser *et al.* 2009; pollution – Eeva *et al.* 1997; lower natural food availability – Perrins 1965). However, as discussed in Chapter One, I mimicked supplementation in gardens through numerous experimental steps, including supplementing a commercial garden bird food, providing food in a diffuse manner to replicate supplementation in individual gardens, and to species that commonly breed in UK gardens (Bland *et al.* 2004). Although logistically challenging, further research in urban/garden habitats (see also Jones & Reynolds 2008) would clearly be of value to explore the broader applicability of my findings.

As well as being prevalent in urban habitats, supplementation is also used to increase reproductive productivity of endangered species. Such supplementation is intentional, often protracted, occurs in the 'natural' breeding habitats of these species, and is often provided to passerines (e.g. stitchbird – Castro *et al.* 2003, Florida scrub jay – Schoech *et al.* 2008, Seychelles magpie-robin – Komdeur 1996). In these respects, my results are highly applicable. The concerning findings of my study suggest that new supplementation initiatives should only be implemented after smaller-scale feeding trials (see also Reynolds *et al*. 2004), especially if dealing with discrete populations since the effects of food supplementation can vary geographically (e.g. Schoech & Hahn 2008) and intraspecifically (e.g. Nager *et al.* 1997; Ramsay & Houston 1997; this study). Indeed, while food supplementation may have pronounced fitness benefits (e.g. Schoech *et al.* 2008), my study demonstrates that it may not be a panacea.

Chapter Three

SHORT-TERM GAINS: FOOD SUPPLEMENTATION INCREASES EGG SIZE BUT NOT NESTLING GROWTH IN BLUE AND GREAT TITS

3.1. Abstract

Egg size of birds can have pronounced positive influences on both nestling growth and survival, particularly early in the nestling phase. Food supplementation studies have examined whether egg size is constrained by food availability but have drawn mixed conclusions. A problem with many previous food supplementation studies is that egg size has been used as a surrogate for egg ‘quality’ (i.e. the nutritional content of the egg) even though the two can vary independently. Here, I examine the influence of food supplementation from pre-laying to post-fledging on egg size and composition, and on nestling growth of blue and great tits. Supplementation increased egg size significantly in great tits but the opposite was true in blue tits. However, in the latter the effect was extremely small and driven by a clutch size × dietary treatment interaction indicating that a negative relationship between egg and clutch size was reduced by food supplementation. Supplemented blue (2006 and 2008) and great (all years) tits had a significantly lower percentage of lipid, and higher percentage of protein, in the yolk than non-supplemented conspecifics. In one year, food supplementation significantly reduced the weight of lipid in the eggs of blue tits. However, the weight of egg components (shell, water, albumen, and yolk) and of macronutrients (lipid and protein) was predicted most significantly by egg size. Nestling growth did not differ significantly between dietary treatments in either species, suggesting that significant effects of food supplementation on egg size and composition, coupled with enhanced food availability during the nestling phase, had little influence on nestling development. These findings build upon those of previous food

supplementation studies and provide insight into effects of supplementation (e.g. advanced clutch initiation and reduced clutch size) presented in Chapter Two.

3.2. Introduction

Egg size can have a positive influence on nestling growth (e.g. Magrath 1992; Smith *et al.* 1995) and, to a lesser extent, on the survival of young to fledging (e.g. Bolton 1991; Blomqvist *et al.* 1997). Although such effects have not been shown in all studies (e.g. see Styrsky *et al.* 2000 and references therein), these substantial benefits suggest that many birds lay eggs that are sub-optimally small. Egg production is energetically and nutritionally demanding (Robbins 1981; Walsberg 1983) and, as such, it is often proposed that egg size is constrained by food availability. Food supplementation has provided support for this proposition. For example, blue tits (Ramsay & Houston 1997) and Florida scrub jays (Reynolds *et al.* 2003b) provided with high-protein supplements produce significantly larger eggs than non-supplemented conspecifics. However, other studies have found mixed (e.g. Källander & Karlsson 1993) or non-significant (Hochachka & Boag 1987) effects of food supplementation on egg size.

Egg size correlates positively with macronutrient (e.g. lipid and protein) content of eggs and, therefore, egg size is usually a good approximation of egg ‘quality’ (see Christians 2002 and references therein). However, the weight of egg components (e.g. yolk and albumen) and of macronutrient content are not necessarily related isometrically to changes in egg size (reviewed in Williams 1994). Thus, egg size as a surrogate for egg quality should be considered with some caution. This might be particularly important within the context of supplementary feeding. For example, Arnold *et al.* (1991) found that supplementation altered egg composition independently of egg size. He supplemented American coots with carbohydrate-rich corn suitable for lipogenesis that produced eggs with higher absolute and proportional lipid content than non-supplemented conspecifics. Such findings might be important in our understanding of the value of food supplementation to breeding birds. For example, in altricial species, such as blue and great tits, the lipid-rich yolk is not usually depleted fully at hatching and acts as a temporary food reserve in the yolk sac of newly-hatched nestlings (Perrins 1979; Rofstad & Sandvik 1987). In the altricial hooded crow *Corvus cornix* egg volume correlates positively with the weight of the yolk sac at hatching (Rofstad & Sandvik 1987) demonstrating a benefit of increased egg size post-hatching. Lipid in the yolk sac may promote nestling survival during a period of food scarcity early in the nestling phase (Schifferli 1973). In addition to lipid, other egg nutrients are also important. Nisbet (1978) suggested that egg protein, rather than lipid, was more important in determining the survival of common tern *Sterna hirundo* nestlings. Protein requirements of egg production form a greater proportion of the total protein requirements of laying females than the equivalent comparison with respect to lipid (reviewed in Meijer & Drent 1999). Therefore, food supplementation might increase protein components of the egg (e.g. Bolton *et al.* 1992). Calcium might also limit egg formation (reviewed in Reynolds *et al.* 2004) so food supplementation could also enhance the ability of birds to sequester calcium allowing higher quality (e.g. heavier) eggshells to be laid (e.g. Bolton *et al.* 1992). Finally, water is also an essential component of the egg and its pool size can be increased through food supplementation (e.g. Reynolds *et al.* 2003b).

Positive effects of food supplementation on egg size and composition, as outlined above, may have a positive influence on nestling growth, particularly early in the nestling phase (reviewed in Williams 1994). Moreover, continued food supplementation throughout the nestling phase should enhance nestling growth further given the substantial energetic and nutritional requirements of adults (Drent & Daan 1980) and young (Perrins 1979) during this period. Indeed, numerous food supplementation studies have found a positive association between nestling growth and supplementation (e.g. Crossner 1977; von Brömssen & Jansson 1980; Arcese & Smith 1988).

Here, I examine the influence of food supplementation on egg size, composition, and nestling growth in blue and great tits. Two supplements were provided: peanut cake (pre-laying to post-fledging) and mealworms (during the nestling phase). The provision of mealworms mimicked recommendations for live invertebrates to be supplemented in UK gardens during chick-rearing (e.g. RSPB 2006; CJ Wildlife 2009). I hypothesised that supplementation would increase egg size and the weight of four egg components (namely shell, water, albumen, and yolk), and of two macronutrients (namely lipid and protein). Finally, I hypothesised that food supplementation would enhance nestling growth and that this effect would be greatest on territories supplemented with mealworms.

3.3. Methods

3.3.1. Study site and experimental design

Please refer to Chapter Two (N.B. ‘feeders’ in the Methods of Chapter Two refer to the supplementation of only peanut cake).

3.3.2. Food supplementation

In each year, one treatment block received no supplementary food and no feeders were present (hereafter ‘control’), one treatment block received peanut cake (described in Chapter Two – hereafter ‘PC’), and the third treatment block received peanut cake and live mealworms (hereafter ‘PCMW’). Peanut cake was provided as described in Chapter Two.

Supplementation with mealworms commenced and ceased on a brood-by-brood basis. Mealworms were supplemented from the day of hatching in a particular box (considered throughout the thesis as day 0 of the nestling phase for a particular brood) to 18 days post-hatch (i.e. about the time of fledging – Perrins 1979) when the mealworm feeder for that particular nestbox was no longer replenished. Mealworms were provided in trays on pole-mounted feeders *c.* 5-8 m from the nestbox (see also Nilsson 1994) and feeders were replenished every other day with *c.* 15 g of live mealworms. The amount of mealworms eaten varied between nestboxes, but trays were not normally found empty. Treatments were rotated over the three years so that each treatment block received each dietary treatment once.

3.3.3. Breeding parameters

3.3.3.1. Egg size

Clutches were removed from a random sub-sample of nests in each year, with each egg weighed to the nearest 0.002 g using an electronic balance (Tanita, Tokyo, Japan). Weighing occurred two days after clutch completion (recorded as described in Chapter Two) to ensure that the female had completed the clutch. The weight of each egg was considered to be the fresh egg weight and this was used as a surrogate for egg size (egg weight and volume were highly related, and the term ‘egg size’ has been used by other authors to describe egg weight or volume – see Williams 1994; Christians 2002; Appendix Two). In this Chapter I use the term ‘egg size’ unless referring specifically to weight or volume (e.g. when citing the details of previous research or to provide clarity regarding details of my study). All eggs were returned to the nestbox, except at a subset of nests where one egg (selected at random) was collected under licence (Natural England 20062699; 20070694; 20080377) for composition analysis (see Section 3.3.3.2). Collected eggs were packaged in cotton wool and transported whole to the laboratory. In 2006 eggs were frozen, and in 2007 and 2008 refrigerated (see details in Section 3.3.4), after collection in the field and prior to composition analyses.

3.3.3.2. Egg composition

Collected eggs were hard-baked at 50-60 ºC so that the albumen and yolk solidified. Shell, albumen, and yolk components were separated by hand and dried at 50-60 ºC to constant weight (see also Nisbet 1978; Bolton *et al.* 1992). Water content was expressed as the difference between the fresh weight of the collected egg and the sum of the dry weights of the shell, albumen, and yolk fractions. Lipid in the egg is confined to the yolk (see Houston *et al.* 1995 and references therein). Therefore, to calculate the weight of lipid in the egg, I extracted lipid from the dry yolk using petroleum ether in a Soxhlet apparatus (see also Eldridge & Krapu 1988; Reynolds *et al.* 2003b) and weighed this amount. Since protein constitutes the majority of the non-shell components of the egg once water and lipid have been removed (Romanoff & Romanoff 1949), I considered the protein content of the egg to be the weight of the dry albumen plus the dry lipid-extracted yolk (see also Bolton *et al.* 1992; Flint & Grand 1999). The percentage of lipid in the yolk was calculated as the weight of the extracted lipid as a percentage of the weight of the dry yolk. The percentage of protein in the yolk was 100 minus the percentage of lipid in the yolk (also expressed as a percentage).

3.3.3.3. Nestling growth

I recorded nestling growth at a subset of nests in each year. Growth was measured as the weight, length of one tarsus (minimum tarsus length – Redfern & Clark 2001), total head length (Redfern & Clark 2001), and condition (expressed as the weight / (minimum tarsus length)^3 – Robb *et al.* 2008b) of *c.* two to three (depending on survivorship) nestlings selected at random per brood. Measures were taken at four time-points: three, six, nine, and 12 days after hatching. At the first time-point each randomly selected nestling was marked using nail varnish on a specific and identifiable claw(s) and these markings were re-applied as necessary at the second and third nest visit. Despite this approach allowing the potential for repeated-measures of the same nestlings on four successive nest visits, this did not occur for all broods due to constraints imposed by brood mortality and time. Therefore, the analyses presented compare growth between treatments at each time-point considered separately. For further details of this approach and information regarding growth curve analyses, see Appendix Three.

3.3.4. Filtering data

Only first clutches were considered in all analyses. In egg size and composition analyses, clutches were only included if active two days after clutch completion. Clutches with laying breaks of > two days were excluded and two dwarf eggs (small residual eggs that did not hatch in the population that I studied) were removed from analyses of egg size and composition due to anomalous and pronounced effects. Eggs that were collected in 2006 for composition analysis were stored in a domestic freezer after collection in the field. This caused many eggs to lyse so that the weight of egg components (shell, water, albumen, and yolk) and of macronutrients (lipid and protein) could not be calculated accurately. However, parts of the yolk were still intact, so the percentage of lipid and protein in the yolk could be assessed (I assumed that the distribution of lipid and protein throughout the yolk was uniform). In 2007 and 2008, eggs were stored in a domestic refrigerator after collection in the field so the above problems associated with freezing were avoided. Therefore, analyses of the weight of egg components and macronutrients have been restricted to 2007 and 2008 whereas analyses of the percentage of lipid and protein in the yolk were conducted in all years. On rare occasions an embryo was visible to the naked eye upon egg-dissection. These eggs were excluded from all analyses of egg composition. Nestling growth measures from the PCMW treatment were excluded on the few occasions that mealworm supplementation commenced after hatching.

3.3.5. Statistical analysis

All statistical analyses were carried out using PROC GLIMMIX in SAS (SAS Institute Inc. 2008) or Minitab 15 (Minitab 2007). Breeding parameters recorded prior to hatching (egg size and composition) were examined at two levels of dietary treatment (i.e. control and supplemented [PC] – as in Chapter Two), whereas nestling growth was examined at three levels of dietary treatment (i.e. control, PC, and PCMW). Random factors were specified as described in Chapter Two. Combined-year analyses were conducted except: (i) analyses of egg component and macronutrient weight of blue tits because of insufficient degrees of freedom after accounting for repeated measures on nestboxes (specified as a random factor) in combined-year analyses; and (ii) if the influence of supplementation differed significantly between years (year × dietary treatment: $P \leq 0.05$). Within-year analyses were carried out in both of these situations.

Analyses of egg weight and nestling growth were conducted on clutch and brood means, respectively. In analyses of egg weight, year (due to annual variation – Perrins & McCleery 1994), clutch initiation date (due to a seasonal increase in egg weight – Perrins 1970), and clutch size (due to a potential trade-off between clutch and egg size – You *et al.* 2009) were included as fixed factors. Clutch initiation date and clutch size were determined as described in Chapter Two. In analyses of the weight of egg components and macronutrients, year, clutch initiation date, and clutch size (all of which can influence egg composition – Arnold *et al.* 1991), and fresh egg weight (to control for differences in egg weight in the sample, and to test the significance of the relationship between the weight of eggs and that of either component or macronutrient) were included as fixed factors. In these analyses, the weight of egg components, macronutrients, and the fresh egg were $\log_{10}$ transformed following Ricklefs *et al.* (1978). One was added to these weights prior to logarithmic transformation to avoid negative characteristics of the transformed values (Sokal & Rohlf 1995). Analyses of the percentage of lipid and protein in the yolk included year (due to annual variation – Arnold *et al.* 1991), clutch initiation date (due to a seasonal decrease in the concentration of lipid – Bourgault *et al.* 2007), clutch size (due to a positive association between clutch size and macronutrient content – Arnold *et al.* 1991), and mean fresh egg weight (due to a decrease in the concentration of lipid with increased egg size – Ojanen 1983) as predictors. The percentage of lipid and protein in the yolk were converted into proportions, and proportions were arcsine square-root transformed prior to analysis (e.g. Poesel & Dabelsteen 2005). Analyses of nestling growth included year to account for annual variation in breeding conditions (Nager *et al.* 1997). Nestling weight usually declines with later hatching and in larger broods (Perrins 1965), so hatching date and brood size (determined as described in Chapter Two) were included as covariates in analyses of nestling growth. All analyses were fitted with normal error structures.

Covariate × dietary treatment interactions were tested as described in Chapter Two. In analyses of nestling growth, treatment block effects could not be controlled when testing the significance of year × dietary treatment interactions, since the two are co-linear. In these models, only box was specified as a random factor. As in Chapter Two, full results for each model are tabulated. Also see Chapter Two for details of figures that are plotted from statistical estimates. In this Chapter, the magnitudes of the effects of food supplementation are described by comparing means generated from statistical estimates.

3.4. Results

3.4.1. Egg size

Supplemented great tits laid significantly heavier eggs than non-supplemented conspecifics (mean increase: 0.04 g; $F_{1,44} = 5.09$, $P = 0.03$) (Fig. 3.1). The opposite was found in blue tits ($F_{1,38} = 6.59$, $P = 0.01$) (Fig. 3.1) but differences between dietary treatments were extremely small (mean difference: 0.001 g). In blue tits, egg weight decreased markedly with increased clutch size in control females, but less substantially in supplemented conspecifics (clutch size × dietary treatment: $F_{1,38} = 6.68$, $P = 0.01$) (Fig. 3.2). When this interaction term is removed

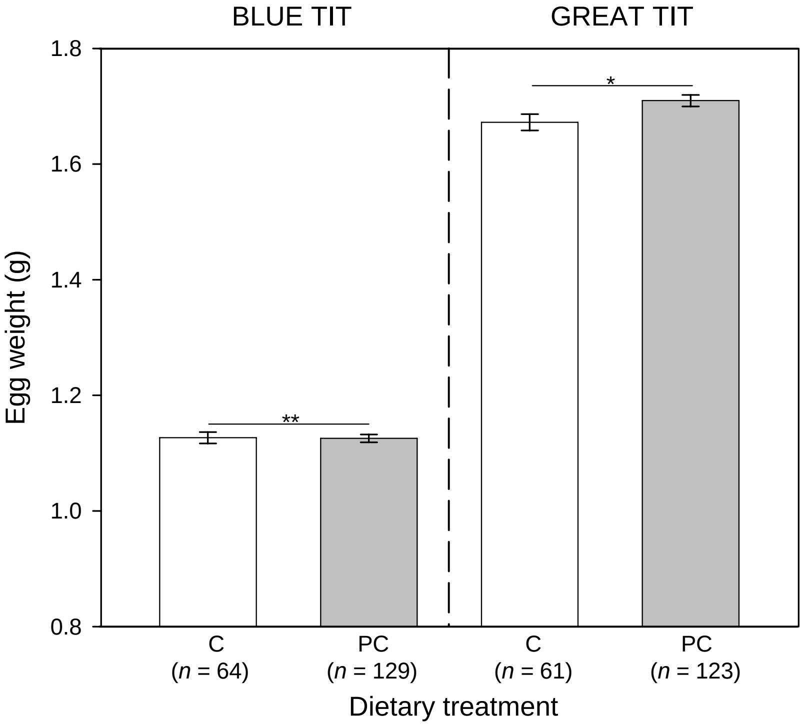

Figure 3.1. Egg weight (mean ± 1 SE from statistical estimates) of blue and great tits at Chaddesley Woods National Nature Reserve in 2006-2008. Dietary treatments: C = control (non-supplemented); PC = peanut cake. * = $P \leq 0.05$; ** = $P \leq 0.01$. Differences between dietary treatments in blue tits are marginal in absolute terms but were statistically significant because of a significant clutch size × dietary treatment interaction in the final model (see Figure 3.2 & Table 3.1). These differences in egg weight of blue tits between dietary treatments appear to be a statistical artefact rather than of biological significance. Number of clutches is in parentheses below dietary treatments. See Table 3.1 for statistical findings and see text for details.

Table 3.1. Models of egg parameters (*F* and associated *P* values) of blue (BT) and great (GT) tits at Chaddesley Woods National Nature Reserve in 2006-2008. The weights of egg components (shell, water, albumen, and yolk) and macronutrients (lipid and protein) were not available in 2006. Combined-year analyses have been conducted except BT egg component and macronutrient weights (insufficient degrees of freedom when controlling for repeated-measures on nestboxes between-years) and BT percentage of lipid and protein in yolk (significant year × dietary treatment interactions: $P = 0.05$). Fixed factors specified in each model are given with significant *P* values in bold text. Directions of significant effects are given: '+' and '-' denote significant positive and negative relationships, respectively, and 'NS' denotes non-significance ($P > 0.05$). Dietary treatments: C = control (non-supplemented); PC = peanut cake. See text for details.

Egg parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Egg weight	BT	2006-08	Dietary treatment	$F_{1,38} = 6.59$	**P = 0.01**	Probable statistical artefact, therefore an unreliable result – see Figure 3.1 and text for details
			Year	$F_{2,38} = 3.70$	**P = 0.03**	2006 = heavier; 2007 = lighter
			Clutch initiation date	$F_{1,38} = 0.33$	$P = 0.57$	NS
			Clutch size	$F_{1,38} = 10.70$	**P = 0.002**	-
			Clutch size × dietary treatment	$F_{1,38} = 6.68$	**P = 0.01**	C = negative association with clutch size; PC = no clear relationship with clutch size
	GT	2006-08	Dietary treatment	$F_{1,44} = 5.09$	**P = 0.03**	C= lighter; PC = heavier
			Year	$F_{2,44} = 0.10$	$P = 0.90$	NS
			Clutch initiation date	$F_{1,44} = 5.72$	**P = 0.02**	+
			Clutch size	$F_{1,44} = 0.77$	$P = 0.39$	NS
Shell weight	BT	2007	Dietary treatment	$F_{1,29} = 0.07$	$P = 0.80$	NS
			Clutch initiation date	$F_{1,29} = 2.73$	$P = 0.11$	NS
			Clutch size	$F_{1,29} = 3.59$	$P = 0.07$	NS
			Egg weight	$F_{1,29} = 37.57$	**P < 0.001**	+
		2008	Dietary treatment	$F_{1,28} = 8.87$	**P = 0.006**	C = lighter; PC = heavier
			Clutch initiation date	$F_{1,28} = 1.23$	$P = 0.28$	NS
			Clutch size	$F_{1,28} = 2.51$	$P = 0.12$	NS
			Egg weight	$F_{1,28} = 62.66$	**P < 0.001**	+
			Clutch size × dietary treatment	$F_{1,28} = 7.82$	**P = 0.009**	C = positive association with clutch size; PC = the opposite
	GT	2007-08	Dietary treatment	$F_{1,3} = 1.24$	$P = 0.35$	NS
			Year	$F_{1,3} = 0.17$	$P = 0.71$	NS
			Clutch initiation date	$F_{1,3} = 0.01$	$P = 0.92$	NS
			Clutch size	$F_{1,3} = 0.61$	$P = 0.49$	NS
			Egg weight	$F_{1,3} = 114.78$	**P = 0.002**	+
Water weight	BT	2007	Dietary treatment	$F_{1,29} = 0.12$	$P = 0.73$	NS
			Clutch initiation date	$F_{1,29} = 0.27$	$P = 0.61$	NS
			Clutch size	$F_{1,29} = 0.24$	$P = 0.62$	NS
			Egg weight	$F_{1,29} = 567.62$	**P < 0.001**	+

Table 3.1. continued

Egg parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Water weight	BT	2008	Dietary treatment	$F_{1,29} = 0.18$	$P = 0.67$	NS
			Clutch initiation date	$F_{1,29} = 0.70$	$P = 0.41$	NS
			Clutch size	$F_{1,29} = 0.26$	$P = 0.61$	NS
			Egg weight	$F_{1,29} = 827.46$	**$P < 0.001$**	+
	GT	2007-08	Dietary treatment	$F_{1,3} = 0.51$	$P = 0.53$	NS
			Year	$F_{1,3} = 1.14$	$P = 0.36$	NS
			Clutch initiation date	$F_{1,3} = 0.00$	$P = 1.00$	NS
			Clutch size	$F_{1,3} = 1.90$	$P = 0.26$	NS
			Egg weight	$F_{1,3} = 5791.59$	**$P < 0.001$**	+
Albumen weight	BT	2007	Dietary treatment	$F_{1,29} = 0.97$	$P = 0.33$	NS
			Clutch initiation date	$F_{1,29} = 1.12$	$P = 0.30$	NS
			Clutch size	$F_{1,29} = 0.99$	$P = 0.33$	NS
			Egg weight	$F_{1,29} = 7.73$	**$P = 0.01$**	+
		2008	Dietary treatment	$F_{1,29} = 2.18$	$P = 0.15$	NS
			Clutch initiation date	$F_{1,29} = 0.01$	$P = 0.93$	NS
			Clutch size	$F_{1,29} = 0.00$	$P = 0.98$	NS
			Egg weight	$F_{1,29} = 9.24$	**$P = 0.005$**	+
	GT	2007-08	Dietary treatment	$F_{1,3} = 5.69$	$P = 0.10$	NS
			Year	$F_{1,3} = 17.79$	**$P = 0.02$**	2007 = heavier; 2008 = lighter
			Clutch initiation date	$F_{1,3} = 3.94$	$P = 0.14$	NS
			Clutch size	$F_{1,3} = 12.64$	**$P = 0.04$**	+
			Egg weight	$F_{1,3} = 30.20$	**$P = 0.01$**	+
Yolk weight	BT	2007	Dietary treatment	$F_{1,29} = 1.26$	$P = 0.27$	NS
			Clutch initiation date	$F_{1,29} = 1.66$	$P = 0.21$	NS
			Clutch size	$F_{1,29} = 1.92$	$P = 0.18$	NS
			Egg weight	$F_{1,29} = 22.44$	**$P < 0.001$**	+
		2008	Dietary treatment	$F_{1,28} = 2.20$	$P = 0.15$	NS
			Clutch initiation date	$F_{1,28} = 0.08$	$P = 0.78$	NS
			Clutch size	$F_{1,28} = 0.06$	$P = 0.81$	NS
			Egg weight	$F_{1,28} = 0.03$	$P = 0.87$	NS
			Clutch initiation date × dietary treatment	$F_{1,28} = 4.14$	**$P = 0.05$**	C = seasonal increase; PC = the opposite
	GT	2007-08	Dietary treatment	$F_{1,3} = 2.85$	$P = 0.19$	NS
			Year	$F_{1,3} = 7.29$	$P = 0.07$	NS

Table 3.1. continued

Egg parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Yolk weight	GT	2007-08	Clutch initiation date	$F_{1,3} = 3.70$	$P = 0.15$	NS
			Clutch size	$F_{1,3} = 7.72$	$P = 0.07$	NS
			Egg weight	$F_{1,3} = 32.61$	**$P = 0.01$**	+
Percentage of lipid and protein in yolk	BT	2006	Dietary treatment	$F_{1,30} = 4.48$	**$P = 0.04$**	C = lipid: high, protein: low; PC = the opposite
			Clutch initiation date	$F_{1,30} = 0.63$	$P = 0.43$	NS
			Clutch size	$F_{1,30} = 0.01$	$P = 0.94$	NS
			Egg weight	$F_{1,30} = 0.01$	$P = 0.93$	NS
			Clutch size × dietary treatment	$F_{1,30} = 5.56$	**$P = 0.03$**	C = lipid: positive association with clutch size, protein: negative association with clutch size; PC = the opposite
		2007	Dietary treatment	$F_{1,27} = 2.47$	$P = 0.13$	NS
			Clutch initiation date	$F_{1,27} = 2.30$	$P = 0.14$	NS
			Clutch size	$F_{1,27} = 2.17$	$P = 0.15$	NS
			Egg weight	$F_{1,27} = 0.01$	$P = 0.93$	NS
		2008	Dietary treatment	$F_{1,31} = 5.47$	**$P = 0.03$**	C = lipid: high, protein: low; PC = the opposite
			Clutch initiation date	$F_{1,31} = 5.06$	**$P = 0.03$**	Lipid: -, protein: +
			Clutch size	$F_{1,31} = 0.23$	$P = 0.63$	NS
			Egg weight	$F_{1,31} = 1.27$	$P = 0.27$	NS
	GT	2006-08	Dietary treatment	$F_{1,13} = 11.02$	**$P = 0.006$**	C = lipid: high, protein: low; PC = the opposite
			Year	$F_{2,13} = 15.96$	**$P < 0.001$**	2006 = lipid: low, protein: high; 2007 = the opposite
			Clutch initiation date	$F_{1,13} = 3.01$	$P = 0.11$	NS
			Clutch size	$F_{1,13} = 1.22$	$P = 0.29$	NS
			Egg weight	$F_{1,13} = 0.16$	$P = 0.70$	NS
Lipid weight in egg	BT	2007	Dietary treatment	$F_{1,26} = 0.14$	$P = 0.71$	NS
			Clutch initiation date	$F_{1,26} = 1.28$	$P = 0.27$	NS
			Clutch size	$F_{1,26} = 2.46$	$P = 0.13$	NS
			Egg weight	$F_{1,26} = 5.90$	**$P = 0.02$**	+
		2008	Dietary treatment	$F_{1,27} = 8.42$	**$P = 0.007$**	C = heavier; PC = lighter
			Clutch initiation date	$F_{1,27} = 2.06$	$P = 0.16$	NS
			Clutch size	$F_{1,27} = 0.10$	$P = 0.75$	NS
			Egg weight	$F_{1,27} = 0.00$	$P = 0.95$	NS
	GT	2007-08	Dietary treatment	$F_{1,3} = 1.32$	$P = 0.33$	NS
			Year	$F_{1,3} = 0.45$	$P = 0.55$	NS
			Clutch initiation date	$F_{1,3} = 2.72$	$P = 0.20$	NS

Table 3.1. continued

Egg parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Lipid weight in egg	GT	2007-08	Clutch size	$F_{1,3} = 6.23$	$P = 0.09$	NS
			Egg weight	$F_{1,3} = 14.88$	$\mathbf{P = 0.03}$	+
Protein weight in egg	BT	2007	Dietary treatment	$F_{1,26} = 0.42$	$P = 0.52$	NS
			Clutch initiation date	$F_{1,26} = 0.92$	$P = 0.35$	NS
			Clutch size	$F_{1,26} = 1.40$	$P = 0.25$	NS
			Egg weight	$F_{1,26} = 21.53$	$\mathbf{P < 0.001}$	+
		2008	Dietary treatment	$F_{1,27} = 2.64$	$P = 0.12$	NS
			Clutch initiation date	$F_{1,27} = 0.24$	$P = 0.63$	NS
			Clutch size	$F_{1,27} = 0.03$	$P = 0.86$	NS
			Egg weight	$F_{1,27} = 15.40$	$\mathbf{P = 0.001}$	+
	GT	2007-08	Dietary treatment	$F_{1,3} = 2.47$	$P = 0.21$	NS
			Year	$F_{1,3} = 3.27$	$P = 0.17$	NS
			Clutch initiation date	$F_{1,3} = 1.91$	$P = 0.26$	NS
			Clutch size	$F_{1,3} = 7.99$	$P = 0.07$	NS
			Egg weight	$F_{1,3} = 70.68$	$\mathbf{P = 0.004}$	+

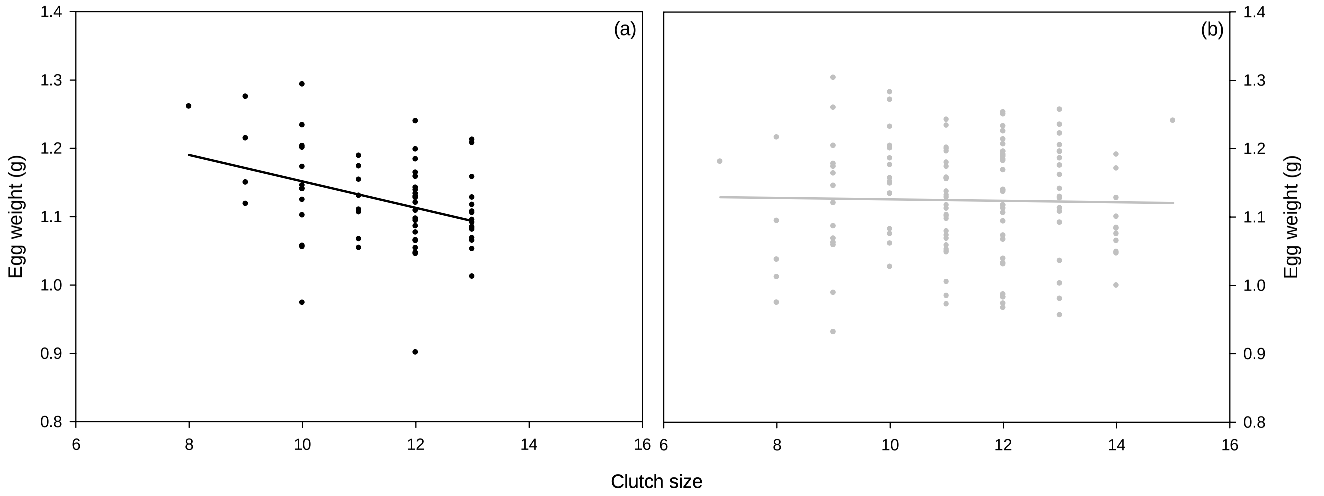

Figure. 3.2. Clutch size × dietary treatment interaction ($P = 0.01$) in the final model of analysis of the egg weight of blue tits at Chaddesley Woods National Nature Reserve in 2006-2008. Dietary treatments: control (a) and peanut cake (b). Number of clutches in each treatment is the same as for blue tits in Figure 3.1. See Table 3.1 for statistical findings and see text for details.

from the final model (Table 3.1), the effect of dietary treatment on egg weight of blue tits is not significant ($F_{1,39} = 0.00$, $P = 0.98$). See Table 3.1 for full model details of analyses of egg weight.

3.4.2. Egg composition

Supplementation of blue tits resulted in increased eggshell weight in 2008 (mean increase: 0.001 g; $F_{1,28} = 8.87$, $P = 0.006$), although the eggshells of supplemented females decreased in weight with increased clutch size, a pattern not found in control conspecifics (clutch size × dietary treatment: $F_{1,28} = 7.82$, $P = 0.009$). Eggshell weight was not influenced significantly by supplementation in blue tits in 2007 ($F_{1,29} = 0.07$, $P = 0.80$) or in great tits ($F_{1,3} = 1.24$, $P = 0.35$). Yolk weight increased seasonally in control, but decreased seasonally in supplemented, blue tits in 2008 (clutch initiation date × dietary treatment: $F_{1,28} = 4.14$, $P = 0.05$). However, supplementation did not influence the weight of water, albumen, or yolk in the eggs of either species (all *P*s > 0.05) (Table 3.1).

In 2006 and 2008 the yolks of control blue tits contained a significantly greater percentage of lipid, and a reduced percentage of protein, compared with those laid by supplemented conspecifics (mean differences in 2006: 4.3%; $F_{1,30} = 4.48$, $P = 0.04$; 2008: 5.9%; $F_{1,31} = 5.47$, $P = 0.03$) (Fig. 3.3). However, the influence of supplementation on the percentage of lipid and protein in the yolk was not consistent between years in blue tits (year × dietary treatment: $F_{2,5} = 5.78$, $P = 0.05$) and was not significant in 2007 ($F_{1,27} = 2.47$, $P = 0.13$) (Fig. 3.3). In 2006, clutch size of control blue tits associated positively with the percentage of lipid in the yolk, and negatively with the percentage of protein in the yolk, with the opposite found in supplemented conspecifics (clutch size × dietary treatment: $F_{1,30} = 5.56$, $P = 0.03$). The weight of lipid in the egg was significantly greater in control, compared with

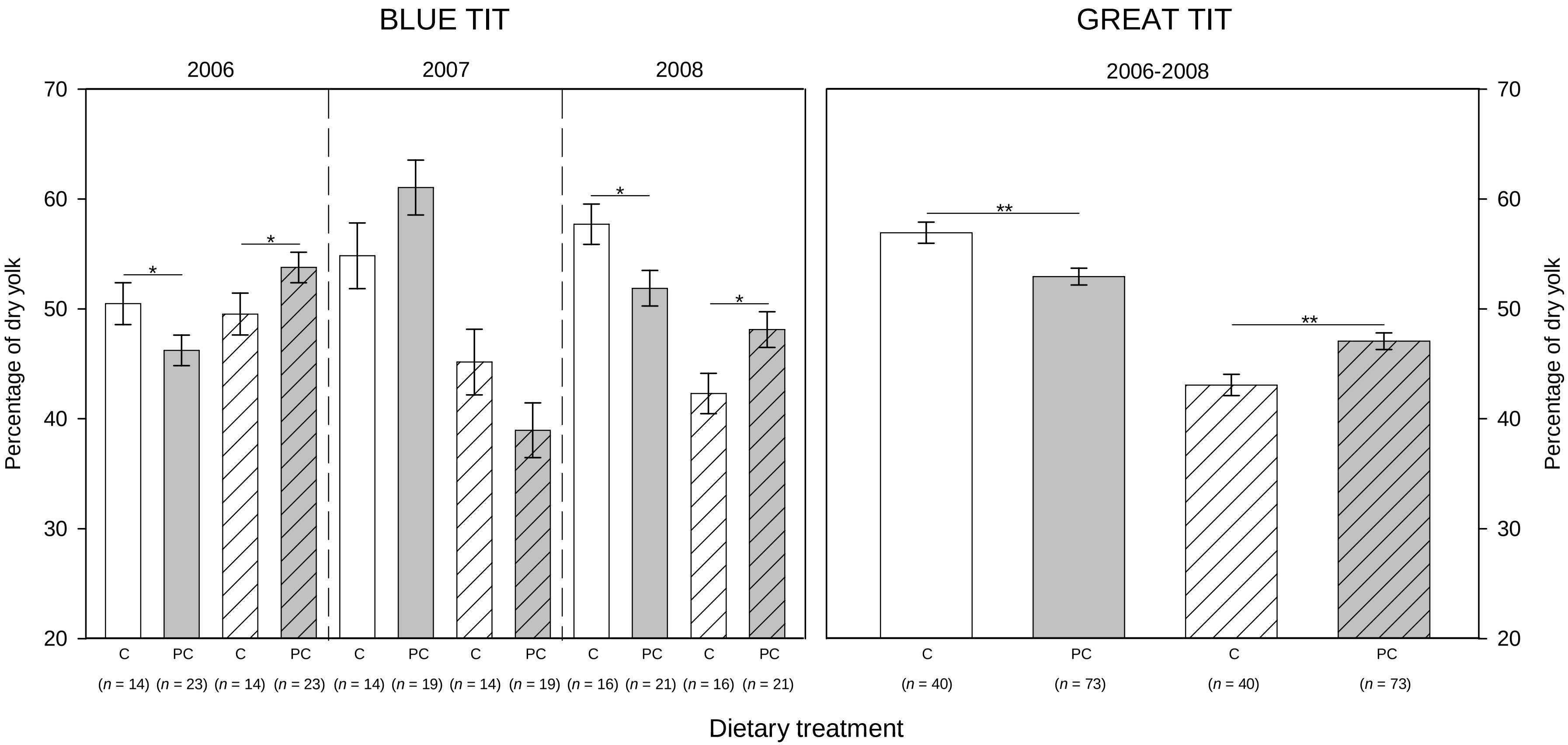

Figure 3.3. Percentage (mean ± 1 SE from statistical estimates) of lipid (non-hatched bars) and protein (hatched bars) in the dry yolk of blue and great tit eggs at Chaddesley Woods National Nature Reserve in 2006-2008. Separate years are presented in blue tits because of a significant year × dietary treatment interaction (lipid and protein: $P = 0.05$). See Figure 3.1 for explanations of dietary treatments. * = $P \leq 0.05$; ** = $P \leq 0.01$. Number of eggs is in parentheses below dietary treatments. See Table 3.1 for statistical findings and see text for details.

supplemented, blue tits in 2008 (mean increase: 0.006 g; $F_{1,27} = 8.42$, $P = 0.007$) but not in 2007 ($F_{1,26} = 0.14$, $P = 0.71$). The weight of protein in the eggs of blue tits did not differ significantly between dietary treatments (2007: $F_{1,26} = 0.42$, $P = 0.52$; 2008: $F_{1,27} = 2.64$, $P = 0.12$).

Yolks of control great tits contained a significantly greater percentage of lipid, and reduced percentage of protein, compared with those in eggs laid by supplemented conspecifics (mean differences: 4.0%; $F_{1,13} = 11.02$, $P = 0.006$) (Fig. 3.3). However, supplementation did not influence the weight of lipid ($F_{1,3} = 1.32$, $P = 0.33$) or protein ($F_{1,3} = 2.47$, $P = 0.21$) in the eggs of great tits. The weight of egg components (shell, water, albumen, and yolk) and of macronutrients (lipid and protein) was explained most significantly by egg weight in both species (Table 3.1). See Table 3.1 for full model details of analyses of egg composition.

3.4.3. Nestling growth

No significant differences were found in nestling weight, tarsus length, total head length, or condition between treatments in either species at three, six, nine, and 12 days after hatching (all *P*s > 0.05) (Fig. 3.4; Table 3.2). Dietary treatment appeared to influence the development of great tits 12 days after hatching (tarsus length: $F_{2,7} = 6.19$, $P = 0.03$; and condition: $F_{2,7} = 7.20$, $P = 0.02$), but pair-wise comparisons between dietary treatments were not significant (all *P*s > 0.05) (Fig. 3.4; Table 3.2). This was caused by a significant hatching date × dietary treatment interaction in both of these models (Table 3.2). Tarsus length increased with later hatching in great tits (Table 3.2), but this occurred most strongly in the PC treatment (hatching date × dietary treatment: $F_{2,7} = 5.57$, $P = 0.04$). However, this seasonal increase in tarsus length was not matched by a proportional increase in weight, so the condition of great

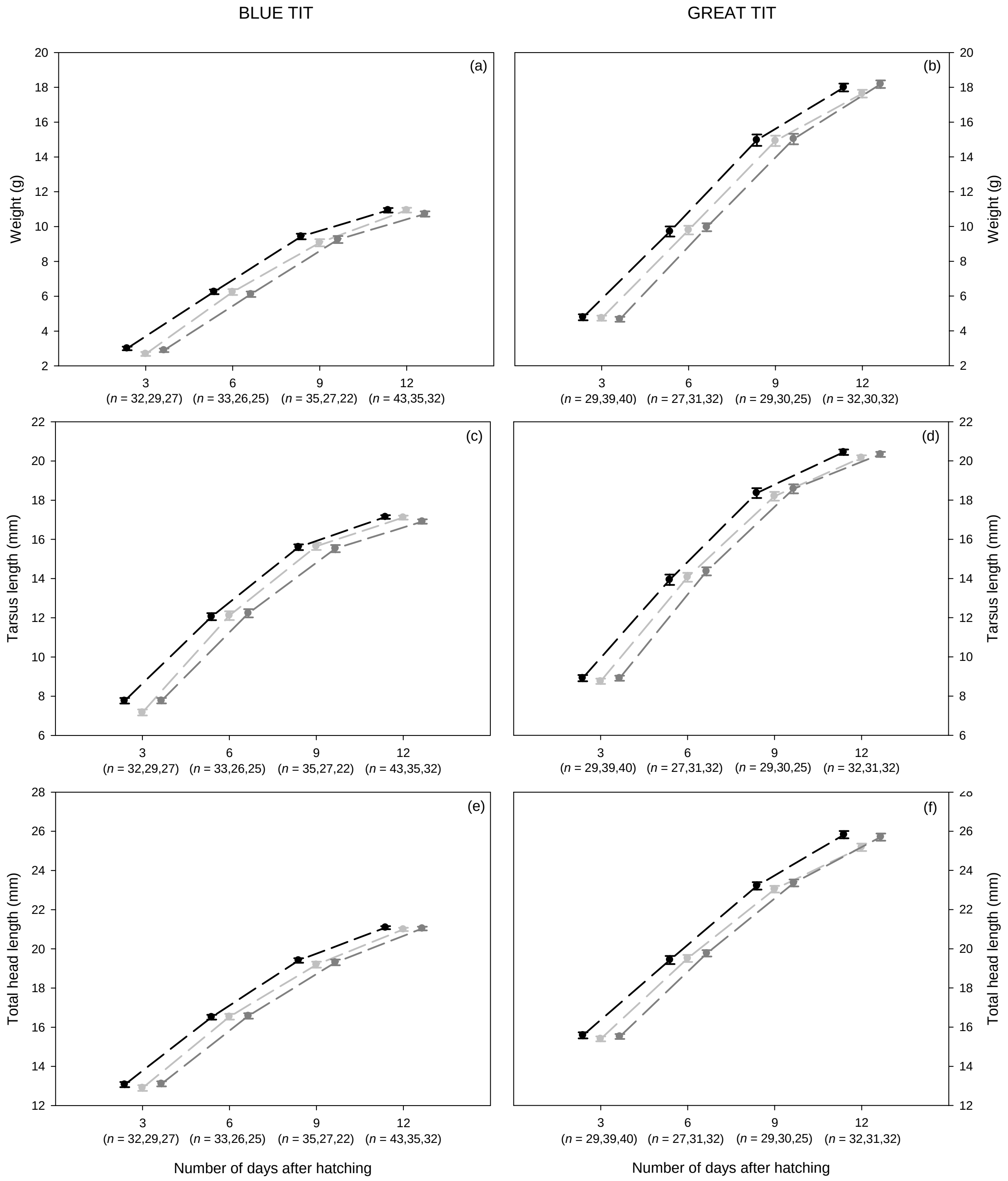

Figure 3.4. Weight (a,b), tarsus length (c,d), and total head length (e,f) (mean ± 1 SE from statistical estimates) of blue and great tit nestlings at three, six, nine, and 12 days after hatching at Chaddesley Woods National Nature Reserve in 2006-2008. Dietary treatments: control (non-supplemented) = black; peanut cake = light grey; peanut cake and mealworms = dark grey. Measures from different dietary treatments are offset on each day of measurement to enable visual comparison. Treatment differences were not significant at any time-point and for any measure. These findings should be considered alongside those regarding brood mortality (see Chapter Four) because differential brood mortality between treatments could have biased the relative 'quality' (e.g. weight, size) of nestlings that were still alive and could, therefore, be measured at the different time points shown above. Lines are dotted because the same broods were not always measured at each time-point. Number of broods is in parentheses below the number of days after hatching. See Table 3.2 for statistical findings and see text for details.

Table 3.2. Models of growth measures (*F* and associated *P* values) of blue (BT) and great (GT) tit nestlings at Chaddesley Woods National Nature Reserve in 2006-2008. Fixed factors specified in each model are given with significant *P* values in bold text. Least squares means tests (adjusted for multiple comparisons via the Tukey method) are given where a significant effect of dietary treatment was found: C = control (non-supplemented); PC = peanut cake; PCMW = peanut cake and mealworms. Directions of significant effects are given: '+' and '-' denote significant positive and negative relationships, respectively, and 'NS' denotes non-significance ($P > 0.05$). See text for details.

						Least squares means (*P* values)			
Growth measures	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**C *vs.* PC**	**C *vs.* PCMW**	**PC *vs.* PCMW**	**Direction**
Nestling weight three days after hatching	BT	2006-08	Dietary treatment	$F_{2,5} = 1.84$	$P = 0.25$				NS
			Year	$F_{2,5} = 0.89$	$P = 0.47$				NS
			Hatch date	$F_{1,5} = 0.41$	$P = 0.55$				NS
			Brood size	$F_{1,5} = 0.37$	$P = 0.57$				NS
	GT	2006-08	Dietary treatment	$F_{2,10} = 0.14$	$P = 0.87$				NS
			Year	$F_{2,10} = 1.44$	$P = 0.28$				NS
			Hatch date	$F_{1,10} = 10.16$	**$P = 0.01$**				+
			Brood size	$F_{1,10} = 4.12$	$P = 0.07$				NS
Nestling weight six days after hatching	BT	2006-08	Dietary treatment	$F_{2,3} = 0.28$	$P = 0.77$				NS
			Year	$F_{2,3} = 0.76$	$P = 0.54$				NS
			Hatch date	$F_{1,3} = 2.45$	$P = 0.22$				NS
			Brood size	$F_{1,3} = 3.16$	$P = 0.17$				NS
	GT	2006-08	Dietary treatment	$F_{2,3} = 0.24$	$P = 0.80$				NS
			Year	$F_{2,3} = 6.44$	$P = 0.08$				NS
			Hatch date	$F_{1,3} = 8.43$	$P = 0.06$				NS
			Brood size	$F_{1,3} = 19.52$	**$P = 0.02$**				-
Nestling weight nine days after hatching	BT	2006-08	Dietary treatment	$F_{2,5} = 0.92$	$P = 0.46$				NS
			Year	$F_{2,5} = 0.27$	$P = 0.77$				NS
			Hatch date	$F_{1,5} = 0.00$	$P = 0.98$				NS
			Brood size	$F_{1,5} = 2.88$	$P = 0.15$				NS
	GT	2006-08	Dietary treatment	$F_{2,3} = 0.03$	$P = 0.97$				NS
			Year	$F_{2,3} = 16.34$	**$P = 0.02$**				2007 = heaviest; 2008 = lightest
			Hatch date	$F_{1,3} = 10.61$	**$P = 0.05$**				+
			Brood size	$F_{1,3} = 24.43$	**$P = 0.02$**				-
Nestling weight 12 days after hatching	BT	2006-08	Dietary treatment	$F_{2,7} = 0.75$	$P = 0.51$				NS
			Year	$F_{2,7} = 8.53$	**$P = 0.01$**				2006 = heaviest; 2007 = lightest
			Hatch date	$F_{1,7} = 10.07$	**$P = 0.02$**				-
			Brood size	$F_{1,7} = 3.16$	$P = 0.12$				NS

Table 3.2. continued

Growth measures	Sp.	Year	Fixed factor	F	P	Least squares means (P values)			Direction
						C *vs.* PC	C *vs.* PCMW	PC *vs.* PCMW	
Nestling weight 12 days after hatching	GT	2006-08	Dietary treatment	$F_{2,9} = 1.64$	$P = 0.25$				NS
			Year	$F_{2,9} = 1.72$	$P = 0.23$				NS
			Hatch date	$F_{1,9} = 1.53$	$P = 0.25$				NS
			Brood size	$F_{1,9} = 16.88$	**P = 0.003**				-
Nestling tarsus length three days after hatching	BT	2006-08	Dietary treatment	$F_{2,5} = 5.11$	$P = 0.06$				NS
			Year	$F_{2,5} = 4.66$	$P = 0.07$				NS
			Hatch date	$F_{1,5} = 2.04$	$P = 0.21$				NS
			Brood size	$F_{1,5} = 0.37$	$P = 0.57$				NS
	GT	2006-08	Dietary treatment	$F_{2,10} = 0.44$	$P = 0.66$				NS
			Year	$F_{2,10} = 4.68$	**P = 0.04**				2007 = longest; 2008 = shortest
			Hatch date	$F_{1,10} = 20.06$	**P = 0.001**				+
			Brood size	$F_{1,10} = 3.22$	$P = 0.10$				NS
Nestling tarsus length six days after hatching	BT	2006-08	Dietary treatment	$F_{2,3} = 0.20$	$P = 0.83$				NS
			Year	$F_{2,3} = 0.66$	$P = 0.58$				NS
			Hatch date	$F_{1,3} = 0.43$	$P = 0.56$				NS
			Brood size	$F_{1,3} = 0.18$	$P = 0.70$				NS
	GT	2006-08	Dietary treatment	$F_{2,3} = 0.93$	$P = 0.49$				NS
			Year	$F_{2,3} = 4.25$	$P = 0.13$				NS
			Hatch date	$F_{1,3} = 10.03$	**P = 0.05**				+
			Brood size	$F_{1,3} = 12.68$	**P = 0.04**				-
Nestling tarsus length nine days after hatching	BT	2006-08	Dietary treatment	$F_{2,5} = 0.12$	$P = 0.89$				NS
			Year	$F_{2,5} = 1.75$	$P = 0.27$				NS
			Hatch date	$F_{1,5} = 0.40$	$P = 0.55$				NS
			Brood size	$F_{1,5} = 0.28$	$P = 0.62$				NS
	GT	2006-08	Dietary treatment	$F_{2,3} = 0.71$	$P = 0.56$				NS
			Year	$F_{2,3} = 9.45$	**P = 0.05**				2006 = longest; 2008 = shortest
			Hatch date	$F_{1,3} = 6.71$	$P = 0.08$				NS
			Brood size	$F_{1,3} = 16.65$	**P = 0.03**				-
Nestling tarsus length 12 days after hatching	BT	2006-08	Dietary treatment	$F_{2,7} = 1.48$	$P = 0.29$				NS
			Year	$F_{2,7} = 3.78$	$P = 0.08$				NS
			Hatch date	$F_{1,7} = 1.38$	$P = 0.28$				NS
			Brood size	$F_{1,7} = 0.00$	$P = 0.99$				NS

Table 3.2. continued

						Least squares means (P values)			
Growth measures	**Sp.**	**Year**	**Fixed factor**	F	P	**C *vs.* PC**	**C *vs.* PCMW**	**PC *vs.* PCMW**	**Direction**
Nestling tarsus length 12 days after hatching	GT	2006-08	Dietary treatment	$F_{2,7}$ = 6.19	**P = 0.03**	P = 0.36	P = 0.83	P = 0.62	Pairwise comparisons NS
			Year	$F_{2,7}$ = 2.19	P = 0.18				NS
			Hatch date	$F_{1,7}$ = 11.63	**P = 0.01**				+
			Brood size	$F_{1,7}$ = 4.05	P = 0.08				NS
			Hatch date × dietary treatment	$F_{2,7}$ = 5.57	**P = 0.04**				PC = steep seasonal increase; C and PCMW = less steep
Nestling total head length three days after hatching	BT	2006-08	Dietary treatment	$F_{2,5}$ = 0.67	P = 0.55				NS
			Year	$F_{2,5}$ = 3.01	P = 0.14				NS
			Hatch date	$F_{1,5}$ = 0.02	P = 0.90				NS
			Brood size	$F_{1,5}$ = 0.95	P = 0.38				NS
	GT	2006-08	Dietary treatment	$F_{2,10}$ = 0.39	P = 0.69				NS
			Year	$F_{2,10}$ = 0.88	P = 0.45				NS
			Hatch date	$F_{1,10}$ = 6.40	**P = 0.03**				+
			Brood size	$F_{1,10}$ = 0.98	P = 0.35				NS
Nestling total head length six days after hatching	BT	2006-08	Dietary treatment	$F_{2,3}$ = 0.06	P = 0.95				NS
			Year	$F_{2,3}$ = 1.13	P = 0.43				NS
			Hatch date	$F_{1,3}$ = 1.50	P = 0.31				NS
			Brood size	$F_{1,3}$ = 0.35	P = 0.60				NS
	GT	2006-08	Dietary treatment	$F_{2,3}$ = 0.97	P = 0.47				NS
			Year	$F_{2,3}$ = 4.75	P = 0.12				NS
			Hatch date	$F_{1,3}$ = 10.66	**P = 0.05**				+
			Brood size	$F_{1,3}$ = 10.18	**P = 0.05**				-
Nestling total head length nine days after hatching	BT	2006-08	Dietary treatment	$F_{2,5}$ = 0.60	P = 0.58				NS
			Year	$F_{2,5}$ = 3.45	P = 0.11				NS
			Hatch date	$F_{1,5}$ = 0.92	P = 0.38				NS
			Brood size	$F_{1,5}$ = 0.01	P = 0.93				NS
	GT	2006-08	Dietary treatment	$F_{2,3}$ = 0.86	P = 0.51				NS
			Year	$F_{2,3}$ = 7.14	P = 0.07				NS
			Hatch date	$F_{1,3}$ = 9.89	**P = 0.05**				+
			Brood size	$F_{1,3}$ = 9.14	P = 0.06				NS

Table 3.2. continued

						Least squares means (*P* values)			
Growth measures	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**C *vs.* PC**	**C *vs.* PCMW**	**PC *vs.* PCMW**	**Direction**
Nestling total head length 12 days after hatching	BT	2006-08	Dietary treatment	$F_{2,7} = 0.26$	$P = 0.78$				NS
			Year	$F_{2,7} = 7.56$	$\mathbf{P = 0.02}$				2007 = shortest; 2008 = longest
			Hatch date	$F_{1,7} = 4.59$	$P = 0.07$				NS
			Brood size	$F_{1,7} = 0.23$	$P = 0.65$				NS
	GT	2006-08	Dietary treatment	$F_{2,9} = 3.24$	$P = 0.09$				NS
			Year	$F_{2,9} = 0.04$	$P = 0.96$				NS
			Hatch date	$F_{1,9} = 1.03$	$P = 0.34$				NS
			Brood size	$F_{1,9} = 2.91$	$P = 0.12$				NS
Nestling condition three days after hatching	BT	2006-08	Dietary treatment	$F_{2,5} = 4.98$	$P = 0.06$				NS
			Year	$F_{2,5} = 7.55$	$\mathbf{P = 0.03}$				2006 = lowest; 2008 = highest
			Hatch date	$F_{1,5} = 1.30$	$P = 0.31$				NS
			Brood size	$F_{1,5} = 0.00$	$P = 0.96$				NS
	GT	2006-08	Dietary treatment	$F_{2,10} = 2.15$	$P = 0.17$				NS
			Year	$F_{2,10} = 10.67$	$\mathbf{P = 0.003}$				2007 = lowest; 2008 = highest
			Hatch date	$F_{1,10} = 22.68$	$\mathbf{P = 0.001}$				-
			Brood size	$F_{1,10} = 0.52$	$P = 0.49$				NS
Nestling condition six days after hatching	BT	2006-08	Dietary treatment	$F_{2,3} = 0.73$	$P = 0.55$				NS
			Year	$F_{2,3} = 2.13$	$P = 0.27$				NS
			Hatch date	$F_{1,3} = 0.00$	$P = 0.98$				NS
			Brood size	$F_{1,3} = 0.73$	$P = 0.45$				NS
	GT	2006-08	Dietary treatment	$F_{2,3} = 1.40$	$P = 0.37$				NS
			Year	$F_{2,3} = 2.57$	$P = 0.22$				NS
			Hatch date	$F_{1,3} = 8.70$	$P = 0.06$				NS
			Brood size	$F_{1,3} = 3.42$	$P = 0.16$				NS
Nestling condition nine days after hatching	BT	2006-08	Dietary treatment	$F_{2,5} = 1.24$	$P = 0.36$				NS
			Year	$F_{2,5} = 3.02$	$P = 0.14$				NS
			Hatch date	$F_{1,5} = 0.28$	$P = 0.62$				NS
			Brood size	$F_{1,5} = 5.25$	$P = 0.07$				NS
	GT	2006-08	Dietary treatment	$F_{2,3} = 0.83$	$P = 0.52$				NS
			Year	$F_{2,3} = 5.06$	$P = 0.11$				NS
			Hatch date	$F_{1,3} = 1.83$	$P = 0.27$				NS
			Brood size	$F_{1,3} = 3.57$	$P = 0.16$				NS

Table 3.2. continued

						Least squares means (*P* values)			
Growth measures	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**C *vs.* PC**	**C *vs.* PCMW**	**PC *vs.* PCMW**	**Direction**
Nestling condition 12 days after hatching	BT	2006-08	Dietary treatment	$F_{2,7} = 0.35$	$P = 0.71$				NS
			Year	$F_{2,7} = 0.55$	$P = 0.60$				NS
			Hatch date	$F_{1,7} = 3.01$	$P = 0.13$				NS
			Brood size	$F_{1,7} = 2.40$	$P = 0.17$				NS
	GT	2006-08	Dietary treatment	$F_{2,7} = 7.20$	$\boldsymbol{P = 0.02}$	$P = 0.65$	$P = 0.65$	$P = 1.00$	Pairwise comparisons NS
			Year	$F_{2,7} = 0.82$	$P = 0.48$				NS
			Hatch date	$F_{1,7} = 8.58$	$\boldsymbol{P = 0.02}$				-
			Brood size	$F_{1,7} = 0.23$	$P = 0.65$				NS
			Hatch date × dietary treatment	$F_{2,7} = 6.83$	$\boldsymbol{P = 0.02}$				PC = steep seasonal decrease; C and PCMW = less steep

tit nestlings 12 days after hatching decreased throughout the season, occurring most strongly in the PC treatment (hatching date × dietary treatment: $F_{2,7} = 6.83$, $P = 0.02$). See Table 3.2 for full model details of analyses of nestling growth.

3.5. Discussion

As hypothesised, food supplementation increased egg size, but this was only found in great tits (Fig. 3.1). The opposite was found in blue tits (Fig. 3.1), but this was caused by a clutch size × dietary treatment interaction that revealed that food supplementation reduced the negative association between clutch and egg size in this species (Fig. 3.2; Table 3.1). Supplemented blue tits produced significantly heavier eggshells than non-supplemented controls in 2008, but the weight of water, albumen, yolk, and protein in the eggs of both species did not differ significantly between treatments (Table 3.1). The yolks of control blue (2006 and 2008) and great (2006-2008) tits contained a significantly higher percentage of lipid, and a reduced percentage of protein, compared with those in eggs laid by supplemented conspecifics (Fig. 3.3). Contrary to my hypotheses, eggs of control blue tits contained significantly more lipid than those of supplemented females, but only in one year (Table 3.1). I found no support for my hypothesis that food supplementation would enhance nestling growth (Fig. 3.4; Table 3.2). I discuss these results within the context of previous studies and findings presented in Chapter Two.

3.5.1. Egg size

Ramsay and Houston (1997) found that blue tits provided with a high-protein supplement increased egg size significantly, but most previous studies of blue and great tits have found no significant effect of food supplementation on egg size (Nilsson & Svensson 1993a,b; Nilsson

1994; Nager *et al.* 1997; Ramsay & Houston 1998). Similarly, in a review across multiple families of birds, Christians (2002) reported that 64% of studies found no significant effect of food supplementation on egg size. To the best of my knowledge, my study is the first to demonstrate a positive influence of food supplementation on egg size of great tits (Fig. 3.1). This finding was notable because peanut cake is lipid-rich but protein-poor (see details in Chapter Two). Florida scrub jays (Reynolds *et al.* 2003b), blue tits (Ramsay & Houston 1997), and zebra finches (Williams 1996) only increased egg size when provided with protein-rich, rather than with lipid-rich, supplements. Therefore, it is probable that egg size of great tits in my study was either constrained energetically, or that peanut cake enabled supplemented great tits to spend longer sequestering natural foods rich in protein, or in specific micronutrients (e.g. see Bolton *et al.* 1992), compared with non-supplemented conspecifics. Dietary intake between treatments is examined in Chapter Five.

In blue tits, there was an apparent trade-off between clutch and egg size that was reduced by food supplementation (Fig. 3.2; Table 3.1). Such a trade-off is not well established (Christians 2002; but see You *et al.* 2009) but appeared to be strong in blue, but not great, tits in the population that I studied (Table 3.1). This trade-off might be caused by a finite amount of nutrients available for egg production (Smith & Fretwell 1974). Therefore, food supplementation should ameliorate such a trade-off (e.g. Fig. 3.2) through enrichment of the foraging environment. Given that control blue tits appeared to incur greater cost of increased clutch size through reduced egg size than supplemented conspecifics (Fig. 3.2), it is surprising that supplemented blue tits laid smaller clutches than controls (Chapter Two). Egg size was significantly larger in control, compared with supplemented, blue tits, but these differences were almost imperceptible (Fig. 3.1). Indeed, when the significant clutch size × dietary treatment interaction was removed from the final model of egg weight in blue tits (Fig. 3.2;

Table 3.1), differences between treatments were far from significant. Therefore, the difference in egg size between dietary treatments in blue tits (Fig. 3.1) appears to be a statistical artefact rather than having a biological foundation.

3.5.2. Egg composition

In 2008, supplemented blue tits laid eggs with significantly heavier shells than non-supplemented conspecifics (Table 3.1). Increased eggshell weight as a consequence of food supplementation has also been found in lesser black-backed gulls (Bolton *et al.* 1992). Peanut cake is not especially rich in calcium (only 1.3% of its fresh weight is inorganic matter – CJ Wildlife pers. comm.) so it is likely that in 2008 this supplement enabled blue tits to sequester calcium from natural food sources more efficiently than control birds. However, it is unclear why food supplementation did not increase eggshell weight of blue tits in 2007, or of great tits in any years of the study (Table 3.1).

Water content did not increase as a consequence of food supplementation in either species (Table 3.1). Reynolds *et al.* (2003b) found that Florida scrub jays supplemented with a high-protein diet incorporated a greater quantity of water into eggs than non-supplemented conspecifics. However, unlike blue and great tits in the UK, this species breeds in arid conditions in which the risk of dehydration of eggs and nestlings is likely to be increased (TJEH pers. obs.). Therefore, it is less surprising that food supplementation did not increase the water content of eggs in my study.

Albumen weight did not increase significantly as a consequence of food supplementation in either species (Table 3.1; also found in Bolton *et al.* 1992). Approximately two-thirds of the protein for the developing embryo is found in the albumen (Romanoff & Romanoff 1949) and, therefore, it is unsurprising that food supplementation did not increase the protein content of the eggs of either species (Table 3.1; also found in Arnold *et al.* 1991). However, supplementation did increase the percentage of protein in the yolk of both species significantly (in two of three years in blue tits – Fig. 3.3). This finding has parallels with Bolton *et al.* (1992) who found that the provision of a protein-rich supplement increased the amount of protein, but not lipid, in the yolk of lesser black-backed gulls. In Chapter Two I suggested that insufficient protein sequestration might have driven reduced clutch sizes of supplemented females. On this evidence, however, this explanation appears unlikely.

The percentage of lipid in the yolks of blue and great tits decreased significantly as a result of food supplementation (in two of three years in blue tits – Fig. 3.3). Indeed, in 2008, supplemented blue tits produced eggs with significantly less lipid content than non-supplemented conspecifics (Table 3.1). To the best of my knowledge, these findings are unique in any avian species. For example, Arnold *et al.* (1991) demonstrated that American coots supplemented with a corn-based diet produced eggs with higher absolute and proportional lipid content compared with non-supplemented conspecifics, whereas Eldridge and Krapu (1988) found that the concentration of lipid in the yolks of mallards *Anas platyrhynchos* did not differ significantly between sibling pairs provided with a high or low-protein diet.

Despite some significant effects of dietary treatment on egg composition (Fig. 3.3; Table 3.1), the most consistent predictor of the weight of egg components and macronutrients was egg size (see ‘egg weight’ as a fixed factor in Table 3.1). Ojanen (1983) found that egg size correlated positively with the weight of eggshell, albumen, yolk, and lipid of great tit eggs, with each of these relationships isometric except for eggshell. It appears, therefore, that the most important effect of food supplementation on egg quality was mediated through an influence on egg size (Figs 3.1 & 3.2; Table 3.1).

3.5.3. Nestling growth

Although food supplementation commonly increases nestling growth rate (57% of studies reviewed in Robb *et al.* 2008a), studies of blue and great tits have usually found no significant effect (e.g. Clamens & Isenmann 1989; Ramsay & Houston 1997,1998; Grieco 2003; this study; but see Svensson & Nilsson 1995; Rytkönen & Orell 2001). In many of these studies (e.g. Clamens & Isenmann 1989; Ramsay & Houston 1997,1998), supplements were withdrawn prior to hatching so a positive influence on nestling growth was perhaps less likely. However, I continued food supplementation throughout the nestling phase and included the provision of mealworms during chick-rearing. Although the latter is recommended in UK gardens to 'help' adults feed nestlings (CJ Wildlife 2009), I found no significant positive influence of mealworm or peanut cake supplementation on nestling growth of either species (Fig. 3.4). Therefore, while it remains possible that food supplementation facilitated brood provisioning (e.g. more time for breeding adults to increase prey selectivity – Grieco 2001), any such benefit did not manifest itself in enhanced nestling development (Fig. 3.4).

Supplementation not only increased food availability during the nestling phase, it also increased egg size of great tits (Fig. 3.1). In this species, egg size correlates positively with hatchling weight, and young hatched from heavier eggs grow more rapidly in the period from hatching to 10 days post-hatch than conspecifics hatched from lighter eggs (Schifferli 1973). Since the last growth measures that I recorded were 12 days post-hatch, it is surprising that great tit nestlings on supplemented territories were not larger than control conspecifics (Fig. 3.4). A possible explanation is that the increase in egg size of great tits as a result of supplementation was too small to be detected in the nestling phase. Indeed, the mean egg size of supplemented great tits was only 2.2% larger than controls (Fig. 3.1). This increase was smaller than that reported in any of the nine comparable studies reviewed in Christians (2002) and was probably too small to have had a lasting biological effect. Indeed, Ramsay and Houston (1997) found that blue tits on a high-protein diet increased egg volume by *c.* 7% compared with non-supplemented conspecifics, but recorded no significant difference in nestling growth between treatments.

Egg composition might have influenced nestling growth. For example, increased eggshell weight (e.g. supplemented blue tits in 2008 – Table 3.1) could enable greater skeletal mineralisation of the embryo (Reynolds *et al.* 2004) potentially causing hatchlings to be larger. Duncan (1988) found that the protein fraction of the yolk (the percentage of which increased significantly as a result of supplementation in my study – Fig. 3.3) in the yolk sac of duckling northern pintails *Anas acuta* was an important resource for growth. However, northern pintails produce precocial, rather than altricial, young so extrapolation of findings recorded in this species to blue and great tits should be considered with caution. Moreover, since the most consistent predictor of the weight of egg components and macronutrients in my study was egg size (Table 3.1; discussed in Section 3.5.2), any influence of egg composition on nestling development was probably linked inextricably to egg size. As discussed, differences in egg size between dietary treatments (e.g. great tits – Fig. 3.1) appeared to have no carry-over effects on nestling growth (Fig. 3.4).

Increased nestling growth of blue and great tits enhances the survival of young both pre and post-fledging (Perrins 1979; Monrós *et al.* 2002). Given these fitness benefits, it is surprising that nestling growth was not enhanced by food supplementation in my study (Fig. 3.4). It is possible that natural food availability was not limiting during the nestling phase and, therefore, supplements contributed little to the foraging environment. Indeed, oak woodland is the most productive breeding habitat of both species in the UK (Perrins 1965), not least because natural foods with which to feed young (e.g. caterpillars) are abundant (Perrins 1979). Therefore, in habitats that are less rich with natural invertebrates (e.g. urban areas – Perrins 1979; Schmidt & Steinbach 1983), supplements such as mealworms could have a positive influence on nestling growth. This possibility is important with respect to food supplementation in gardens, and requires further investigation. In Chapter Four I examine the availability of caterpillars between treatments while in Chapter Five I investigate the intake of supplementary and natural foods by adults and nestlings.

3.5.4. General discussion and conclusions

Egg size was increased by food supplementation in great tits (Fig. 3.1), but the magnitude of this effect was small compared with previous food supplementation studies. Egg size is highly repeatable within-individuals and is more heritable than both clutch initiation date and clutch size, so a small effect-size with regard to supplementation is not unusual (reviewed in Christians 2002). Egg composition might be more plastic than egg size (Bourgault *et al.* 2007) but, despite some significant differences in egg composition between dietary treatments (Fig. 3.3; Table 3.1), the most significant predictor of the weight of egg components and macronutrients was egg size (Table 3.1).

Despite peanut cake being lipid-rich, the percentage of lipid in the yolks of both species was reduced significantly by its supplementation (Fig. 3.3). Moreover, in one year, supplemented blue tits had significantly less lipid in their eggs than non-supplemented conspecifics (Table 3.1). This suggests that peanut cake might not have been used heavily by supplemented blue and great tits during egg formation. It also questions a recent suggestion by Bourgault *et al.* (2007) that the egg composition of tits could be diagnostic of their foraging environment during reproduction. Indeed, a counter-hypothesis is that females should invest less in egg nutrients (e.g. lipid) that are readily available in the environment in which nestlings will be raised.

Nestling growth did not differ significantly between dietary treatments (Fig. 3.4) despite the provision of mealworms during the nestling phase. Changes in egg size and composition as a result of food supplementation also appeared to have no lasting effect on nestling growth (Fig. 3.4; Tables 3.1 & 3.2). A positive association between egg size and nestling growth is stronger in precocial, rather than altricial, species (reviewed in Williams 1994). Therefore, a positive influence of food supplementation on egg size in a precocial species might have a more pronounced, long-lasting, influence on nestling development. Indeed, in my study, it is possible that the first growth measures at three days post-hatch were too late for differences in growth attributable to egg size to be detected.

Some of the findings in this Chapter highlight possible mechanisms behind those presented in Chapter Two. For example, egg size of great tits increased throughout the breeding season (Table 3.1) suggesting that egg formation was constrained early in spring. Since supplementation increased egg size of great tits (Fig. 3.1), this might have enabled eggs to surpass a minimum ‘threshold’ of size early in the season and, thereby, advance clutch initiation (Chapter Two). The surface area:volume ratio of eggs correlates negatively with egg size, so large eggs retain heat more efficiently than small ones (see Williams 1994 and references therein). Therefore, increased egg size of great tits as a consequence of supplementation might also have contributed to reduced incubation periods (Chapter Two). However, neither of these mechanisms are supported in blue tits despite supplementation also causing advanced clutch initiation and reduced incubation periods (Chapter Two).

With respect to the applied aspects of my research (e.g. food supplementation in gardens and as part of conservation initiatives – see Chapter One) my findings are somewhat equivocal. Food supplementation increased egg size of great tits (Fig. 3.1), and reduced the decline of egg size with increased clutch size of blue tits (Fig. 3.2). However, these apparent benefits represented only short-term gains, and did not manifest themselves in enhanced nestling growth (Fig. 3.4). This latter finding suggests that the survival of both species pre and post-fledging might have been similar between treatments. This contention is investigated in Chapter Four.

Chapter Four

A CURATE'S EGG: FEEDING BIRDS IS 'GOOD IN PARTS' FOR THE PRODUCTION AND SURVIVAL OF YOUNG

4.1. Abstract

Food supplementation during spring and early summer reduces brood sizes of blue and great tits in Chaddesley Woods NNR, UK (Chapter Two). This is concerning given that sustained food supplementation of birds during reproduction is recommended in UK gardens, and is also used to increase breeding productivity of some endangered species. Here, I compare the influence of food supplementation on longer-term measures of reproductive success in the same population of blue and great tits. Birds were supplemented with peanut cake (pre-laying to post-fledging phases) and mealworms (nestling phase), peanut cake (pre-laying to post-fledging phases), or with nothing (control). Control blue tits had significantly higher fledging success than supplemented conspecifics and fledged, on average, 2.0 more young. Control great tits had significantly higher fledging success than conspecifics supplemented with peanut cake and fledged, on average, 1.4 more young than supplemented pairs. Fledglings were recaptured several months post-fledging to estimate survival. In both species, apparent survival was highest in birds fledged from territories supplemented with peanut cake and mealworms, and was significant compared with control blue tits, and peanut cake-supplemented great tits. Therefore, surprisingly, food supplementation reduced nestling phase productivity, but appeared to increase the survival of fledglings when mealworms were provided during the nestling period. These findings inform current debate regarding the true value of food supplementation to avian populations.

4.2. Introduction

Food supplementation of birds during reproduction is recommended in UK gardens (e.g. RSPB 2006; Toms & Sterry 2008) and is also used as a tool to increase reproductive output in some endangered species (e.g. Spanish imperial eagle – Blanco 2006; San Clemente loggerhead shrike – Heath *et al.* 2008). However, a recent study of blue and great tits at Chaddesley Woods NNR, UK, has highlighted concerns regarding this practice. In both species, food supplementation reduced clutch and brood size significantly while in blue tits hatching success was also significantly reduced (Chapter Two). Moreover, supplementation with live invertebrates (mealworms) during the nestling phase, as is recommended in UK gardens to 'help' adults to provision nestlings (e.g. CJ Wildlife 2009), failed to enhance nestling growth significantly in either species (Chapter Three).

These findings provide important insight into proximate effects of food supplementation on reproduction. However, it is only through the examination of longer-term measures that broader implications of food supplementation during reproduction can be appreciated (Martin 1987). In this regard, measures such as fledging success, the number of young fledged, and post-fledging survival rate are informative. Fledging success provides a measure of the efficiency with which investment in the initial brood is maintained through to fledging; number of young fledged provides a compound measure of clutch size, hatching success, and fledging success; and post-fledging survival rate describes the relative endurance of fledglings.

Fledging success is usually influenced positively by food supplementation (64% of studies reviewed in Robb *et al.* 2008a) and only rarely have fewer young fledged as a consequence (e.g. Källander & Karlsson 1993). A broadly positive influence of food supplementation on fledging success is likely because reproduction is energetically and nutritionally demanding in both adults (e.g. egg formation – Walsberg 1983; provisioning bouts – Drent & Daan 1980) and nestlings (e.g. due to the rapid rate of growth required to fledge successfully – Perrins 1979). Food supplementation during reproduction can also enhance the survival rate of fledglings (e.g. Dewey & Kennedy 2001) and increase the number of independent young (e.g. Arcese & Smith 1988). In many species, mortality rate is greatest in the first year of life, with predation and starvation major causes of loss (Lack 1954). Food requirements of newly-fledged young can exceed those of nestlings (e.g. great tits – Royama 1966) probably because of increased activity and greater heat loss once leaving the nest (Perrins 1979). Energetic and nutritional stress might also affect independent young due to social subordination in feeding flocks (Gosler 1996). Therefore, food supplementation can reduce the risk of energetic or nutritional shortfalls during both pre and post-fledging periods.

In this Chapter, I examine the influence of protracted food supplementation during reproduction, including the provision of live invertebrates (mealworms) during the nestling phase, on long-term measures of breeding success of blue and great tits. Four measures are examined: (i) fledging success; (ii) number of young fledged; (iii) proportion of fledglings recaptured several months post-fledging; and (iv) number of fledglings recaptured several months post-fledging. Since food supplementation augments the foraging environment, I hypothesised that all four measures would be enhanced, and particularly by the provision of mealworms.

4.3. Methods

4.3.1. Study site, experimental design, and food supplementation

Please refer to Chapter Three.

4.3.2. Breeding parameters

Brood size was determined as described in Chapter Two. The number of nestlings that fledged (hereafter 'number fledged') was defined as those that survived until 10-15 days after hatching (when each nestling received a standard British Trust for Ornithology metal ring) minus any chicks found dead during fledging checks. Fledging success was defined as the number fledged as a proportion of the brood size.

4.3.3. Survival estimation

To census fledglings from the preceding spring, 12 mist-net sessions were conducted in October and November of each year with sessions spread evenly over a *c.* six week period. The period between the median hatch date and first mist-net session was 150 ± 6 days and 154 ± 6 days over the three years in blue and great tits, respectively. The same three mist-net sites were used four times in rotational sequence each year. Mist-net sites were selected based on their suitability for mist-netting rather than on their location relative to each treatment (juvenile blue and great tits are gregarious and relatively fluid in movement in the autumn – Cramp & Perrins 1993a,b) (see Fig. 1.2.A in Appendix One). The standard protocol in each session was to open five 40-ft (*c.* 12.2 m) mist-nets at dawn for *c.* 4-5 hours. This protocol was only deviated from on rare occasions (e.g. due to inclement weather). Temporary feeding stations (providing peanut cake and sunflower hearts) were established to bait the mist-net sites. The number of fledglings recaptured was expressed per brood (hereafter 'number recaptured'). Recapture success was also expressed per brood, and was defined as the number recaptured as a proportion of the number fledged. Since the aim of this work was to examine apparent survival from fledging until the autumn, survival estimates between the 12 mist-net sessions in each year (intervals of *c.* three-four days) were not of interest. As a result, the 12 mist-net sessions in each year were treated as a single sampling event.

4.3.4. Filtering data

Only first clutches from which at least one nestling hatched were considered in all analyses. Broods that succumbed to predation (i.e. those where chick remains and/or disturbed nesting material was found during fledging checks) were extremely rare, were not clearly biased in number by food supplementation, and were excluded from all analyses. Subsidiary to these levels of filtering, the following were also implemented. Since peanut cake supplementation reduced brood size significantly in both species (Chapter Two), it was of interest to follow the same cohort of broods though to independence (in the autumn). In order for this to be achieved, number fledged and number recaptured analyses had the same filtering criteria as brood size analyses (see Chapter Two for details). Number recaptured analyses included all successful (i.e. from which at least one nestling fledged) and all unsuccessful (i.e. from which no nestlings fledged) broods and, thereby, provided a compound measure of pre and post-fledging productivity. Recapture success analyses excluded unsuccessful broods and, thereby, provided an estimate of only post-fledging productivity. Broods in which some or all of the fledged young were not ringed (< 10 broods over the study period) were excluded from number recaptured analyses. Broods on PCMW territories were excluded from all analyses on rare occasions when mealworm supplementation commenced after hatching.

4.3.5. Statistical analysis

4.3.5.1. Model structure

Year was included as a fixed factor in all analyses (to account for annual variation in breeding conditions – Nager *et al.* 1997). Hatching date (determined as described in Chapter Two) was included as covariate in all analyses (early-hatched young are usually heavier and more young fledge and subsequently survive – Perrins & McCleery 1989; Norris 1993). Brood size was included as covariate in fledging and recapture success analyses (nestlings are smaller in larger broods and this can reduce nestling phase and post-fledging survival – Martin 1987; Naef-Daenzer *et al.* 2001). To control for possible natal-site fidelity post-fledging, the distance between each nestbox and the centre of its closest mist-net site (hereafter 'minimum fledging distance') was included as a covariate in the recapture success and number recaptured analyses. There was no *a priori* reason that this covariate would be influential so minimum fledging distance was excluded where non-significant ($P > 0.05$). Minimum fledging distances were calculated from a diagram of the nestbox grid assuming exactly equal 40 m spacing between nestboxes (see Fig. 1.2.A Appendix One for schematic representation). Covariate × dietary treatment interactions were tested as described in Chapter Two.

Nestbox nested in treatment block was specified as a random factor in the fledging success and number fledged analyses due to repeated measures on nestboxes and blocks between years, and the spatial nesting of nestboxes within blocks. Since number recaptured was a compound measure of productivity pre and post-fledging, nestbox nested in treatment block was also specified as a random factor in these analyses. Nestbox effects were not considered in recapture success analyses (juveniles may move away from their natal territory soon after fledging – Perrins 1979), but treatment block did appear important (perhaps due to the positioning of the mist-net sites and/or surrounding habitat characteristics), so treatment block was included as a random factor. I could not account for treatment block effects when testing the significance of year × dietary treatment interactions, since the two are co-linear. For the few models in which year × dietary treatment was significant ($P \leq 0.05$), treatment block differences appeared to be the cause ($P \leq 0.05$ when tested as a fixed effect in replacement of year × dietary treatment, indicating systematic treatment block differences rather than a year × dietary treatment interaction, that would be less likely to reveal such systematic effects). Therefore, relevant treatment block terms were included in the random statement (described above) and year × dietary treatment was excluded. Combined-year analyses were conducted for all breeding parameters. Fledging and recapture success analyses were fitted with binomial errors, whereas poisson errors were specified in the number fledged and recaptured analyses.

4.3.5.2. Additional breeding parameters

Fledging success and number fledged analyses were complemented by three subsidiary analyses, namely of partial brood mortality, complete brood mortality, and number fledged (successful broods only) (see Table 4.1). Analyses of partial brood mortality followed the same methods as the fledging success analyses, but excluded dead broods. Similarly, analyses of number fledged (successful broods only) followed the same criteria as number fledged analyses, but excluded dead broods. Complete brood mortality analyses included the same broods as fledging success analyses, but success (at least one young fledged) or failure (brood death) was specified as a binomial response variable.

4.3.5.3. Additional information

All analyses were conducted using PROC GLIMMIX in SAS (SAS Institute Inc. 2008) or Minitab 15 (Minitab 2007). Full results for each model are provided in Table 4.1. See Chapter Two for details of figures that are plotted from statistical estimates. Fledging and recapture success were analysed as proportions (details in Section 4.3.2 & 4.3.3, respectively) but are presented as percentages in this Chapter. The magnitudes of the effects of supplementation presented in the Results are described by comparing means generated from statistical estimates.

4.4. Results

Fledging success of blue tits was significantly higher on control, compared with PC (mean difference: 10.7%; *P* = 0.001) and PCMW (mean difference: 8.0%; *P* = 0.009), territories (Fig. 4.1). Control blue tits fledged significantly more young than both PC (mean difference: 2.1 fledglings; *P* = 0.001) and PCMW (mean difference: 1.9 fledglings; *P* = 0.001) conspecifics (Fig. 4.2). In great tits, fledging success was highest on control territories and was significant compared with PC broods (mean difference: 11.4%; *P* = 0.001) (Fig. 4.1). Control great tits fledged significantly more young than both PC (mean difference: 1.6 fledglings; *P* = 0.007) and PCMW (mean difference: 1.2 fledglings; *P* = 0.05) conspecifics (Fig. 4.2).

Recapture success was highest in birds fledged from PCMW territories in both species and was significant compared with control broods of blue tits (mean difference: 3.1%; *P* = 0.02) and with PC broods of great tits (mean difference: 6.8%; *P* = 0.02) (Fig. 4.3). The number of recaptured blue tits was significantly greater in PCMW, compared with control (mean difference: 0.2 fledglings; *P* = 0.04), broods (Fig. 4.4). The number of recaptured great

Table 4.1. Models of breeding parameters (*F* and associated *P* values) of blue (BT) and great (GT) tits at Chaddesley Woods National Nature Reserve in 2006-2008. Combined-year analyses were conducted for all breeding parameters. Fixed factors specified in each model are given with significant *P* values in bold text. Least squares means tests (adjusted for multiple comparisons via the Tukey method) are given where a significant effect of dietary treatment was found: C = control; PC = peanut cake; PCMW = peanut cake and mealworms. Directions of significant effects are given: '+' and '-' denote significant positive and negative relationships, respectively, and 'NS' denotes non-significance ($P > 0.05$). See text for details.

					Least squares means (*P*-values)			
Breeding parameter	**Sp.**	**Fixed factor**	***F***	***P***	**C *vs.* PC**	**C *vs.* PCMW**	**PC *vs.* PCMW**	**Direction**
Fledging success	BT	Dietary treatment	$F_{2,138} = 4.88$	**$P = 0.009$**	**$P = 0.001$**	**$P = 0.009$**	$P = 0.74$	C = highest; PC = lowest
		Year	$F_{2,138} = 41.78$	**$P < 0.001$**				2006 = highest; 2007 = lowest
		Hatch date	$F_{1,138} = 17.98$	**$P < 0.001$**				-
		Brood size	$F_{1,138} = 0.01$	$P = 0.93$				NS
		Hatch date × dietary treatment	$F_{2,138} = 3.43$	**$P = 0.04$**				C = little seasonal variation; PC and PCMW = seasonal increase
	GT	Dietary treatment	$F_{2,67} = 7.00$	**$P = 0.002$**	**$P = 0.001$**	$P = 0.18$	$P = 0.17$	C = highest; PC = lowest
		Year	$F_{2,67} = 17.49$	**$P < 0.001$**				2006 = highest; 2007 = lowest
		Hatch date	$F_{1,67} = 0.21$	$P = 0.65$				NS
		Brood size	$F_{1,67} = 1.29$	$P = 0.26$				NS
Partial brood mortality	BT	Dietary treatment	$F_{2,103} = 0.98$	$P = 0.38$				NS
		Year	$F_{2,103} = 26.55$	**$P < 0.001$**				2006 = lowest; 2007 = highest
		Hatch date	$F_{1,103} = 49.30$	**$P < 0.001$**				+
		Brood size	$F_{1,103} = 1.80$	$P = 0.18$				NS
	GT	Dietary treatment	$F_{2,54} = 5.42$	**$P = 0.007$**	**$P = 0.02$**	**$P = 0.01$**	$P = 0.93$	C = lowest; PCMW = highest
		Year	$F_{2,54} = 9.81$	**$P < 0.001$**				2006 = lowest; 2008 = highest
		Hatch date	$F_{1,54} = 0.49$	$P = 0.49$				NS
		Brood size	$F_{1,54} = 6.65$	**$P = 0.01$**				+
Complete brood mortality	BT	Dietary treatment	$F_{2,140} = 4.40$	**$P = 0.01$**	**$P = 0.01$**	**$P = 0.04$**	$P = 0.92$	C = lowest; PC = highest
		Year	$F_{2,140} = 15.05$	**$P < 0.001$**				2007 = highest; 2008 = lowest
		Hatch date	$F_{1,140} = 0.38$	$P = 0.54$				NS
		Brood size	$F_{1,140} = 0.03$	$P = 0.86$				NS
	GT	Dietary treatment	$F_{2,232} = 2.06$	$P = 0.13$				NS
		Year	$F_{2,232} = 8.15$	**$P < 0.001$**				2006 = lowest; 2007 = highest
		Hatch date	$F_{1,232} = 0.73$	$P = 0.39$				NS
		Brood size	$F_{1,232} = 4.26$	**$P = 0.04$**				-
Number fledged	BT	Dietary treatment	$F_{2,123} = 6.13$	**$P = 0.003$**	**$P = 0.001$**	**$P = 0.001$**	$P = 0.97$	C = highest; PC = lowest
		Year	$F_{2,123} = 40.65$	**$P < 0.001$**				2006 = highest; 2007 = lowest

Table 4.1. continued

					Least squares means (P-values)			
Breeding parameter	**Sp.**	**Fixed factor**	F	P	**C *vs.* PC**	**C *vs.* PCMW**	**PC *vs.* PCMW**	**Direction**
Number fledged	BT	Hatch date	$F_{1,123} = 17.17$	**$P < 0.001$**				-
		Hatch date × dietary treatment	$F_{2,123} = 4.49$	**$P = 0.01$**				C = little seasonal variation; PC and PCMW = seasonal increase
	GT	Dietary treatment	$F_{2,64} = 4.57$	**$P = 0.01$**	**$P = 0.007$**	**$P = 0.05$**	$P = 0.70$	C = highest; PC = lowest
		Year	$F_{2,64} = 6.50$	**$P = 0.003$**				2006 = highest; 2007 = lowest
		Hatch date	$F_{1,64} = 0.99$	$P = 0.32$				NS
		Hatch date × dietary treatment	$F_{2,64} = 3.54$	**$P = 0.03$**				C = small seasonal increase; PC and PCMW = large seasonal increase
Number fledged (successful broods only)	BT	Dietary treatment	$F_{2,93} = 4.38$	**$P = 0.02$**	$P = 0.12$	**$P = 0.01$**	$P = 0.71$	C = highest; PCMW = lowest
		Year	$F_{2,93} = 28.67$	**$P < 0.001$**				2006 = highest; 2007 = lowest
		Hatch date	$F_{1,93} = 38.80$	**$P < 0.001$**				-
	GT	Dietary treatment	$F_{2,52} = 5.61$	**$P = 0.006$**	$P = 0.14$	**$P = 0.03$**	$P = 0.78$	C = highest; PCMW = lowest
		Year	$F_{2,52} = 10.40$	**$P < 0.001$**				2006 = highest; 2008 = lowest
		Hatch date	$F_{1,52} = 2.05$	$P = 0.16$				NS
		Hatch date × dietary treatment	$F_{2,52} = 4.61$	**$P = 0.01$**				C = seasonal decrease; PC and PCMW = seasonal increase
Recapture success	BT	Dietary treatment	$F_{2,296} = 3.64$	**$P = 0.03$**	$P = 0.52$	**$P = 0.02$**	$P = 0.28$	PCMW = highest; C = lowest
		Year	$F_{2,296} = 8.00$	**$P < 0.001$**				2006 = highest; 2007 = lowest
		Hatch date	$F_{1,296} = 9.67$	**$P = 0.002$**				-
		Brood size	$F_{1,296} = 0.03$	$P = 0.86$				NS
		Brood size × dietary treatment	$F_{2,296} = 3.00$	**$P = 0.05$**				C and PC = positive relationship; PCMW = negative relationship
	GT	Dietary treatment	$F_{2,205} = 3.54$	**$P = 0.03$**	$P = 0.39$	$P = 0.42$	**$P = 0.02$**	PCMW = highest; PC = lowest
		Year	$F_{2,205} = 13.76$	**$P < 0.001$**				2006 = highest; 2007 = lowest
		Hatch date	$F_{1,205} = 14.71$	**$P < 0.001$**				-
		Brood size	$F_{1,205} = 3.19$	$P = 0.08$				NS
Number recaptured	BT	Dietary treatment	$F_{2,123} = 3.65$	**$P = 0.03$**	$P = 0.83$	**$P = 0.04$**	$P = 0.14$	PCMW = highest; C = lowest
		Year	$F_{2,123} = 37.07$	**$P < 0.001$**				2006 = highest; 2007 = lowest
		Hatch date	$F_{1,123} = 33.29$	**$P < 0.001$**				-
		Minimum fledging distance	$F_{1,123} = 8.02$	**$P = 0.005$**				-
	GT	Dietary treatment	$F_{2,65} = 6.43$	**$P = 0.003$**	**$P = 0.05$**	$P = 0.67$	**$P = 0.002$**	PCMW = highest; PC = lowest
		Year	$F_{2,65} = 15.60$	**$P < 0.001$**				2006 = highest; 2007 = lowest
		Hatch date	$F_{1,65} = 7.71$	**$P = 0.007$**				-

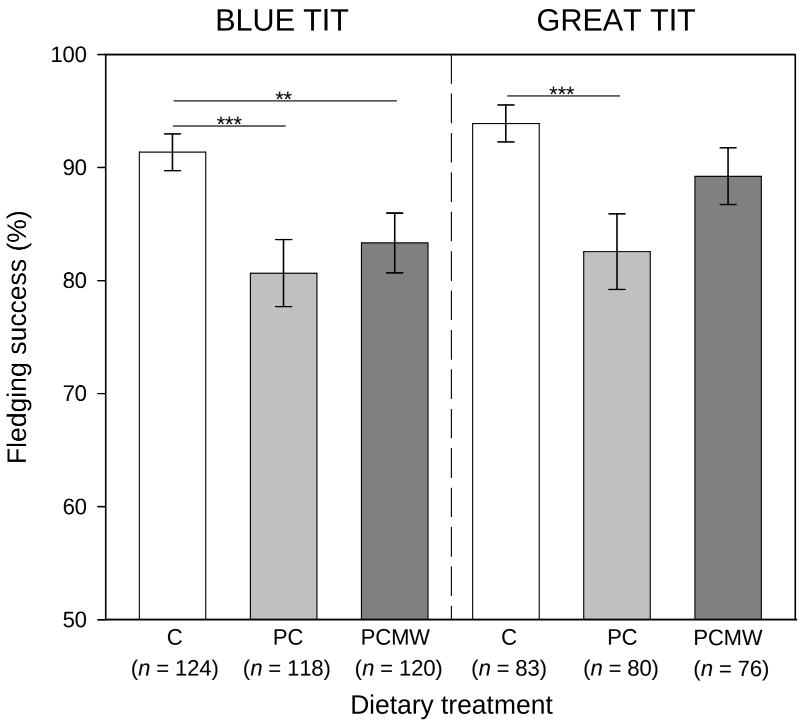

Figure 4.1. Fledging success (mean ± 1 SE from statistical estimates) of blue and great tits at Chaddesley Woods National Nature Reserve in 2006-2008. Dietary treatments: C = control (non-supplemented); PC = peanut cake; PCMW = peanut cake and mealworms. ** = $P \leq 0.01$; *** = $P \leq 0.001$. Number of broods is in parentheses below dietary treatments. See Table 4.1 for statistical findings and see text for details.

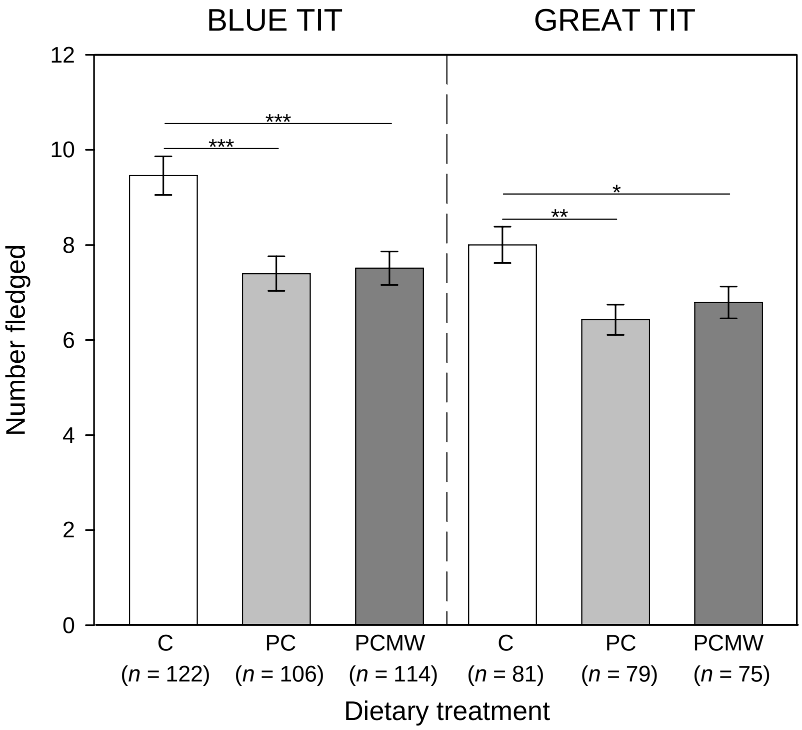

Figure 4.2. Number fledged (mean ± 1 SE from statistical estimates) from blue and great tit broods at Chaddesley Woods National Nature Reserve in 2006-2008. See Figure 4.1 for explanations of dietary treatments and sample sizes. * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$. See Table 4.1 for statistical findings and see text for details.

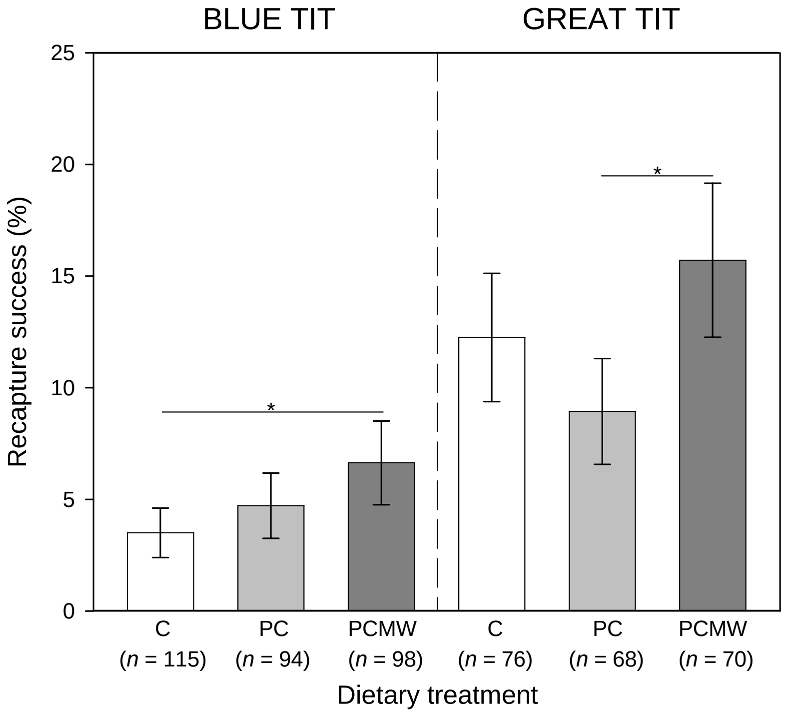

Figure 4.3. Recapture success (mean ± 1 SE from statistical estimates) of juvenile blue and great tits in October and November each year following fledging at Chaddesley Woods National Nature Reserve in 2006-2008. See Figure 4.1 for explanations of dietary treatments and sample sizes. * = $P \leq 0.05$. See Table 4.1 for statistical findings and see text for details.

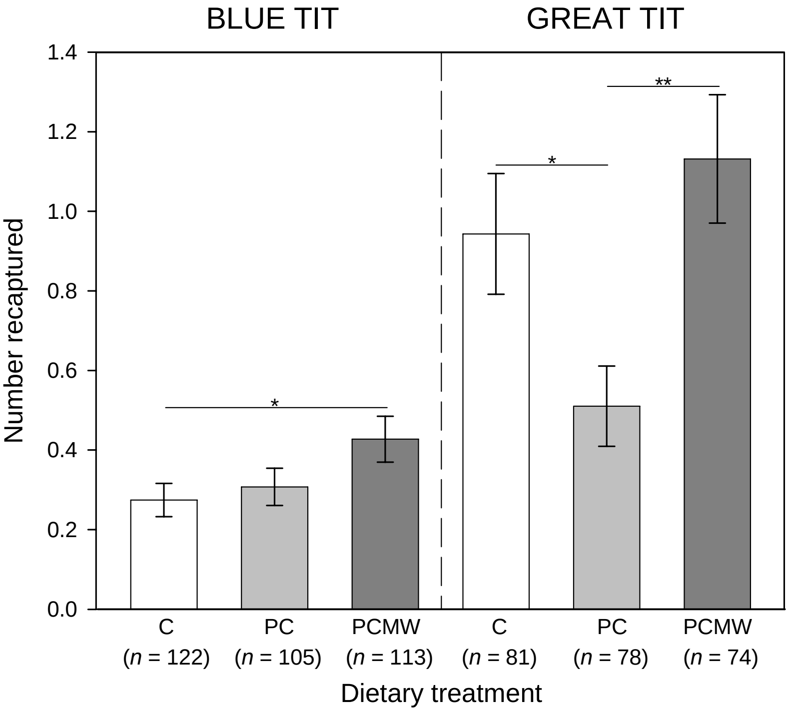

Figure 4.4. Number of juvenile blue and great tits recaptured (mean ± 1 SE from statistical estimates) in October and November each year following fledging at Chaddesley Woods National Nature Reserve in 2006-2008. See Figure 4.1 for explanations of dietary treatments and sample sizes. * = $P \leq 0.05$; ** = $P \leq 0.01$. See Table 4.1 for statistical findings and see text for details.

tits was significantly lower in PC, compared with control (mean difference: 0.4 fledglings; *P* = 0.05) and PCMW (mean difference: 0.6 fledglings; *P* = 0.002), broods (Fig. 4.4).

4.5. Discussion

Food supplementation reduced nestling phase productivity significantly (Figs 4.1 & 4.2). Supplemented blue and great tits fledged, on average, 2.0 and 1.4 fewer young than controls, respectively (Fig. 4.2). However, recapture success and number recaptured (hereafter 'apparent survival') were highest in birds fledged from PCMW territories in both species (Figs 4.3 & 4.4). Indeed, significantly more PCMW blue tits were recaptured per brood than control conspecifics (Fig. 4.4) despite fledging, on average, 1.9 fewer young (Fig. 4.2). However, great tits fledged from PC territories had both the lowest nestling phase productivity (Figs 4.1 & 4.2) and apparent survival (Figs 4.3 & 4.4). These findings only partially support my hypotheses. Mechanisms determining these results, the importance of these findings with reference to effects of food supplementation earlier in the breeding cycle (described in Chapters Two & Three), and broader considerations of the influence of food supplementation during avian reproduction are discussed below.

4.5.1. Fledging success and number fledged

Although most studies have reported an increase in nestling phase productivity as a result of food supplementation (reviewed in Robb *et al.* 2008a), a small number have reported declines (e.g. Reese & Kadlec 1984; Clamens & Isenmann 1989; Källander & Karlsson 1993; Nilsson 1994). As in Nilsson (1994), I found that reduced fledging success in supplemented blue tits (Fig. 4.1) was driven by increased complete, but not partial, brood mortality (Table 4.1). Conversely, in great tits, partial brood mortality was more influential (Table 4.1). However, in this species models of complete brood mortality did not run successfully when nestbox nested in treatment block was included in the random statement (see details in Section 4.3.5.1 & 4.3.5.2). This was probably because of low failure rates, especially in 2006. To enable model the model to run successfully these random terms were omitted so these results should be interpreted with caution. When only successful broods (i.e. broods that fledged at least one young) were considered, supplemented broods fledged fewer young than controls in both species (mean reduction in the number fledged compared with controls in blue / great tits, respectively: PC = 0.7 / 0.6; PCMW = 0.9 / 0.8) (Table 4.1).

Adverse effects of food supplementation during the nestling period might be due to peanut cake and/or mealworms being less suitable to provision nestlings than are natural foods. Peanut cake may be a particularly inappropriate food since the diet of nestlings in UK woodland consists almost entirely of invertebrates (Cramp & Perrins 1993a,b). In gardens, *c.* 15% of food for nestling blue and great tits may be anthropogenic and nestlings may die through the consumption of unsuitable supplements (Cowie & Hinsley 1988a). In this respect, mealworms may have been more suitable than peanut cake but PCMW broods did not have significantly higher nestling phase productivity than PC broods in either species (Figs 4.1 & 4.2). Therefore, the extent to which the provision of live invertebrates (e.g. mealworms) during the nestling period, as is recommended in UK gardens (e.g. CJ Wildlife 2009), can alleviate nutritional constraints appears limited. Feeder visitation might also lead to exposure to pathogens that can cause mortality (Pennycott *et al.* 2002). During my study I collected a number of dead nestlings for which the cause of death was unknown but could be investigated in future research.

Supplementation advanced hatching in both species (Fig. 4.5; Chapter Two). Therefore, reduced nestling phase productivity of supplemented broods might have been

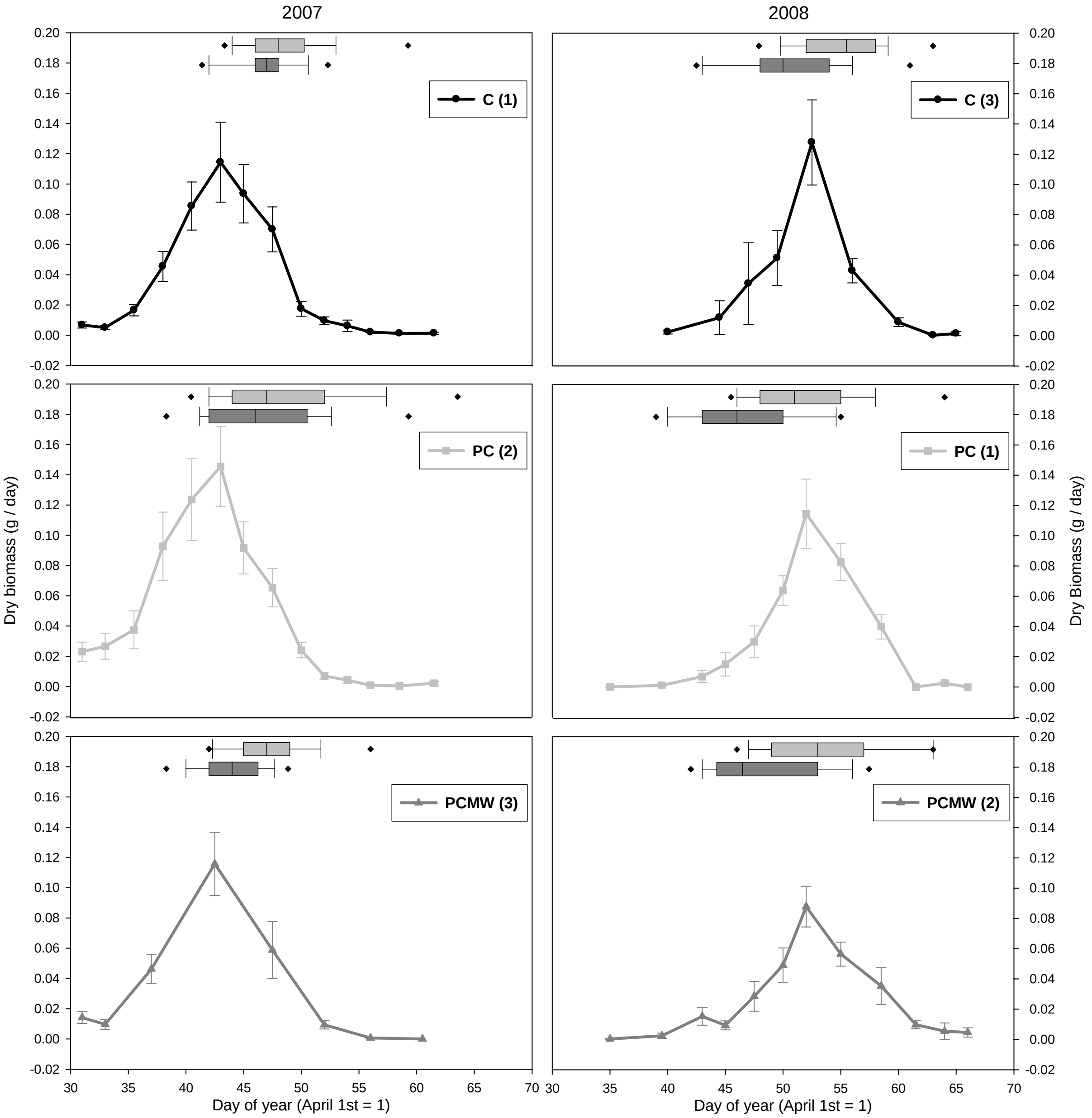

Figure 4.5. Geometer caterpillar dry biomass expressed as g / day (mean ± 1 SE, plotted at the mid-point between successive caterpillar samples) at Chaddesley Woods National Nature Reserve in 2007 and 2008. Legend denotes dietary treatment (C = control; PC = peanut cake; PCMW = peanut cake and mealworms) with treatment block number in parentheses (dietary treatments were rotated across treatment blocks between years). Box-plots are of hatching dates + 10 days (a period of peak nestling provisioning – Perrins 1991) of first clutches in blue (light grey) and great (dark grey) tits. The vertical line within each box denotes the median hatching date. The right of each box is the 75th, and the left the 25th, percentile of dates. The right whisker represents the 90th, and the left the 10th, percentile of the dates. Outlying data points are the 95th (right) and 5th (left) percentiles of dates. See Appendix Four for methods of caterpillar sampling and see text for details.

caused by greater asynchrony of the peak food demands of broods (*c.* 10 days after hatching – Perrins 1991) with peak caterpillar availability (the most common food of nestlings – Cramp

& Perrins 1993a,b) compared with control broods (Fig. 4.5). Caterpillar abundance was monitored in 2007 and 2008 (data for 2006 were unavailable – Fig. 4.5; see Appendix Four for methods). Differences in synchrony between the timing of peak caterpillar availability and peak brood demands between treatments could not be tested precisely since the intervals between successive caterpillar samples were *c.* three days, a similar magnitude to the advancement of hatching through supplementation (Fig. 4.5). However, greater asynchrony in supplemented broods seems an unlikely cause of the pronounced treatment differences in nestling phase productivity (Figs 4.1 & 4.2) because of the considerable overlap of hatching dates between dietary treatments (Fig. 4.5). Indeed, other studies that have reported reduced nestling phase productivity as a result of food supplementation have also found considerable phenological overlap between treatments (e.g. Clamens & Isenmann 1989; Källander & Karlsson 1993; Nilsson 1994). Absolute abundance of caterpillars during the peak (dry biomass / day) also did not differ significantly between treatments (2007: $F_{2,27} = 0.51$, $P = 0.61$; 2008: $F_{2,27} = 0.83$, $P = 0.45$ – Fig. 4.5).

In previous studies, supplement withdrawal (e.g. around the time of egg laying – Reese & Kadlec 1984; Clamens & Isenmann 1989; Källander & Karlsson 1993; Nilsson 1994) could explain reduced nestling phase productivity in supplemented broods. However, my study demonstrates that food supplementation throughout the breeding period can also cause such effects (Figs 4.1 & 4.2). Indeed, perhaps the most important factor that unifies these studies is food supplementation itself. Although rarely considered, the addition of a rich, localised resource may have effects beyond those of increased food availability (e.g. increased territorial intrusion and confrontation – Ewald & Rohwer 1982; Schoech *et al.* 2008) that could incur reproductive costs. In my study, any such costs might have been associated particularly with peanut cake that was positioned equidistantly between nestboxes in supplemented treatment blocks, perhaps on the boundaries of adjacent territories.

First clutches of blue and great tits usually hatch synchronously (Perrins 1979) and clutch size is adjusted relative to the rearing capacity of individual pairs (Pettifor *et al.* 1988). Indeed, food-supplemented great tits experienced significantly higher partial brood mortality than control conspecifics (Table 4.1), but increased partial brood mortality did not correspond with enhanced recapture success ($F_{1,204} = 1.51$, $P = 0.22$) suggesting that such loss was not adaptive. In both species, food supplementation reduced the number of fledglings per successful brood (Table 4.1). Of these successful broods, the number fledged was associated positively with the number recaptured in blue ($F_{1,91} = 5.50$, $P = 0.02$), but not significantly in great ($F_{1,52} = 1.90$, $P = 0.17$), tits. Therefore, although reduced nestling phase productivity was probably a maladaptive response to food supplementation in both species, this was most apparent in blue tits.

4.5.2. Apparent survival

Food supplementation during the breeding season has been found to enhance the survival rates of fledglings and/or increase the production of independent young in a number of species (e.g. northern goshawk – Dewey & Kennedy 2001; Florida scrub jay – Schoech *et al.* 2008; song sparrow – Arcese & Smith 1988). Higher apparent survival in PCMW broods (Figs 4.3 & 4.4) was expected due to richer foraging conditions compared with control and PC broods, and provides support for the provision of live invertebrates (e.g. mealworms) during the nestling period in UK gardens (e.g. CJ Wildlife 2009). Interestingly, any effect of mealworm supplementation must have operated through a carry-over effect (e.g. Grieco *et al.* 2002; Robb *et al.* 2008b) because this supplement was withdrawn at fledging. Heavier nestlings have greater survival prospects post-fledging (Naef-Daenzer *et al.* 2001) and it is possible that mealworm supplementation enhanced nestling growth prior to fledging. Increased nestling development was not apparent in PCMW, compared with PC and control, broods (both species – Chapter Three) but mealworms are relatively large and chitinous (e.g. compared with caterpillars that are used to provision young) so peak provisioning may have occurred after 12 days post-hatch when nestling growth was last recorded (see Chapter Three).

However, it is also possible that mealworm supplementation influenced post-fledging dispersal by perhaps 'encouraging' parents to keep fledglings close to feeders (i.e. areas of perceived food richness) and, thereby, increasing apparent survival. I did not examine post-fledging dispersal but two interesting patterns have emerged, one in each species. In blue tits, number recaptured associated negatively with minimum fledging distance (Table 4.1), a consistent pattern across treatments (minimum fledging distance × dietary treatment: $F_{2,121} = 0.11$, $P = 0.90$). Therefore, although this does not reveal rates of dispersal between treatments, it does suggest that patterns in movement (i.e. fidelity to natal territories) were similar.

In great tits, minimum fledging distance had no significant effect on apparent survival, but there were intriguing sex-specific patterns in fledglings that were recaptured. It is known that female juvenile great tits disperse further than males (reviewed in Payevsky 2006). In support of this, I recaptured many more males than females post-fledging. However, strikingly, 78% of control juveniles that were recaptured were male compared with 62% of both PC and PCMW juveniles. This was a significant difference when supplemented treatments were combined in comparison with the control ($F_{1,113} = 4.63$, $P = 0.03$). It is possible that food supplementation altered the sex ratio of great tit broods, but a greater male bias would be predicted in supplemented, not control, broods (e.g. kakapo – Clout *et al.*

2002). Therefore, a more likely explanation is that either control females dispersed further and/or control males were more sedentary than in great tits fledged from supplemented territories. Either possibility would alter current estimates of apparent survival (Figs 4.3 & 4.4). Sex-specific patterns in apparent survival were not investigated in blue tits since sexing is less reliable in the hand during autumn than in great tits.

Future research should examine the role of food supplementation in influencing sex-specific survival and dispersal in both species (e.g. by mist-netting in nearby habitats – Dhondt 1979; and/or by using radio telemetry/colour rings – Naef-Daenzer *et al.* 2001). Establishing the costs (e.g. through inbreeding depression – e.g. Kempenaers *et al.* 1996) and the benefits (e.g. through residency in oak woodland breeding habitat – Perrins 1965) of remaining resident in the population that I studied, along with the factors that influence post-fledging dispersal distance, will be important to establish so that such research is interpreted accurately.

A disadvantage of my statistical approach is that encounter rate (the probability of a living, marked individual being encountered) was not examined. Specialist mark-recapture analyses (e.g. Program MARK – White & Burnham 1999) control for encounter rate when generating survival estimates. However, I feel that my approach was appropriate for two reasons. First, data were collected to estimate survival over a single period, from fledging to the autumn. Although 12 mist-net sessions were conducted in each year, survival between the 12 sessions was not of interest. Second, the encounter rate (in this case, the number of mist-net sessions in which a juvenile was recaptured, expressed per brood / 12) of recaptured juveniles did not differ significantly between treatments: blue tits – 0.14 (control), 0.15 (PC), and 0.14 (PCMW) ($F_{2,117} = 0.52$, $P = 0.59$); great tits – 0.17 (all treatments) ($F_{2,106} = 0.14$, $P =$

0.87). Therefore, this suggests that differences in apparent survival between treatments were driven by differences in survival and/or dispersal, not encounter probability.

4.5.3. Consequences of breeding phenology and brood size

Two key results presented earlier in this thesis were the advancement of breeding phenology and reduction of brood size as a result of supplementation with peanut cake in both species (Chapter Two). Since hatching date and brood size were both specified as covariates in many of the analyses in this Chapter (see Table 4.1), this provides an opportunity to consider long-term consequences of both advanced phenology and reduced brood size in the population that I studied.

Early-hatched blue tits were significantly heavier 12 days after hatching than conspecifics that hatched later (Chapter Three), experienced significantly higher fledging success (through lower partial brood mortality), and fledged in significantly greater numbers (Table 4.1). Early-hatched great tits tended to be lighter, smaller, but in better condition than conspecifics hatched later (Chapter Three) but seasonal variation in nestling phase productivity was not pronounced (Table 4.1). However, apparent survival decreased significantly with later hatching in both species (Table 4.1). Therefore, it appears that advanced breeding in supplemented pairs (Chapter Two) was a strategy to maximise productivity. However, there was evidence that early-breeding supplemented pairs 'underperformed' relative to later-breeding pairs in the same treatment, a tendency that was not common on control territories (hatch date × dietary treatment interactions in Table 4.1: blue tit – fledging success and number fledged; great tit – number fledged). In supplemented pairs, these patterns could be attributable to reduced supplement use later in the season as natural invertebrates became more available (Perrins 1979; assuming that the former were sub-optimal to the latter). The considerable phenological overlap between supplemented and control broods (Fig. 4.5) means that if this mechanism operated, it is unlikely that early-breeding supplemented pairs avoided natural foods because of their absence but, instead, that they changed their foraging strategy across the season, relying heavily upon supplements until natural food availability surpassed a certain threshold. Patterns in supplement use between treatments are explored in Chapter Five.

It is difficult to identify benefits of smaller brood sizes of supplemented pairs (Chapter Two). Nestling growth of great tits associated negatively with brood size but the same was not true of blue tits (Chapter Three). Brood size had a conflicting relationship with partial and complete brood mortality of great tits (Table 4.1) but brood size did not predict fledging success significantly in either species (Table 4.1). Indeed, reduced fledging success in supplemented broods (Fig. 4.1) suggests that these broods were larger than could be reared successfully. Unlike other studies (e.g. Gustafsson & Sutherland 1988; Perrins & McCleery 1989), brood size was not significantly negatively related to recapture success in either species (although approached significance in great tits – Table 4.1). Therefore, it appears that the principal means with which smaller broods were adaptive was through advanced hatching (Table 4.1).

4.5.4. Conclusions

In both species, food supplementation significantly reduced the number of young fledged (Fig. 4.2) but supplementation with mealworms may have increased post-fledging survival (Figs 4.3 & 4.4). Invertebrate supplements, such as mealworms, are advocated for use in UK gardens during the breeding season (e.g. RSPB 2006; CJ Wildlife 2009). My study suggests some support for this advice (Figs 4.3 & 4.4). Indeed, since gardens contain fewer natural invertebrates with which to feed young than broadleaved woodland (e.g. due to the spraying of pesticides and the presence of exotic flora in gardens – Schmidt 1988; Burghardt *et al.* 2009), provision of live invertebrates might enhance breeding productivity substantially. However, there is almost no empirical evidence regarding the influence of different food supplements on avian reproduction in urban (e.g. garden) habitats.

Despite marked habitat differences, my findings show great similarity with patterns in blue and great tit reproduction in urban habitats, namely reduced nestling phase productivity but increased apparent survival post-fledging (reviewed in Chamberlain *et al.* 2009). Therefore, it is possible that food supplementation, that is widespread in UK gardens (Davies *et al.* 2009), could contribute to these patterns in avian reproduction in urban habitats. In addition, my research is relevant to food supplementation of endangered species during reproduction (e.g. stitchbird – Castro *et al.* 2003; Florida scrub jay – Schoech *et al.* 2008). To this end, my study contributes to a growing body of literature in which concern has been raised over adverse consequences of food supplementation (e.g. see Chapter One). My study challenges the notion that food supplementation enhances breeding productivity, but also demonstrates that the appropriate use of food supplements might elicit long-term benefits.

Chapter Five

MECHANISMS OF EFFECTS OF FOOD SUPPLEMENTATION ON AVIAN REPRODUCTION AS REVEALED BY STABLE ISOTOPE ANALYSIS

5.1. Abstract

Food supplementation of blue and great tits throughout the breeding season at Chaddesley Woods NNR has multiple significant effects on reproduction. Food supplementation advances clutch initiation, reduces productivity in egg (via clutch size) and nestling (via fledging success) phases, but increases apparent survival of fledglings when mealworms are provided during the nestling period (Chapters Two & Four). In one breeding season (2007) the relative contributions of food supplements and natural foods to the diet of adult and nestling blue and great tits were investigated using stable isotope analysis of carbon and nitrogen. Three tissues (egg albumen, claw, and blood) were sampled to examine dietary intake over different temporal scales. The two supplements, peanut cake and mealworms, were isotopically distinct from each other and from naturally occurring foods. Between supplemented and non-supplemented (control) treatments, the $\delta^{13}C$ and $\delta^{15}N$ values of tissues varied significantly but differences were not widespread across tissue types in either species. In both species, mealworm use did not differ significantly between treatments and peanut cake use showed few significant differences between treatments. Both food supplements, but particularly mealworms, formed only a subsidiary part of the diet. However, increased supplement intake associated significantly with various measures of breeding success, some of which (e.g. larger clutches and, in great tits, higher fledging success) contradicted effects of providing food supplements on breeding territories (e.g. reduced clutch size and fledging success – Chapters Two & Four). I conclude that supplements need not be consumed in great quantities to elicit

significant effects on reproduction. I propose a behavioural basis for the action of food supplementation on avian reproduction.

5.2. Introduction

Recent research at Chaddesley Woods NNR, UK, has revealed numerous significant, and some unexpected, effects of protracted food supplementation on reproduction of blue and great tits. Food-supplemented pairs advance clutch initiation (both species), lay smaller clutches (both species), have shorter incubation periods (both species), and experience lower hatching (blue tits) and fledging (both species) success compared with non-supplemented (control) conspecifics (Chapters Two & Four). However, supplementation with mealworms during the nestling period increases the apparent survival of fledglings (Chapter Four). These significant effects were detected following food supplementation in three spatially distinct treatment blocks in each year. Given the influence of food supplementation on reproduction, it would be reasonable to assume that food intake of birds differed substantially between the treatment blocks and was driven by the availability of supplementary food.

This assumption could be tested through a number of approaches. Previous studies have monitored food supplement use through visual inspections of supplements (e.g. Svensson & Nilsson 1995; Nager *et al.* 1997) or through recording the weight of food eaten (e.g. Cowie & Hinsley 1988b; Robb *et al.* 2008b) over known periods of time. These methods are advantageous in that they are quick, inexpensive, and data can be quickly collated and analysed. However, visual inspections are susceptible to subjective error and both methods may be complicated by supplements being consumed by other species and/or by non-focal (e.g. control) individuals. Feeder watches (e.g. Cowie & Hinsley 1988b; Soler & Soler 1996) provide intake information for specific individuals but they must be identifiable at distance (e.g. through colour-ringing), foraging away from feeders is not recorded, and data collection is labour-intensive. To refine feeder watch methods, passive integrated transponder (PIT) tag technology can be used where PIT-tags are attached to individuals whose visitation to feeders is monitored automatically by loggers positioned on feeders. This technology can even be adapted to supplement specific focal individuals (i.e. feeder recognition technology – Schoech *et al.* 2008). However, such approaches are prohibitively expensive currently and foraging away from feeders is not examined. The above approaches investigate foraging patterns in fledged birds. The diet of nestlings can be investigated using nest cameras (e.g. Cowie & Hinsley 1988a) but footage can sometimes be inconclusive (e.g. due to obscured views). More generally, all of the above methods measure only food intake rather than nutrient assimilation.

To counter some of these problems, interest has grown recently in the use of stable isotope analysis (SIA) to trace supplement use by birds (e.g. Gloutney *et al.* 1999; Davis *et al.* 2005; Robb *et al.* In review). Supplements can be provided whose $\delta^{13}C$ and/or $\delta^{15}N$ values differ from corresponding $\delta^{13}C$ and/or $\delta^{15}N$ values of foods available naturally. Isotopic signatures of foods are assimilated predictably into the tissues of consumers (DeNiro & Epstein 1978, 1981) so, by sampling consumer tissues, the relative contributions of natural and supplementary foods to the diet can be modelled. Importantly, because different tissues have different turnover rates of carbon (C) and nitrogen (N), food intake can be examined over several temporal scales (e.g. in adult passerines: over several months by sampling claw – Bearhop *et al.* 2003; during egg formation by egg collection – Meijer & Drent 1999; over days to weeks by sampling blood – Hobson & Bairlein 2003). In food supplementation studies SIA provides information about supplement use in each dietary treatment, about treatment fidelity, and about exclusion of particular individuals (e.g. subordinate birds) from supplement sources.

In this study, SIA was used to estimate the relative contributions of supplementary and natural foods to the diet of adult and nestling blue and great tits. Three tissue types were examined (namely egg albumen, claw, and blood) with supplement use compared between treatments and against individual measures of breeding success (e.g. clutch size, hatching success, fledging success – Chapters Two & Four). I hypothesised that consumption of each supplement would be highest in the treatment block in which that particular supplement was provided, and that differences in supplement use would explain differences in breeding parameters between treatments.

5.3. Methods

5.3.1. Study site, experimental design, and food supplementation

Please refer to Chapter Three.

5.3.2. Tissue sampling

All tissues were sampled in 2007. One egg per clutch was collected and stored as described in Chapter Three. Hatching date was recorded at each nest (as described in Chapter Two). Adults were tissue sampled after capture on the nest (usually using a spring trap) *c.* 10-14 days after hatching. Nestlings were tissue sampled 12 days after hatching. Blood and claw (*c.* 2 mm trimmed using springbow scissors) samples were collected under licence (Home Office PPL 40/2926) from each adult, and from *c.* three nestlings per brood selected at random. Blood samples were taken from the brachial vein by venipuncture and collected in non-heparinised glass capillary tubes. Blood was stored on ice in the field and was centrifuged within *c.* two hours of collection to separate plasma and red blood cell components. Blood components were separated and stored in a domestic freezer, and claw samples were stored in a domestic refrigerator, until SIA.

5.3.3. Stable isotope analysis

Each food supplement was delivered in a single batch at the beginning of the 2007 breeding season from which samples were collected and stored in a domestic freezer. Mealworms were raised on a diet of bran and 20% fishmeal to ensure isotopic separation from other foods (Robb *et al.* In review). Natural foods were sampled from across the study area. The natural diet of adult and nestling blue and great tits has been studied intensively (e.g. Cramp & Perrins 1993a,b) so important natural foods at different points of the annual cycle are well known. Adult claws represent dietary intake over the preceding months (Bearhop *et al.* 2003) so coleoptera, diptera and arachnida (combined due to a similar $\delta^{13}C$ and $\delta^{15}N$), other invertebrates (primarily under-bark invertebrates that might be available during winter), seeds (beech *Fagus* spp., birch *Betula* spp., and hazel *Corylus* spp. – combined due to a similar $\delta^{13}C$ and $\delta^{15}N$), and peanut cake were considered. Albumen reflects dietary intake during egg formation (Meijer & Drent 1999), so the same foods specified for analyses of adult claws were again appropriate. Adult blood represents dietary intake over the preceding days to weeks (Hobson & Bairlein 2003), so lepidoptera (caterpillars), coleoptera, diptera and arachnida, peanut cake, and mealworms were considered. Analyses of nestling tissues (claw and blood) specified the same foods as analyses of adult blood, but excluded coleoptera. These food-groupings are hereafter referred to as ‘food types’ in this Chapter.

The isotope signature of proteinaceous tissues such as claw, albumen, and blood is most influenced by the isotope signature of protein fractions of the foods consumed (a process known as isotopic routing – e.g. see Bearhop *et al.* 2002; Podlesak *et al.* 2005). As a consequence, the isotopic signature of whole foods might not always predict the isotopic signature of a tissue reliably. In my study, after initial SIA of tissues, it was apparent that isotopic routing was likely to be influential, particularly with respect to peanut cake that was 70.5% fat and only 17.1% protein (CJ Wildlife pers. comm.). To account for this, $\delta^{13}C$ values were calculated from fat-extracted foods types ($\delta^{15}N$ values were derived from non fat-extracted counterparts – see Sears *et al.* 2009). The $\delta^{13}C$ of lipid-rich food types was enriched by fat-extraction, particularly in peanut cake that caused isotopic separation of this food from other food types to be less pronounced (see Appendix Five).

Food samples were rinsed in distilled water (except peanut cake), decanted into plastic weighing boats, and oven-dried at 50-60 ºC for *c.* two days. To minimise sample loss, samples were ground *in situ* in the weighing boats using a pestle after drying. Lipid was extracted from all foods using multiple rinses in 1:1 chloroform:methanol. Eggs were hard-baked, dissected, and albumen fractions were dried as described in Chapter Three. Blood components were oven-dried at 50-60 ºC or freeze-dried for *c.* 12 hrs and *c.* 2 hrs, respectively. To maximise the probability of supplement use being detected in adult claws, I gripped the proximal (i.e. more recent growth) end of each claw in a pair of tweezers and I trimmed 1 mm from the distal (tip) end. The proximal section underwent SIA. All samples (*c.* 0.7 mg for animal material and *c.* 1.0 mg for seeds and peanut cake) were loaded into tin capsules and were analysed at the Scottish Universities Environmental Research Centre (SUERC) at East Kilbride using a continuous flow isotope ratio mass spectrometer (Thermo Fisher Scientific, Delta Plus XP IRMS – Bremen, Germany) coupled to an elemental analyser (Costech, Costech ECS 4010 – Milan, Italy) to determine stable isotope ratios of C and N. Stable isotope ratios were expressed in parts per thousand (‰) using the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 1000$$

where *X* is ^{13}C or ^{15}N and *R* is the corresponding isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ is the international standard for C (PDB) and N (AIR). Reproducibility was around 0.25‰ for $\delta^{15}N$ and 0.10‰ for $\delta^{13}C$, as indicated by gelatine replicates and alanine internal references.

5.3.4. Isotopic analytical considerations

The proportion of different food types in the diet of blue and great tits was estimated on an individual basis for adult tissues and egg albumens, and on brood means for nestlings. In analyses of blood, the red blood cell and plasma fractions were treated as two data points per individual or brood because this provided more robust estimates of dietary contributions. The trophic enrichment factors (otherwise known as fractionation or discrimination factors; hereafter 'TEFs' – Inger & Bearhop 2008) used in analyses reflected values in similar passerines – claw (from values for feather that is also keratin-rich): $\Delta^{13}C = +2.9‰$, $\Delta^{15}N = +3.7‰$; blood: $\Delta^{13}C = +1.1‰$, $\Delta^{15}N = +2.3‰$ (Hobson & Bairlein 2003; Pearson *et al.* 2003). The TEFs for albumens were from less-related species (e.g. waterfowl and raptors): $\Delta^{13}C = +1.1‰$, $\Delta^{15}N = +3.0‰$ (Hobson 1995) due to an absence of estimates in more-similar species. The TEF for $\Delta^{13}C_{diet\text{-}blood}$ was adjusted for the $\delta^{13}C$ of each food type (*sensu* Caut *et al.* 2009). Potential error regarding these TEFs (± 1 SD) was specified in each statistical model (see Section 5.3.6). Concentration dependence (mean ± 1 SD of the % C and N of each food type) was controlled (Phillips & Koch 2002; Pearson *et al.* 2003).

5.3.5. Filtering data

Since multiple replicates of each individual food source underwent SIA, any outlying $\delta^{13}C$ and $\delta^{15}N$ values were identified but were only excluded if unreliable (e.g. due to the weight of the sample being too heavy or light and/or suspected sample contamination). In the final analyses, the δ^{13}C and δ^{15}N values of each food source were determined from a minimum of two replicates (Bearhop *et al.* 1999; Sears *et al.* 2009). One albumen sample appeared to be contaminated with yolk and was excluded from all analyses.

5.3.6. Statistical analysis

The proportion of different foods in the diet was estimated using Stable Isotope Analysis in R (SIAR) (Parnell & Jackson 2008). Each model using SIAR produced a range of solutions regarding the proportional contribution of each food type to the diet. The median of these values represented the maximum likelihood value (i.e. the most probable solution). This value was used to test for differences in the intake of different food types between treatments, and considered all breeding attempts. The maximum likelihood value was also used to test associations between supplement intake and various breeding parameters in 2007: clutch initiation date, clutch size, incubation period, hatching success, fledging success, and recapture success (see Chapters Two & Four for definitions and for details of how data were filtered, covariates used, and error structures). These parameters were selected because of significant differences between dietary treatments (Chapters Two & Four). In these analyses data were pooled across all dietary treatments, and the latter was not included as a predictor in any analysis since supplement intake was predicted to be synonymous with dietary treatment. All predictors were specified as fixed factors with analyses conducted using PROC GLIMMIX in SAS (SAS Institute Inc. 2008) and Minitab 15 (Minitab 2007).

Sex-specific differences in adult supplement use were not examined between treatments due to relatively small sample sizes, particularly with respect to blood. However, sex-specific patterns in adult supplement use *versus* breeding parameters were examined due to the pooling of data across treatments. In addition, supplement intake per pair (mean of the

$\delta^{13}C$ and $\delta^{15}N$ of each tissue per pair) *versus* breeding parameters were also examined. Where both members of a pair were not sampled, data for either the breeding male or female were used.

5.4. Results

5.4.1. Isotopic separation between food supplements and natural foods

For descriptive purposes, the isotopic separation between food supplements and natural foods is presented in Figure 5.1. The isotopic separation of mealworms was pronounced with respect to $\delta^{15}N$, whereas peanut cake had the most positive $\delta^{13}C$ value of all food types (Fig. 5.1).

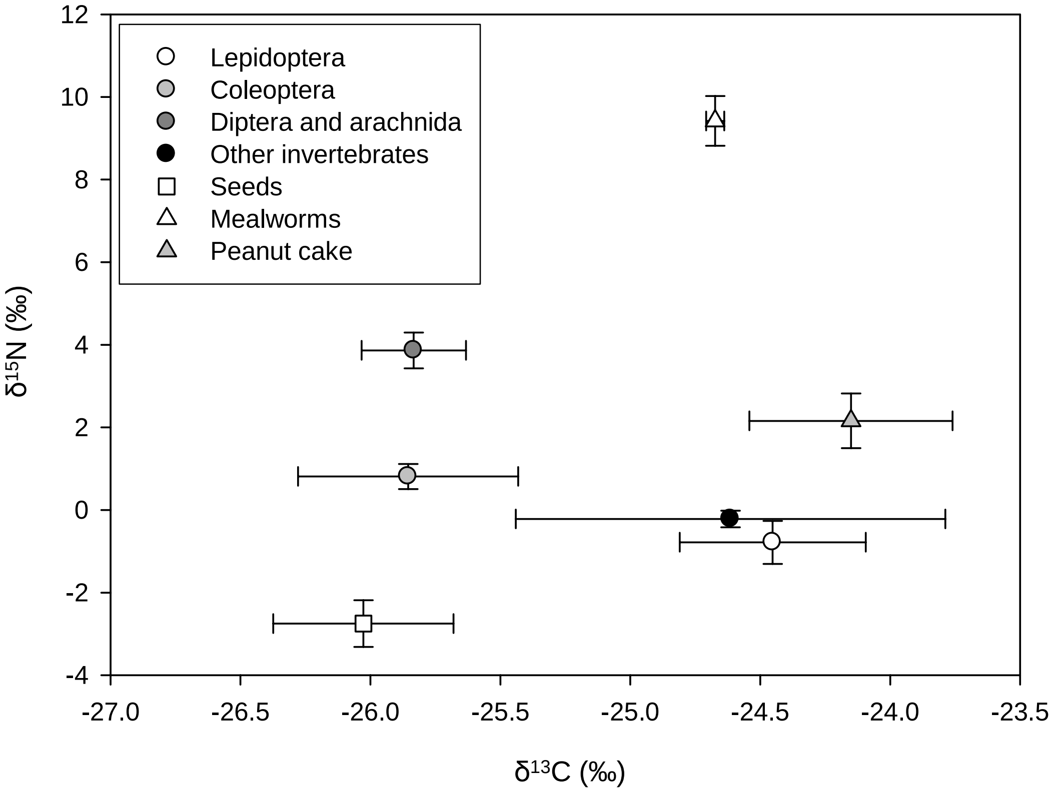

Figure 5.1. $\delta^{13}C$ and $\delta^{15}N$ values (mean ± 1 SD) of food types used in stable isotope analyses of tissues of blue and great tits sampled at Chaddesley Woods National Nature Reserve in 2007. $\delta^{13}C$ is from fat-extracted samples and $\delta^{15}N$ is from non-fat-extracted samples. Supplements are denoted by triangles and naturally occurring food types by circles (invertebrates) or by a square (seeds). Not all food types were considered in the analyses of each tissue type (egg albumen, claw, or blood) and/or age class (adults or nestlings). See text for details.

5.4.2. Differences in diet between treatments

Despite some significant differences in δ^{13}C and δ^{15}N values between treatments (Table 5.1), estimated consumption of different food types in each treatment was similar (Figs 5.2 & 5.3). There was some evidence that adult blue tits on supplemented territories consumed more

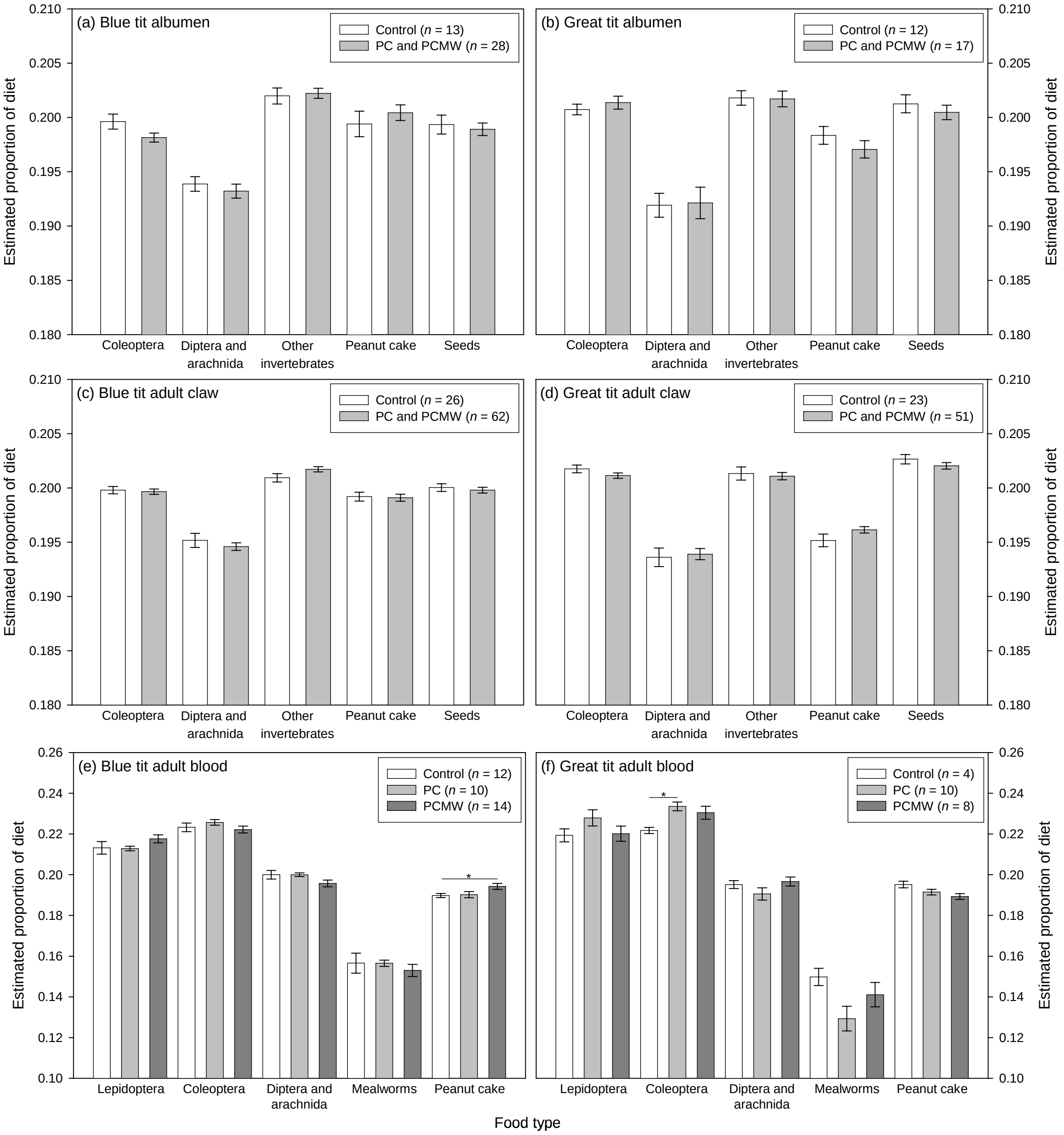

Figure 5.2. The proportion of different food types in the diet of adult blue and great tits (mean ± 1 SE of the maximum likelihood values per individual estimated using SIAR) at Chaddesley Woods National Nature Reserve in 2007. Tissues: albumen (a,b), claw (c,d), and blood (plasma and red blood cells) (e,f). Samples were from three dietary treatments: control (non-supplemented), PC (peanut cake), and PCMW (peanut cake and mealworms). PC and PCMW are combined for albumen and claw (see Table 5.1 for explanation). * = $P \leq 0.05$. See text for details.

Table 5.1. δ^{13}C and δ^{15}N values (mean ± 1 SD) of tissues of adult and nestling blue (BT) and great (GT) tits sampled at Chaddesley Woods National Nature Reserve in 2007. Samples from three treatments: C = control (non-supplemented), PC = peanut cake, and PCMW = peanut cake and mealworms. PC and PCMW are combined for albumen and adult claw because mealworm intake would not be detected (mealworms were not supplemented during tissue formation). Differences between treatments are tested: * = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$. Significant least squares means tests (adjusted, where applicable, for multiple comparisons via the Tukey method) are given. 'NS' denotes non-significance ($P > 0.05$), 'N/A' = not applicable. See text for details.

						δ^{13}C	δ^{15}N	Significant least squares means	
Age class	**Tissue**	**Sp.**	**Treatment**	**δ^{13}C (‰)**	**δ^{15}N (‰)**	***P***	***P***	**δ^{13}C**	**δ^{15}N**
Breeding adult	Albumen	BT	C	-23.83 (±0.97)	0.85 (±0.72)	NS	NS	N/A	N/A
			PC and PCMW	-23.85 (±1.22)	1.05 (±0.70)				
		GT	C	-24.56 (±1.38)	2.14 (±1.05)	NS	NS	N/A	N/A
			PC and PCMW	-24.85 (±1.15)	2.50 (±0.81)				
	Claw	BT	C	-22.40 (±0.20)	1.06 (±0.80)	NS	**	N/A	C *vs.* PC and PCMW **
			PC and PCMW	-22.38 (±0.32)	1.47 (±0.66)				
		GT	C	-22.87 (±0.33)	3.21 (±0.90)	NS	**	N/A	C *vs.* PC and PCMW **
			PC and PCMW	-22.85 (±0.32)	2.69 (±0.78)				
	Red blood cells	BT	C	-24.59 (±0.32)	0.54 (±0.82)	***	NS	C *vs.* PCMW *** PC *vs.* PCMW *	N/A
			PC	-24.33 (±0.57)	0.70 (±0.39)				
			PCMW	-23.81 (±0.37)	0.85 (±0.70)				
		GT	C	-24.58 (±0.27)	1.15 (±0.79)	NS	NS	N/A	N/A
			PC	-24.54 (±0.27)	1.79 (±0.60)				
			PCMW	-24.48 (±0.25)	1.50 (±0.57)				
	Plasma	BT	C	-25.99 (±0.48)	1.39 (±0.66)	*	NS	C *vs.* PCMW *	N/A
			PC	-25.58 (±0.37)	1.31 (±0.44)				
			PCMW	-25.53 (±0.47)	1.50 (±0.78)				
		GT	C	-26.72 (±0.31)	1.61 (±0.92)	***	NS	C *vs.* PC ** C *vs.* PCMW ***	N/A
			PC	-25.81 (±0.35)	2.37 (±0.44)				
			PCMW	-25.68 (±0.49)	1.98 (±0.79)				
Nestling	Claw	BT	C	-24.17 (±0.34)	-0.30 (±0.70)	**	NS	C *vs.* PCMW ***	N/A
			PC	-23.79 (±0.47)	0.03 (±1.09)				
			PCMW	-23.45 (±0.50)	-0.16 (±0.79)				
		GT	C	-23.99 (±0.39)	0.15 (±0.71)	NS	NS	N/A	N/A
			PC	-23.74 (±0.46)	0.39 (±0.84)				
			PCMW	-23.52 (±0.43)	0.37 (±0.76)				
	Red blood cells	BT	C	-25.75 (±0.41)	0.02 (±0.88)	**	NS	C *vs.* PCMW **	N/A
			PC	-25.38 (±0.49)	0.27 (±1.25)				
			PCMW	-25.00 (±0.38)	0.15 (±0.56)				
		GT	C	-25.56 (±0.44)	0.25 (±0.63)	NS	NS	N/A	N/A

Table 5.1. continued

						$\delta^{13}C$	$\delta^{15}N$	**Significant least squares means**	
Age class	**Tissue**	**Sp.**	**Treatment**	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	***P***	***P***	**$\delta^{13}C$**	**$\delta^{15}N$**
Nestling	Red blood cells	GT	PC	-25.16 (±0.49)	0.21 (±0.84)				
			PCMW	-24.91 (±0.47)	0.06 (±0.79)				
	Plasma	BT	C	-27.87 (±0.36)	0.55 (±0.73)	NS	NS	N/A	N/A
			PC	-27.56 (±0.82)	0.77 (±0.98)				
			PCMW	-27.39 (±0.96)	0.65 (±0.71)				
		GT	C	-27.99 (±0.63)	0.75 (±0.77)	NS	NS	N/A	N/A
			PC	-27.20 (±0.46)	0.86 (±0.78)				
			PCMW	-27.33 (±0.92)	0.39 (±0.86)				

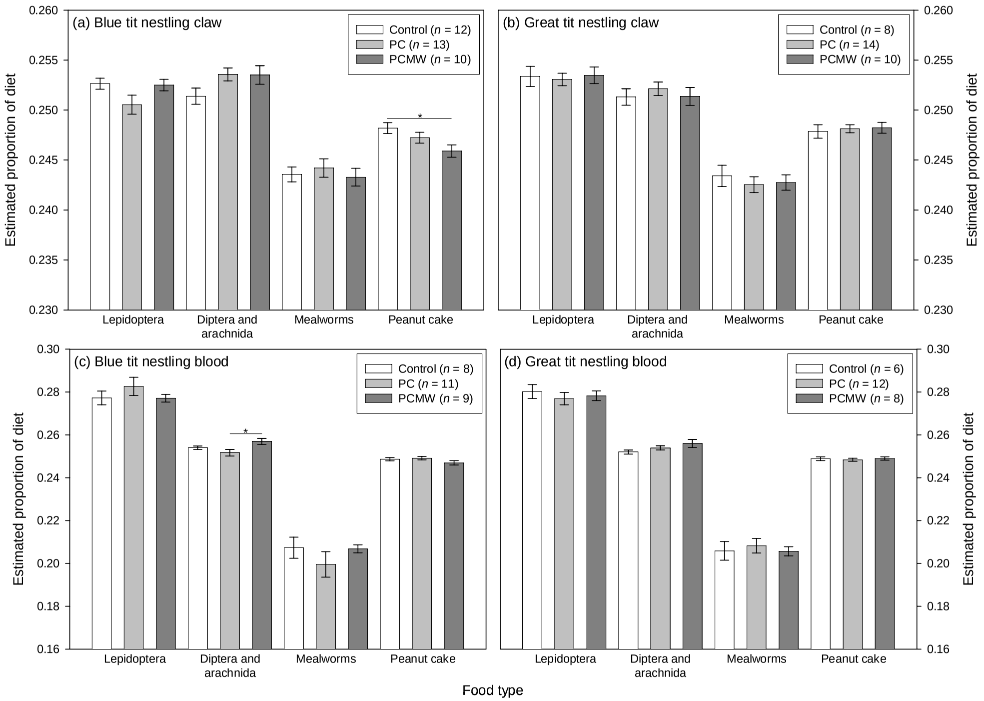

Figure 5.3. The proportion of different food types in the diet of nestling blue and great tits (mean ± 1 SE of the maximum likelihood values per brood estimated using SIAR) at Chaddesley Woods National Nature Reserve in 2007. Tissues: claw (a,b) and blood (plasma and red blood cells) (c,d). See Figure 5.2 for explanations of treatments. * = $P \leq 0.05$. See text for details.

peanut cake than controls (blood: $F_{2,33} = 3.65$, $P = 0.04$) (Fig. 5.2e) but the opposite was found in blue tit nestlings (claw: $F_{2,32} = 3.81$, $P = 0.03$) (Fig. 5.3a). However, all other comparisons of the proportion of peanut cake and mealworm intake between treatments were non-significant (all *P*s > 0.05) (Figs 5.2 & 5.3). Moreover, while some significant differences in the intakes of natural food types between treatments were apparent, these differences were rare (Figs 5.2 & 5.3).

Proportions of the diet presented in Figures 5.2 and 5.3 were calculated on an individual (i.e. adult) or brood (i.e. nestling) basis. This small sample size per estimate appeared to cause some uncertainty in the absolute values produced. For example, when five potential food types were specified, the proportional contribution of each tended to centre on 0.20 (Fig. 5.2). When four potential sources were specified, proportions centred on 0.25 (Fig. 5.3). Indeed, blood revealed greater absolute differences in the intake of different food types compared with albumen or claw (Figs 5.2 & 5.3) because two data points (i.e. plasma and red blood cells) were used per individual or brood, rather than one data point as in analyses of albumen and claw. It should be considered, therefore, that these estimates (Figs 5.2 & 5.3) provide an indication of relative, rather than absolute, contributions of different food types to the diet.

In order to obtain more accurate values in absolute terms, I combined the $\delta^{13}C$ and $\delta^{15}N$ values for all individuals or broods in each treatment for each tissue illustrated in Figures 5.2 and 5.3. After differences in sample size and, therefore, statistical power between treatments was controlled (by selecting the same number of samples per treatment, based on the treatment with the smallest sample size), maximum likelihood values for peanut cake intake did not exceed 0.22 (blue tit albumen, PC and PCMW) and averaged 0.11 (albumen), 0.09 (adult claw), 0.09 (adult blood), 0.16 (nestling claw), and 0.09 (nestling blood) across species and treatments. Maximum likelihood values for mealworm intake did not exceed 0.06 (great tit nestling claw, both control and PCMW) and averaged 0.01 (adult blood), 0.05 (nestling claw), and 0.01 (nestling blood) across species and treatments. To exemplify this low supplement intake a selection of results are provided in Figures 5.4 and 5.5.

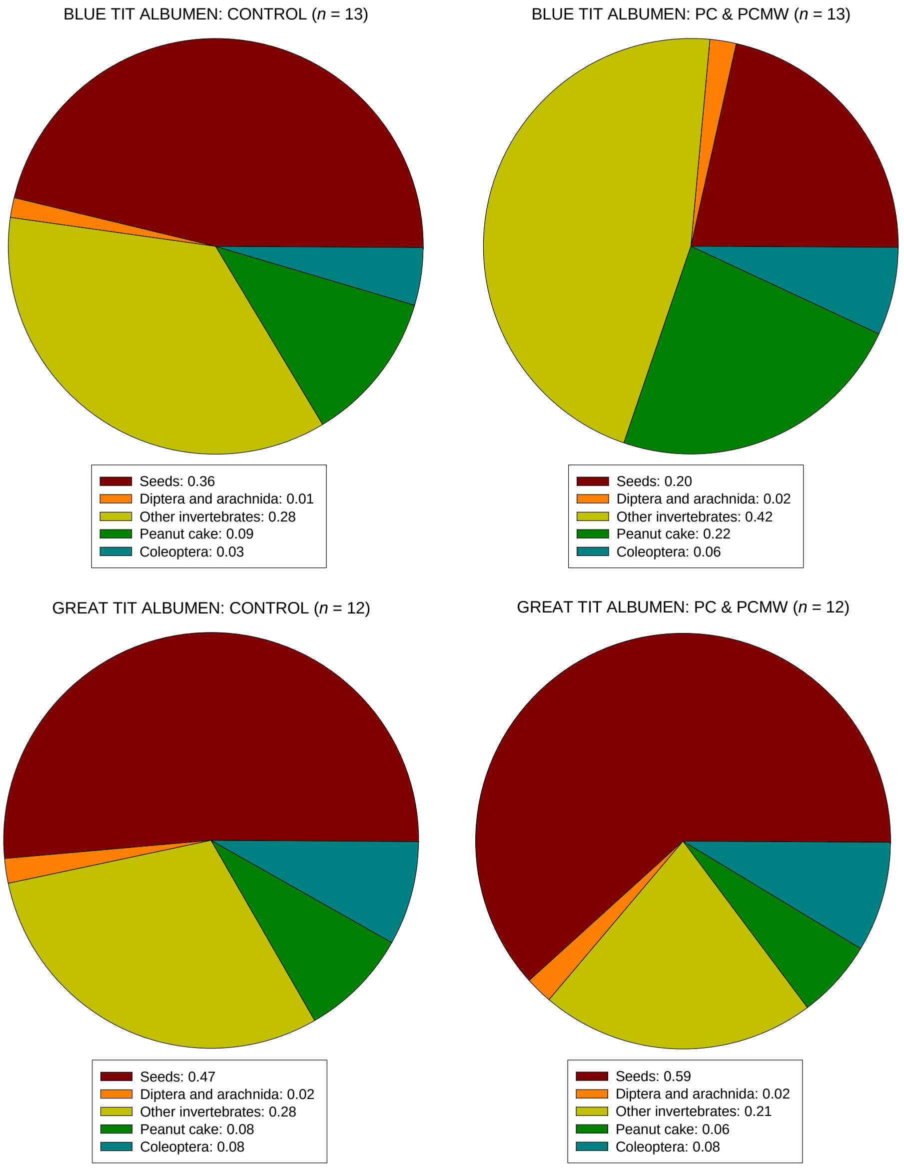

Figure 5.4. The proportion of natural and supplementary (peanut cake) food in the diet of blue and great tits at Chaddesley Woods National Nature Reserve in 2007, examined through stable isotope analysis of egg albumen. See Figure 5.2 for explanations of treatments. The proportion of each food type is the maximum likelihood value calculated using SIAR from combined δ^{13}C and δ^{15}N values for all eggs across each treatment (controlling for differences in sample size). Since maximum likelihood values represent the median, rather than the mean, of all possible solutions, the sum of the maximum likelihood values per treatment does not necessarily equal one. See text for details.

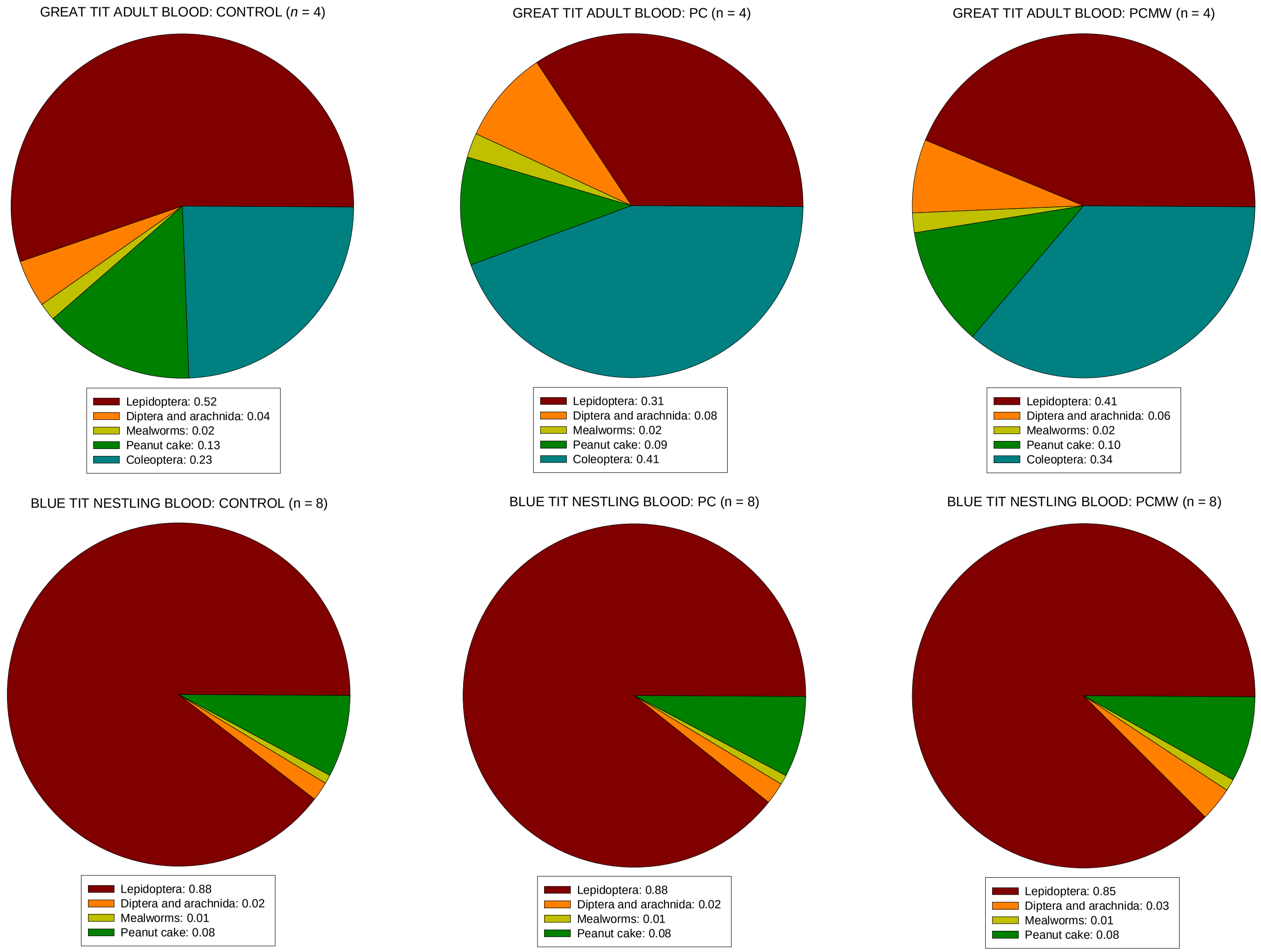

Figure 5.5. The proportion of natural and supplementary (peanut cake and mealworms) foods in the diet of adult great tits and nestling blue tits at Chaddesley Woods National Nature Reserve in 2007, examined through stable isotope analysis of blood (plasma and red blood cells). See Figure 5.2 for explanations of treatments. The proportion of each food type is the maximum likelihood value calculated using SIAR from combined $\delta^{13}C$ and $\delta^{15}N$ values for all individuals (i.e. adults) or broods (i.e. nestlings) across each treatment (controlling for differences in sample size). Since maximum likelihood values represent the median, rather than the mean, of all possible solutions, the sum of the maximum likelihood values per treatment does not necessarily equal one. See text for details.

5.4.3. Supplement use versus breeding parameters

In blue tits, there was evidence that when pairs consumed proportionately more peanut cake, clutch initiation advanced significantly (claw: $F_{1,52} = 3.86$, $P = 0.05$; blood: $F_{1,24} = 4.47$, $P = 0.05$) (Fig. 5.6a). However, such patterns did not extend to albumen of blue tits, or any tissue of great tits (all Ps > 0.05) (Table 5.2). Proportionately greater intake of peanut cake associated positively with clutch size in blue (male claw: $F_{1,29} = 8.48$, $P = 0.007$) and great (albumen: $F_{1,25} = 4.37$, $P = 0.05$; female and male blood: $F_{1,9} = 5.54$, $P = 0.04$) tits (Fig. 5.6b). However, all other comparisons with respect to clutch size were non-significant (all Ps > 0.05) (Table 5.2). Incubation period and hatching success were not explained significantly by the proportion of peanut cake in the diet (all Ps > 0.05) (Table 5.2), although the latter tended to be higher in blue tits that consumed proportionately more peanut cake (albumen: $F_{1,37} = 3.63$, $P = 0.06$).

Fledging success associated negatively with the proportion of peanut cake in the diet in female blue tits (blood: $F_{1,18} = 6.08$, $P = 0.02$) (Fig. 5.6c). Moreover, there was evidence that fledging success of blue tits declined when nestlings were provisioned with proportionately more mealworms (claw: $F_{1,30} = 4.17$, $P = 0.05$). Conversely, great tit pairs that consumed proportionately more peanut cake experienced significantly greater fledging success (blood: $F_{1,8} = 272.68$, $P < 0.001$) (Fig. 5.6d), an effect driven mostly by females (blood: $F_{1,6} = 219.68$, $P < 0.001$). An increased proportion of mealworms in the diet of female great tits (blood: $F_{1,6} = 849.61$, $P < 0.001$) (Fig. 5.6e) also associated with significantly higher fledging success. Fledging success of great tits increased when nestlings were fed with proportionately more peanut cake (blood: $F_{1,17} = 5.48$, $P = 0.03$) (Fig. 5.6f). All other adult and nestling tissue comparisons with respect to fledging success were non-significant (all Ps > 0.05) (Table 5.2).

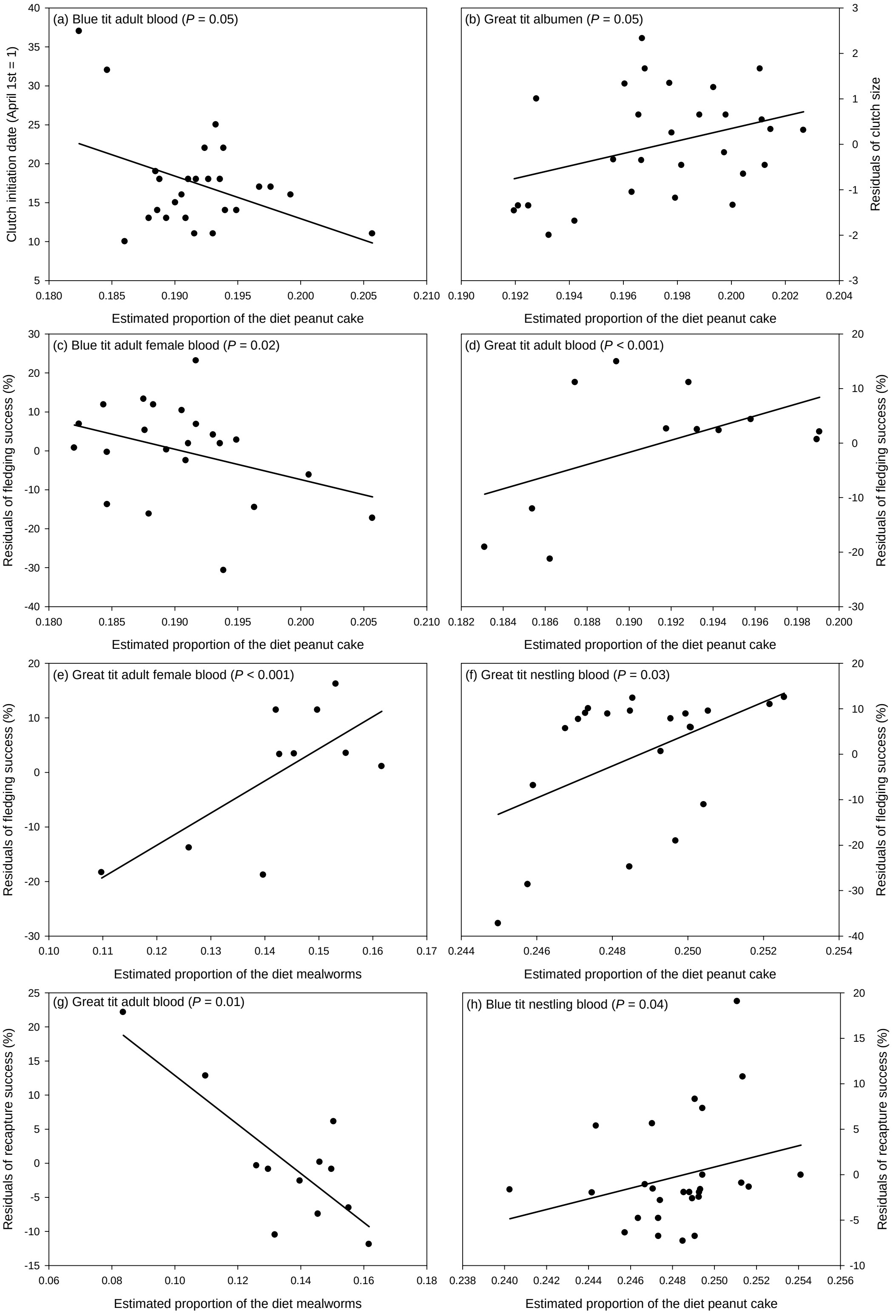

Figure 5.6. Significant relationships between breeding parameters of blue and great tits and the proportion of peanut cake or mealworms in the diet (maximum likelihood values per individual or brood estimated using SIAR) at Chaddesley Woods National Nature Reserve in 2007. Species, age class, tissue (blood = plasma and red blood cells), and sex (where results are restricted to one sex) are specified. Residuals show the relationship between relative supplement intake and each dependent variable while accounting (where applicable) for all other predictors in the model. See Table 5.2 for statistical tests and see text for details.

Table 5.2. Relationships (*F* and associated *P* values) between breeding parameters of blue (BT) and great (GT) tits and the proportion of peanut cake or mealworms in the diet (maximum likelihood values per individual or brood estimated using SIAR) of adults and nestlings at Chaddesley Woods National Nature Reserve in 2007. Tissues sampled specified (blood = plasma and red blood cells), as is sex ('F' = female, 'M' = male, 'N/A' = not applicable). Significant *P* values are in bold text with directions given: '+' and '-' denote significant positive and negative associations, respectively. 'NS' denotes non-significance ($P > 0.05$). Additional predictors were included in some models, see text for details.

						Effect of proportion of supplement in diet		
Breeding parameter	**Supplement**	**Age class**	**Tissue**	**Sp.**	**Sex**	***F***	***P***	**Direction**
Clutch initiation date	Peanut cake	Breeding adult	Albumen	BT	N/A	$F_{1,39} = 0.64$	$P = 0.43$	NS
				GT	N/A	$F_{1,26} = 0.82$	$P = 0.37$	NS
			Claw	BT	F	$F_{1,47} = 1.21$	$P = 0.28$	NS
					M	$F_{1,31} = 0.56$	$P = 0.46$	NS
					F&M	$F_{1,52} = 3.86$	$\boldsymbol{P = 0.05}$	-
				GT	F	$F_{1,31} = 1.64$	$P = 0.21$	NS
					M	$F_{1,30} = 0.03$	$P = 0.86$	NS
					F&M	$F_{1,37} = 0.15$	$P = 0.71$	NS
			Blood	BT	F	$F_{1,21} = 2.48$	$P = 0.13$	NS
					M	$F_{1,10} = 1.77$	$P = 0.21$	NS
					F&M	$F_{1,24} = 4.47$	$\boldsymbol{P = 0.05}$	-
				GT	F	$F_{1,8} = 0.06$	$P = 0.81$	NS
					M	$F_{1,4} = 1.59$	$P = 0.28$	NS
					F&M	$F_{1,10} = 0.90$	$P = 0.37$	NS
Clutch size	Peanut cake	Breeding adult	Albumen	BT	N/A	$F_{1,37} = 0.03$	$P = 0.87$	NS
				GT	N/A	$F_{1,25} = 4.37$	$\boldsymbol{P = 0.05}$	+
			Claw	BT	F	$F_{1,45} = 1.26$	$P = 0.27$	NS
					M	$F_{1,29} = 8.48$	$\boldsymbol{P = 0.007}$	+
					F&M	$F_{1,50} = 2.91$	$P = 0.09$	NS
				GT	F	$F_{1,30} = 0.25$	$P = 0.62$	NS
					M	$F_{1,29} = 1.26$	$P = 0.27$	NS
					F&M	$F_{1,36} = 0.00$	$P = 0.97$	NS
			Blood	BT	F	$F_{1,19} = 0.33$	$P = 0.57$	NS
					M	$F_{1,9} = 2.27$	$P = 0.17$	NS
					F&M	$F_{1,22} = 0.12$	$P = 0.73$	NS
				GT	F	$F_{1,7} = 4.24$	$P = 0.08$	NS
					M	$F_{1,3} = 0.40$	$P = 0.57$	NS
					F&M	$F_{1,9} = 5.54$	$\boldsymbol{P = 0.04}$	+
Incubation period	Peanut cake	Breeding adult	Albumen	BT	N/A	$F_{1,37} = 2.62$	$P = 0.11$	NS
				GT	N/A	$F_{1,24} = 1.04$	$P = 0.32$	NS

Table 5.2. continued

						Effect of proportion of supplement in diet		
Breeding parameter	**Supplement**	**Age class**	**Tissue**	**Sp.**	**Sex**	***F***	***P***	**Direction**
Incubation period	Peanut cake	Breeding adult	Claw	BT	F	$F_{1,43} = 1.14$	$P = 0.29$	NS
					M	$F_{1,28} = 0.46$	$P = 0.50$	NS
					F&M	$F_{1,48} = 2.00$	$P = 0.16$	NS
				GT	F	$F_{1,29} = 0.29$	$P = 0.60$	NS
					M	$F_{1,28} = 0.02$	$P = 0.89$	NS
					F&M	$F_{1,35} = 0.16$	$P = 0.69$	NS
			Blood	BT	F	$F_{1,18} = 0.05$	$P = 0.82$	NS
					M	$F_{1,8} = 0.35$	$P = 0.57$	NS
					F&M	$F_{1,21} = 0.00$	$P = 0.97$	NS
				GT	F	$F_{1,6} = 0.00$	$P = 0.98$	NS
					M	$F_{1,2} = 1.10$	$P = 0.41$	NS
					F&M	$F_{1,8} = 0.07$	$P = 0.80$	NS
Hatching success	Peanut cake	Breeding adult	Albumen	BT	N/A	$F_{1,37} = 3.63$	$P = 0.06$	NS
				GT	N/A	$F_{1,25} = 2.87$	$P = 0.10$	NS
			Claw	BT	F	$F_{1,43} = 1.31$	$P = 0.26$	NS
					M	$F_{1,28} = 0.08$	$P = 0.78$	NS
					F&M	$F_{1,48} = 1.29$	$P = 0.26$	NS
				GT	F	$F_{1,29} = 0.12$	$P = 0.74$	NS
					M	$F_{1,28} = 0.42$	$P = 0.52$	NS
					F&M	$F_{1,35} = 0.25$	$P = 0.62$	NS
			Blood	BT	F	$F_{1,18} = 1.07$	$P = 0.32$	NS
					M	$F_{1,9} = 0.09$	$P = 0.78$	NS
					F&M	$F_{1,21} = 1.85$	$P = 0.19$	NS
				GT	F	$F_{1,7} = 0.16$	$P = 0.70$	NS
					M	$F_{1,3} = 2.94$	$P = 0.18$	NS
					F&M	$F_{1,9} = 0.32$	$P = 0.58$	NS
Fledging success	Peanut cake	Breeding adult	Albumen	BT	N/A	$F_{1,37} = 1.63$	$P = 0.21$	NS
				GT	N/A	$F_{1,23} = 3.95$	$P = 0.06$	NS
			Claw	BT	F	$F_{1,43} = 0.39$	$P = 0.54$	NS
					M	$F_{1,29} = 3.38$	$P = 0.08$	NS
					F&M	$F_{1,48} = 0.01$	$P = 0.93$	NS
				GT	F	$F_{1,28} = 0.02$	$P = 0.90$	NS
					M	$F_{1,27} = 0.14$	$P = 0.71$	NS
					F&M	$F_{1,34} = 0.07$	$P = 0.79$	NS
			Blood	BT	F	$F_{1,18} = 6.08$	$\mathbf{P = 0.02}$	-

Table 5.2. continued

						Effect of proportion of supplement in diet		
Breeding parameter	**Supplement**	**Age class**	**Tissue**	**Sp.**	**Sex**	***F***	***P***	**Direction**
Fledging success	Peanut cake	Breeding adult	Blood	BT	M	$F_{1,9} = 1.39$	$P = 0.27$	NS
					F&M	$F_{1,22} = 3.32$	$P = 0.08$	NS
				GT	F	$F_{1,6} = 219.68$	$\boldsymbol{P < 0.001}$	+
					M	$F_{1,2} = 0.00$	$P = 0.99$	NS
					F&M	$F_{1,8} = 272.68$	$\boldsymbol{P < 0.001}$	+
	Mealworms	Breeding adult	Blood	BT	F	$F_{1,18} = 2.15$	$P = 0.16$	NS
					M	$F_{1,9} = 3.82$	$P = 0.08$	NS
					F&M	$F_{1,22} = 3.38$	$P = 0.08$	NS
				GT	F	$F_{1,6} = 849.61$	$\boldsymbol{P < 0.001}$	+
					M	$F_{1,2} = 0.00$	$P = 1.00$	NS
					F&M	$F_{1,8} = 2.70$	$P = 0.14$	NS
	Peanut cake	Nestling	Claw	BT	N/A	$F_{1,30} = 1.66$	$P = 0.21$	NS
				GT	N/A	$F_{1,22} = 0.00$	$P = 0.97$	NS
			Blood	BT	N/A	$F_{1,23} = 1.76$	$P = 0.20$	NS
				GT	N/A	$F_{1,17} = 5.48$	$\boldsymbol{P = 0.03}$	+
	Mealworms	Nestling	Claw	BT	N/A	$F_{1,30} = 4.17$	$\boldsymbol{P = 0.05}$	-
				GT	N/A	$F_{1,22} = 0.17$	$P = 0.69$	NS
			Blood	BT	N/A	$F_{1,23} = 2.10$	$P = 0.16$	NS
				GT	N/A	$F_{1,17} = 0.89$	$P = 0.36$	NS
Recapture success	Peanut cake	Breeding adult	Albumen	BT	N/A	$F_{1,24} = 0.48$	$P = 0.50$	NS
				GT	N/A	$F_{1,15} = 0.17$	$P = 0.68$	NS
			Claw	BT	F	$F_{1,41} = 1.61$	$P = 0.21$	NS
					M	$F_{1,29} = 1.98$	$P = 0.17$	NS
					F&M	$F_{1,47} = 0.91$	$P = 0.35$	NS
				GT	F	$F_{1,26} = 0.27$	$P = 0.60$	NS
					M	$F_{1,25} = 0.14$	$P = 0.72$	NS
					F&M	$F_{1,33} = 0.17$	$P = 0.68$	NS
			Blood	BT	F	$F_{1,16} = 1.14$	$P = 0.30$	NS
					M	$F_{1,9} = 0.07$	$P = 0.80$	NS
					F&M	$F_{1,21} = 0.49$	$P = 0.49$	NS
				GT	F	$F_{1,6} = 5.97$	$\boldsymbol{P = 0.05}$	-
					M	$F_{1,2} = 8056.94$	$\boldsymbol{P < 0.001}$	+
					F&M	$F_{1,8} = 0.63$	$P = 0.45$	NS
	Mealworms	Breeding adult	Blood	BT	F	$F_{1,16} = 2.22$	$P = 0.16$	NS
					M	$F_{1,9} = 11.23$	$\boldsymbol{P = 0.009}$	+

Table 5.2. continued

						Effect of proportion of supplement in diet		
Breeding parameter	**Supplement**	**Age class**	**Tissue**	**Sp.**	**Sex**	***F***	***P***	**Direction**
Recapture success	Mealworms	Breeding adult	Blood	BT	F&M	$F_{1,20} = 2.34$	$P = 0.14$	NS
				GT	F	$F_{1,6} = 5.06$	$P = 0.07$	NS
					M	$F_{1,2} = 21004.7$	**P < 0.001**	-
					F&M	$F_{1,8} = 10.97$	**P = 0.01**	-
	Peanut cake	Nestling	Claw	BT	N/A	$F_{1,30} = 0.25$	$P = 0.62$	NS
				GT	N/A	$F_{1,21} = 0.02$	$P = 0.89$	NS
			Blood	BT	N/A	$F_{1,23} = 4.91$	**P = 0.04**	+
				GT	N/A	$F_{1,16} = 0.21$	$P = 0.65$	NS
	Mealworms	Nestling	Claw	BT	N/A	$F_{1,30} = 0.08$	$P = 0.78$	NS
				GT	N/A	$F_{1,21} = 0.78$	$P = 0.39$	NS
			Blood	BT	N/A	$F_{1,23} = 0.22$	$P = 0.64$	NS
				GT	N/A	$F_{1,16} = 0.71$	$P = 0.41$	NS

Recapture success of fledglings associated positively with the proportion of mealworms in the diet of male blue tits (blood: $F_{1,9} = 11.23$, $P = 0.009$). However, recapture success associated negatively with the proportion of mealworms in the diet of great tit pairs (blood: $F_{1,8} = 10.97$, $P = 0.01$) (Fig. 5.6g), an effect driven most significantly by males (blood: $F_{1,2} = 21004.7$, $P < 0.001$). A negative association with recapture success was also found with the proportion of peanut cake in the diet of great tit females (blood: $F_{1,6} = 5.97$, $P = 0.05$), although the opposite was found in males (blood: $F_{1,2} = 8056.94$, $P < 0.001$). All other adult tissue comparisons with respect to recapture success were non-significant (all *P*s > 0.05) (Table 5.2). Proportionately more peanut cake in the diet of blue tit nestlings associated positively with recapture success (blood: $F_{1,23} = 4.91$, $P = 0.04$) (Fig. 5.6h), but all other relationships between recapture success and the proportion of either peanut cake or mealworms in the diet of nestlings were non-significant in both species (all *P*s > 0.05) (Table 5.2).

5.5. Discussion

Significant differences in the isotopic signatures of tissues between treatments were found (Table 5.1), but these differences were not universal and were usually small (maximum difference between means: 1.04‰), suggesting that diets in each treatment were similar. Indeed, few significant differences were found in the estimated intake of different food types between treatments (Figs 5.2 & 5.3). Increased statistical power revealed that supplements formed only a subsidiary part of the diet (e.g. Figs 5.4 & 5.5). Despite minimal intake, proportionately greater food supplement use related significantly to numerous breeding parameters (Fig. 5.6; Table 5.2), some of which (e.g. larger clutches and, in great tits, higher fledging success) contradicted effects of food supplements being provided on breeding territories (e.g. reduced clutch size and fledging success – Chapters Two & Four). These results do not support my hypotheses that peanut cake and mealworm use would be highest in treatments in which these supplements were provided, nor that differences in supplement use would explain differences in breeding parameters between treatments. Instead, these findings suggest other, unexpected, mechanisms with which food supplementation can influence avian reproduction.

5.5.1. Supplement use between treatments

5.5.1.1. Peanut cake

Peanut cake was a subsidiary food in both species (e.g. Figs 5.4 & 5.5), with similar relative intakes across treatments (Figs 5.2 & 5.3). This suggests low peanut cake intake across individuals and broods, and a lack of treatment fidelity. The latter is possible particularly because parid foraging ranges can extend *c.* 300 m for some nutrients (e.g. calcium – Wilkin *et al.* 2009). However, both species are territorial during reproduction (Gosler 1993) and the centre of home ranges are likely to be held exclusively by resident pairs (Naef-Daenzer 1994). Moreover, it is questionable why control birds would forage in supplemented territories unless peanut cake was an important resource. Field observations suggest that peanut cake consumption was, at least at a population level, widespread (TJEH pers. obs.) so low intake across individuals and broods is surprising.

Therefore, another possibility for low peanut cake use and similar intake between treatments, is that peanut cake intake was detected poorly. Isotopic separation of peanut cake from other food types was not pronounced (Fig. 5.1) so estimates of intake could be unreliable (Figs 5.2-5.5) despite robust statistical analyses. Furthermore, peanut cake is relatively fat-rich and protein-poor, so assessment of use via its fat-extracted δ^{13}C signature in proteinaceous tissues (i.e. egg albumen, claw, and blood) may not be most appropriate. For example, an apparently low contribution to the diet (e.g. Figs 5.4 & 5.5) could still represent substantial calorific intake. Finally, with respect to nestlings, it is possible that intake of peanut cake peaked beyond 12 days post-hatch when tissue sampling occurred. Nestlings are predominantly fed invertebrates (Cramp & Perrins 1993a,b) so provision of peanut cake to nestlings, particularly when they are young, seems unlikely. Current estimates of peanut cake intake in nestlings might, therefore, be conservative.

5.5.1.2. Mealworms

Isotopic separation of mealworms from other food types was pronounced with respect to $\delta^{15}N$ (Fig. 5.1). Therefore, it is reasonable to assume that the lack of differences in mealworm use between treatments (Figs 5.2 & 5.3), coupled with the low contribution of mealworms to the diet (e.g. Fig. 5.5), reflects a lack of utilisation across all treatments, rather than poor detection or a lack of treatment fidelity. However, as suggested in Chapter Four, mealworms are relatively large and chitinous invertebrates, so peak provisioning to nestlings may have occurred beyond 12 days post-hatch when nestling tissues were sampled. Field observations suggest that mealworm use was variable in all three years, and that interspecific use (e.g. by great spotted woodpeckers *Dendrocopos major*) could have contributed to incidents of heavy utilisation (TJEH pers. obs.).

5.5.2. Supplement use versus breeding parameters

5.5.2.1. Clutch initiation date

Clutch initiation date of both species advanced significantly as a result of food supplementation (Chapter Two). Food may be scarce early in the breeding season and this might constrain egg production (the constraint hypothesis: Perrins 1965; Lack 1966). Food supplementation could alleviate such constraints and advance laying. In blue tits, there was evidence that an increased proportion of peanut cake in the diet advanced laying significantly (Fig. 5.6a; Table 5.2). However, this result was not transferable across all tissues of blue tits, and was not found in great tits (Table 5.2). Moreover, the use of peanut cake was similar across treatments (Fig. 5.2) and the relative proportion of peanut cake in the diet was always small.

Therefore, possible effects of peanut cake supplementation that do not necessarily involve considerable supplement intake are interesting to consider. For example, the presence of peanut cake in supplemented treatments might have acted as a visual cue that food availability was increased and that peak food abundance at some point later in the season was advanced, so laying should commence (the cue/anticipation hypothesis: Lack 1954; Perrins 1965). Alternatively, the reliable presence of peanut cake in supplemented treatment blocks could have acted as an ‘insurance cue’ that early breeding was possible. Early-breeding blue and great tits usually recruit most young into the breeding population (Verhulst & Tinbergen 1991) but very early breeding can reduce offspring survival (Norris 1993) and/or the survival of breeding females (Nilsson 1994). Such costs of very early breeding might be because natural food availability is reduced early in the breeding season. Therefore, the presence of peanut cake could have acted as an insurance resource that stimulated early laying. Interestingly, a response to such cues need not be shared across all pairs. For example, these cues could advance territorial behaviour (e.g. singing) in some males that might stimulate reciprocal behaviour in neighbouring males (Foote *et al.* 2008), thereby causing a cascade of advanced territoriality in food-supplemented treatment blocks. Since territorial song can prime both sexes for reproduction (Staicer *et al.* 1996; Helm *et al.* 2006), this could have been the main cause of earlier laying in supplemented treatments.

5.5.2.2. Clutch size

Clutch size of both species reduced significantly as a consequence of food supplementation (Chapter Two). However, the proportion of peanut cake in the diet of adult blue and great tits not only showed few differences between dietary treatments (Fig. 5.2) but associated positively with clutch size on numerous occasions (Fig. 5.6b; Table 5.2). It is likely, therefore, that in supplemented treatment blocks the presence of feeders incurred costs to pairs that did not relate to supplement intake. One possible mechanism is increased territorial intrusion and conflict (Ewald & Rohwer 1982; Schoech *et al.* 2008). For example, male great tits may defend supplemented territories more vigorously than non-supplemented conspecifics (Ydenberg 1984) thereby incurring reproductive costs. Future research should examine in detail measures of condition (e.g. based upon morphometric measures such as those used in Chapter Three) and stress (e.g. levels of corticosterone – Schoech *et al.* 2004) in breeding adults from different dietary treatments.

5.5.2.3. Incubation period

Incubation period of both species shortened significantly as a result of food supplementation (in two of three years in blue tits – Chapter Two). No association was found between the proportion of peanut cake in the diet and the length of the incubation period in either species (Table 5.2). As discussed (see Section 5.5.2.1), food supplementation might have acted as a cue that peak food availability later in the season was advanced and/or that early breeding was less risky. Therefore, the reliable availability of peanut cake in supplemented treatments, rather than its consumption, could have induced shorter incubation periods to advance hatching/fledging. This reliability might also have reduced the risk of food shortage in incubating females (Eikenaar *et al.* 2003), perhaps facilitating more intensive incubation in supplemented treatment blocks. Alternatively, incubation might have commenced earlier in the laying sequence of supplemented, compared with control, clutches because the reliable availability of peanut cake insured against potential adverse effects of hatching asynchrony (as discussed in Chapter Two).

5.5.2.4. Hatching success

Food supplementation significantly reduced hatching success of blue tits, but had no significant effect on that of great tits (Chapter Two). Increased peanut cake intake did not influence hatching success significantly in great tits (Table 5.2). However, in blue tits there was a positive (but marginally non-significant) association (albumen – Table 5.2). Therefore, a direct link between peanut cake use and lower hatching success seems unlikely. An alternative explanation may lie in differences in incubation behaviour (that can influence hatching success – Perrins 1979; Lyon & Montgomerie 1985; Chapter Two) between treatments caused by the presence, rather than by intake, of peanut cake. For example, the presence of peanut cake might have encouraged incubation earlier in the laying sequence (discussed in Section 5.5.2.3) that can result in reduced hatching success (Perrins 1979).

5.5.2.5. Fledging success

Fledging success was reduced significantly in the PC, compared with the control, dietary treatment in both species (Chapter Four). In blue tits, fledging success was also significantly lower in the PCMW treatment compared with the control (Chapter Four). There were significant negative associations between supplement use and fledging success in female (Fig. 5.6c; Table 5.2) and nestling (Table 5.2) blue tits, but all other comparisons were non-significant. Intriguingly, however, supplement use by adult great tits associated positively with fledging success (Figs 5.6d,e; Table 5.2) as did peanut cake intake by great tit nestlings (Fig. 5.6f; Table 5.2). These findings, and the relative lack of treatment differences in supplement use (Figs 5.2 & 5.3), suggest that the pronounced differences in fledging success between dietary treatments were caused by effects of food supplementation beyond those of increased supplement intake. As with clutch size (Section 5.5.2.2), a testable hypothesis is that supplemented pairs experience greater territorial intrusion and conflict, elicit more territorial behaviour, and are more physiologically stressed than control pairs.

5.5.2.6. Recapture success

Supplementation with mealworms enhanced recapture success of fledglings in both species (Chapter Four). In support of this finding, mealworm intake by male blue tits associated positively with recapture success (Table 5.2), but the opposite was true in great tit pairs (Fig. 5.6g; Table 5.2). Importantly, however, there were no significant associations between the proportion of mealworms in the diet of nestlings of either species and their subsequent recapture probability (Table 5.2). Therefore, the two mechanisms that were proposed to explain increased recapture success as a result of mealworm supplementation in Chapter Four are still possible. First, mealworms may have been provided to nestlings after tissue samples were taken at day 12 post-hatch, causing increased fledging weight and subsequent survival (Naef-Daenzer *et al.* 2001). Second, the presence of mealworms may have reduced post-fledging dispersal by ‘encouraging’ pairs to keep their fledglings close to these areas of food richness. The latter might have occurred without considerable supplement intake (Figs 5.2, 5.3, & 5.5), particularly if mealworms were perceived as an insurance resource.

5.5.3. Critical appraisal

As discussed in Section 5.5.1, while estimates of mealworm intake appear to be robust, there is scope for improvement with regard to estimates of peanut cake utilisation. This could incorporate other methods of recording supplement use (e.g. focal feeder watches, nestbox cameras – Cowie & Hinsley 1988a,b), examination of fat-rich tissues such as egg yolk (e.g. through SIA or fatty acid signatures – e.g. Jacobs *et al.* 2009), or the use of a tracer to improve isotopic separation (e.g. Robb *et al.* In review).

Estimates of dietary intake per individual (i.e. adult – Fig. 5.2) and per brood (i.e. nestling – Fig. 5.3) resulted in a lack of statistical power and some uncertainty in the absolute values derived (see Section 5.4.2). However, this approach was necessary in order to examine relative supplement intake *versus* breeding parameters (Fig. 5.6; Table 5.2). Future work could obtain a greater number of replicates of a particular tissue type per individual or brood (e.g. albumen samples taken from multiple eggs of the same clutch, or blood samples taken on different days during the nestling period). Non-independence of data and current regulations regarding tissue sampling (e.g. Home Office, UK) would need to be considered in such approaches.

Significant associations between supplement use and early season breeding parameters (e.g. clutch initiation date, clutch size, hatching success) were more common in adult tissues representing intake during pre-breeding and early in the breeding season (i.e. claw and albumen – Table 5.2). Significant associations with late season parameters (e.g. fledging success, recapture success) in adult tissues were only found in blood (Table 5.2), representing dietary intake during incubation and the nestling period. Since changes in the foraging environment are likely to have proximate effects on reproduction of income-breeding passerines such as blue and great tits, this suggests confidence in my findings. However, the significant associations presented in Figure 5.6 and Table 5.2 should be treated with some caution. First, it is of concern that relative supplement intake correlated poorly between different tissues sampled from the same individual or brood (Table 5.3). In adults this variation might be because relative supplement use changed throughout the breeding season. However, in nestlings both claw and blood are assimilated mostly between hatching and fledging, so supplement use as calculated from these two tissues should be highly correlated.

Species	**Age class**	**Supplement**	**Sex**	**Tissues**	r_s	***P***
BT	Adult	Peanut cake	F	Claw *vs.* albumen	$r_s = 0.09$	NS
			F	Blood *vs.* albumen	$r_s = -0.23$	NS
			F	Claw *vs.* blood	$r_s = -0.17$	NS
			M	Claw *vs.* blood	$r_s = 0.68$	**$P < 0.05$**
			F&M	Claw *vs.* blood	$r_s = 0.22$	NS
	Nestling	Peanut cake	N/A	Claw *vs.* blood	$r_s = 0.06$	NS
		Mealworm	N/A	Claw *vs.* blood	$r_s = -0.20$	NS
GT	Adult	Peanut cake	F	Claw *vs.* albumen	$r_s = -0.09$	NS
			F	Blood *vs.* albumen	$r_s = 0.19$	NS
			F	Claw *vs.* blood	$r_s = 0.06$	NS
			M	Claw *vs.* blood	$r_s = 0.10$	NS
			F&M	Claw *vs.* blood	$r_s = 0.32$	NS
	Nestling	Peanut cake	N/A	Claw *vs.* blood	$r_s = -0.06$	NS
		Mealworm	N/A	Claw *vs.* blood	$r_s = 0.15$	NS

Table 5.3. Relationships (Spearman's rank correlation coefficient and associated significance at $P = 0.05$) between the proportion of peanut cake or mealworms in the diet (maximum likelihood values per individual or brood estimated using SIAR) as calculated from tissues of adult and nestling blue (BT) and great (GT) tits at Chaddesley Woods National Nature Reserve in 2007. Tissues sampled are specified (blood = plasma and red blood cells), as is sex ('F' = female, 'M' = male, 'N/A' = not applicable). In adults, correlations between tissues are restricted to peanut cake use because only blood was used to examine mealworm use (mealworms were provided only during chick-rearing). Correlations that involve egg albumen have been restricted to females. Significant *P* values are in bold text, 'NS' denotes non-significance ($P > 0.05$). See text for details.

Second, a small contribution of a food supplement to the diet (e.g. mealworms – e.g. Fig. 5.5) may not have a biologically important influence. Third, a proportional increase or decrease in supplement use in the diet is associated with a concomitant increase or decrease of another food type. Therefore, the significant relationships recorded (Fig. 5.6; Table 5.2) may be determined by the intake of other food types (although still driven by manipulation of the foraging environment through food supplementation). Finally, it is possible that 2007 was not a representative year. Although I have no reason to suspect this, repetition of this work in future years would, undoubtedly, be of value.

5.5.4. Conclusions

My study demonstrates that food supplementation can have multiple significant effects on avian reproduction without forming a substantial component of the diet. The latter finding supports suggestions following analyses of egg composition (Chapter Three) that birds in supplemented treatment blocks did not rely heavily upon peanut cake. Interestingly, the influence of providing food supplements (e.g. reduced clutch size and fledging success – Chapters Two & Four) often differed from the influence of food supplements being consumed in proportionately greater quantities (e.g. larger clutches and, in great tits, increased fledging success – Figs 5.6b,d-f). This discrepancy might be explained by my experimental design. In most previous food supplementation studies of blue and great tits, supplements have been provided close to the nest (e.g. as with mealworms in my study) and in none have findings such as reduced clutch size and hatching success been reported (e.g. Svensson & Nilsson 1995; Nager *et al.* 1997; Ramsay & Houston 1998; see Chapter Two). By contrast, peanut cake in my study was positioned equidistantly between nestboxes in supplemented treatment blocks, perhaps at the boundaries of adjacent breeding territories. This might have reversed nutritional benefits of supplementation (e.g. increased clutch size – Table 5.2) through factors such as increased intrusion pressure and territorial defence. In light of these findings, I suggest that behavioural effects of food supplementation are afforded greater attention in conjunction with studies of physiological effects. Linking the behavioural and physiological consequences of food supplementation will be an exciting avenue for future research.

Chapter Six

ADVANCED LAYING AND DECREASED PRODUCTIVITY OF BLUE AND GREAT TITS ACROSS A UK URBAN GRADIENT

6.1. Abstract

Breeding phenology (clutch initiation date) and productivity (clutch and brood size) of blue and great tits were examined across an urban gradient using data obtained from across the UK. Urban land cover (ULC) was quantified objectively using satellite-derived land cover data, as was broadleaved land cover (BLC), the most productive breeding habitat of both species in the UK. ULC and BLC were identified at a resolution of 1-km^2. Increased ULC associated negatively with: (i) clutch initiation date (both species); (ii) clutch size (great tits); (iii) brood size (both species); and (iv) brood size as a proportion of clutch size (blue tits). Many of these findings are similar to effects of food supplementation of the same species during the spring and summer at a rural woodland site (Chapters Two & Four) raising the possibility that food supplementation, that is widespread in urban habitats, could influence breeding patterns in urban parids. Increased BLC associated positively with breeding productivity in blue, but not in great, tits. I discuss the significance of these findings with respect to food supplementation, urban adaptation, and dependence on BLC.

6.2. Introduction

Urbanisation has marked effects on the reproduction of passerines, often advancing breeding phenology (e.g. clutch initiation date) and reducing productivity (e.g. clutch and brood size) (Chamberlain *et al.* 2009). The human population is expanding (from just fewer than seven billion currently to over nine billion by 2050 – UN 2008) and is becoming increasingly urbanised (*c.* 50% of the world's population live in urban areas, set to increase to 70% by 2050 – UN 2008). Therefore, detailed study into the influence of urbanisation on avian reproduction is important as many species come into increasingly closer contact with humans. Numerous species of birds, including some of conservation concern (Bland *et al.* 2004; Chapter One), already breed in urban habitats such as gardens. Since many species experience reduced productivity within urban habitats (Chamberlain *et al.* 2009), the suitability of these habitats for breeding birds is of concern. This concern is amplified given that it is the every-day actions of householders, through the provision of food supplements and artificial nest sites in gardens (Davies *et al.* 2009), that could be a cause of birds breeding in sub-optimal urban areas. Indeed, such 'benevolence' could set an ecological trap (as discussed in Robb *et al.* 2008a).

A number of species are suitable for comparison of reproduction between urban and non-urban habitats. For example, blue and great tits breed in a wide range of habitats (Cramp & Perrins 1993a; Gosler 1993) and take readily to nestboxes enabling breeding attempts to be monitored easily (Perrins 1979). This ease of study has resulted in reproduction in these species being characterised across numerous habitats (e.g. gardens – Cowie & Hinsley 1987; broadleaved deciduous woodland – Perrins & McCleery 1989; broadleaved evergreen woodland – Blondel *et al.* 1993; coniferous woodland – Tilgar *et al.* 1999). Compared with non-urban habitats, blue and great tits in urban areas advance clutch initiation (e.g. Schmidt & Steinbach 1983; Dhondt *et al.* 1984) and have smaller clutch and brood sizes (e.g. Perrins 1965; Berressem *et al.* 1983). Advanced laying is likely to be caused by factors such as supplementary feeding that might advance breeding condition (Robb *et al.* 2008b), and warmer temperatures (Haggard 1990) that could act as a cue that seasonal peaks in natural foods with which to rear young are relatively advanced (Visser *et al.* 2009). Smaller clutches and broods might be caused by factors such as a poor quality pre-breeding diet (Solonen 2001) and lower natural invertebrate availability (Perrins 1979). In contrast, productivity of blue and great tits in non-urban habitats can be increased compared with urban areas. In the UK, productivity is usually greatest in broadleaved woodland (Perrins 1965). Given the concerns regarding decreased productivity in urban habitats, it is interesting to consider the role that more productive habitats could have in ameliorating these effects.

Previous comparisons of reproduction of blue and great tits (and most other species) between urban and non-urban habitats have been restricted to localised scales (e.g. within a single city – Perrins 1965; Cowie & Hinsley 1987), with habitat definitions susceptible to subjective error (e.g. interpretation of habitat proximate to the nest – Perrins 1965; Cowie & Hinsley 1987; description of surrounding habitats – Dhondt *et al.* 1984; distance from sea coast corresponding to degree of urbanisation – Solonen 2001). Here, I compare breeding phenology (defined by clutch initiation date) and productivity (defined by clutch and brood size) of blue and great tits across two land-cover types, urban land cover (ULC) and broadleaved land cover (BLC), throughout the UK. Both ULC and BLC were identified objectively from satellite images. I hypothesised that increased ULC would advance breeding phenology and reduce productivity, whereas increased BLC would enhance productivity.

6.3. Methods

6.3.1. Selection and filtering of nest records

Breeding data were obtained from the BTO’s NRS (Crick 1992). The NRS was established in 1939 and holds over 1.2 million nest records of UK-breeding species (BTO 2005b). A nest record consists of the details of a breeding attempt as documented by a volunteer nest-recorder. I selected nest records for blue and great tits over five consecutive years, namely

2000 to 2004 inclusive. For each nest record, the nest-recorder provided a site name and a grid reference. One nest record was selected randomly per site in each year to minimise non-independence in the sample due to multiple records from the same site (and, therefore, usually from the same recorder). Each nest record was allocated to the 1-km grid square (Ordnance Survey) from which the record was obtained, and was combined with land cover data (see Section 6.3.2), latitude (northings), longitude (eastings) and mean altitude within the corresponding grid square. Nest records were obtained from throughout the UK (see Appendix Six; range: northings 34000-882000; eastings 161000-654000) (Universal Transverse Mercator grid system), although there was some variation between analyses due to the inclusion or exclusion of nest records based on their suitability (see below).

Nest records were filtered as described in Crick *et al.* (2003). In brief, clutch initiation date was defined as the mid-point between the earliest and latest possible clutch initiation date (rounded to the nearest day). If the difference between these two dates was > 10 days then uncertainty regarding clutch initiation date was considered to be too great and the record was discarded (see Crick *et al.* 2003). Clutch and brood sizes were recorded as the maximum observed, but were discarded if > 16 (such records may have been a result of egg dumping or recorder error, since the clutch size of these species does not usually exceed 16 – Cramp & Perrins 1993a,b). Brood sizes of zero (i.e. dead broods) were excluded. Since NRS methodology does not necessarily allow the fate of every egg in each clutch to be determined, hatching success and/or partial brood mortality were examined through the calculation of brood size as a proportion of clutch size (the same filtering criteria as above were employed).

6.3.2. Land cover data

Land cover data were extracted from the Land Cover Map 2000 database (LCM2000 – Fuller *et al.* 2002). LCM2000 presents classifications of satellite images of land cover, and incorporates external data to refine these classifications (Tipping *et al.* 2008). Of the 16 land cover types (‘Target classes’; measured with an accuracy of *c.* 85% – Fuller *et al.* 2002) distinguished in LCM2000, I considered two (see Centre for Ecology and Hydrology 2009 for full definitions): (i) ‘Built-up areas, gardens’ (ULC), defined as built-up areas (e.g. urban land and rural development), waste and derelict ground, transport infrastructure (e.g. roads and railways), gardens and urban trees; and (ii) ‘Broad-leaved / mixed woodland’ (BLC), defined as > 20% broadleaved tree-cover in stands > 5 m high, or mixed woodland if > 20% broadleaved. LCM2000 expresses ULC and BLC as percentages of a 1-km grid square.

6.3.3. Statistical analysis

All statistical analyses were conducted using PROC GLIMMIX in SAS (SAS Institute 2008) and Minitab 15 (Minitab 2007). All predictors were specified as fixed factors. ULC, altitude, and year were included in all models (annual and altitudinal differences in breeding phenology and productivity – e.g. Perrins 1979; Beldal *et al.* 1998; Fargallo 2004). Latitude (northings) and longitude (eastings) (both standardised because of their large numerical size) were included in all models to control for any spatial correlation of nest records. BLC was not included in clutch initiation date analyses (no clear hypothesis), but was tested with respect to clutch and brood size (a positive relationship expected – e.g. Perrins 1965). Clutch and brood size analyses included clutch initiation date as a covariate (seasonal decline expected – e.g. Perrins 1979; Verhulst & Tinbergen 1991). Brood size as a proportion of clutch size included the same predictors as the clutch and brood size analyses. ULC interaction terms (e.g. year ×

ULC; northings × ULC) were of interest to test whether the influence of ULC was consistent, for example, between years and geographical locations (the latter, in particular, a surrogate for climate variation). I had no *a priori* expectation that these interactions would be significant, so ULC interaction terms were not included in all models, but rather were tested for significance independently of one another, with non-significant interactions ($P > 0.05$) removed from models if there was no significant change in model deviance. Co-linearity between predictors was low (Spearman rank correlation: all r^2s ≤ 0.15). Clutch initiation date analyses were fitted with a normal error structure after square root transformation. Clutch and brood size analyses were fitted with poisson errors, whereas binomial errors were specified when examining brood size as a proportion of clutch size.

Detailed statistics for each model are provided in Table 6.1. The magnitude of significant associations between ULC or BLC and the breeding parameters examined are described from a linear regression equation of the residuals generated after accounting for all other predictors in the final model (excluding any significant ULC interaction terms that cannot be included when ULC is removed – see Table 6.1).

6.4. Results

6.4.1. Phenology: clutch initiation date

Clutch initiation date of blue tits advanced significantly with increased ULC ($F_{1,716} = 7.34$, $P = 0.007$) (Fig. 6.1). In blue tits, laying advanced by 0.3 days for every 10% increase in ULC (Fig. 6.1). This was also found in great tits where the size of the effect was not consistent across years (year × ULC: $F_{4,583} = 2.51$, $P = 0.04$), but was always negative (Fig. 6.2). In great tits, within-year analyses revealed a significant negative association between ULC and clutch initiation date in 2000 ($F_{1,179} = 22.51$, $P < 0.001$), 2001 ($F_{1,130} = 9.33$, $P = 0.003$), 2002 ($F_{1,95} =$

Table 6.1. Models of reproductive parameters (F and associated P values) of blue (BT) and great (GT) tits in the UK in 2000-2004. Combined-year analyses except GT clutch initiation date (significant year × ULC interaction: $P = 0.04$). Fixed factors specified in each model are given with significant P values in bold text. ULC = urban land cover, BLC = broadleaved land cover. BLC not included in clutch initiation date analyses because of no clear hypothesis to do so. Directions of significant effects are given: '+' and '-' denote significant positive and negative associations, respectively, and 'NS' denotes non-significance ($P > 0.05$). See text for details.

Breeding parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Clutch initiation date	BT	2000-04	ULC	$F_{1,716} = 7.34$	**$P = 0.007$**	-
			Year	$F_{4,716} = 59.70$	**$P < 0.001$**	Significant annual variation
			Northings	$F_{1,716} = 50.47$	**$P < 0.001$**	+
			Eastings	$F_{1,716} = 4.23$	**$P = 0.04$**	-
			Altitude	$F_{1,716} = 21.81$	**$P < 0.001$**	+
	GT	2000	ULC	$F_{1,179} = 22.51$	**$P < 0.001$**	-
			Northings	$F_{1,179} = 21.61$	**$P < 0.001$**	+
			Eastings	$F_{1,179} = 1.38$	$P = 0.24$	NS
			Altitude	$F_{1,179} = 3.72$	$P = 0.06$	NS
		2001	ULC	$F_{1,130} = 9.33$	**$P = 0.003$**	-
			Northings	$F_{1,130} = 4.80$	**$P = 0.03$**	+
			Eastings	$F_{1,130} = 0.17$	$P = 0.68$	NS
			Altitude	$F_{1,130} = 0.04$	$P = 0.84$	NS
		2002	ULC	$F_{1,95} = 5.93$	**$P = 0.02$**	-
			Northings	$F_{1,95} = 4.92$	**$P = 0.03$**	+
			Eastings	$F_{1,95} = 0.63$	$P = 0.43$	NS
			Altitude	$F_{1,95} = 0.59$	$P = 0.45$	NS
		2003	ULC	$F_{1,79} = 0.64$	$P = 0.43$	NS
			Northings	$F_{1,79} = 11.89$	**$P = 0.001$**	+
			Eastings	$F_{1,79} = 0.45$	$P = 0.50$	NS
			Altitude	$F_{1,79} = 12.31$	**$P = 0.001$**	+
			ULC × Altitude	$F_{1,79} = 6.39$	**$P = 0.01$**	Advancement of laying with increased ULC more pronounced at high than at low altitude.
		2004	ULC	$F_{1,87} = 4.33$	**$P = 0.04$**	-
			Northings	$F_{1,87} = 5.65$	**$P = 0.02$**	+
			Eastings	$F_{1,87} = 1.96$	$P = 0.17$	NS
			Altitude	$F_{1,87} = 1.11$	$P = 0.30$	NS
			ULC × Eastings	$F_{1,87} = 9.29$	**$P = 0.003$**	Advancement of laying with increased ULC more pronounced in the west than the east of the UK.
Clutch size	BT	2000-04	ULC	$F_{1,393} = 1.39$	$P = 0.24$	NS
			BLC	$F_{1,393} = 7.78$	**$P = 0.006$**	+
			Year	$F_{4,393} = 3.63$	**$P = 0.006$**	Significant annual variation

Table 6.1. continued

Breeding parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Clutch size	BT	2000-04	Northings	$F_{1,393} = 10.95$	**$P = 0.001$**	+
			Eastings	$F_{1,393} = 1.43$	$P = 0.23$	NS
			Altitude	$F_{1,393} = 0.91$	$P = 0.34$	NS
			Clutch initiation date	$F_{1,393} = 61.80$	**$P < 0.001$**	-
	GT	2000-04	ULC	$F_{1,273} = 6.25$	**$P = 0.01$**	-
			BLC	$F_{1,273} = 0.03$	$P = 0.86$	NS
			Year	$F_{4,273} = 2.01$	$P = 0.09$	NS
			Northings	$F_{1,273} = 0.06$	$P = 0.80$	NS
			Eastings	$F_{1,273} = 3.88$	**$P = 0.05$**	+
			Altitude	$F_{1,273} = 0.95$	$P = 0.33$	NS
			Clutch initiation date	$F_{1,273} = 3.99$	**$P = 0.05$**	-
Brood size	BT	2000-04	ULC	$F_{1,560} = 9.38$	**$P = 0.002$**	-
			BLC	$F_{1,560} = 3.72$	**$P = 0.05$**	+
			Year	$F_{4,560} = 2.31$	$P = 0.06$	NS
			Northings	$F_{1,560} = 3.34$	$P = 0.07$	NS
			Eastings	$F_{1,560} = 0.09$	$P = 0.77$	NS
			Altitude	$F_{1,560} = 0.22$	$P = 0.64$	NS
			Clutch initiation date	$F_{1,560} = 26.06$	**$P < 0.001$**	-
	GT	2000-04	ULC	$F_{1,472} = 6.86$	**$P = 0.009$**	-
			BLC	$F_{1,472} = 0.91$	$P = 0.34$	NS
			Year	$F_{4,472} = 7.42$	**$P < 0.001$**	Significant annual variation
			Northings	$F_{1,472} = 4.35$	**$P = 0.04$**	+
			Eastings	$F_{1,472} = 3.50$	$P = 0.06$	NS
			Altitude	$F_{1,472} = 2.30$	$P = 0.13$	NS
			Clutch initiation date	$F_{1,472} = 13.21$	**$P < 0.001$**	-
Brood size as a proportion of clutch size	BT	2000-04	ULC	$F_{1,295} = 3.83$	**$P = 0.05$**	-
			BLC	$F_{1,295} = 0.02$	$P = 0.88$	NS
			Year	$F_{4,295} = 2.08$	$P = 0.08$	NS
			Northings	$F_{1,295} = 0.51$	$P = 0.47$	NS
			Eastings	$F_{1,295} = 0.06$	$P = 0.80$	NS
			Altitude	$F_{1,295} = 1.64$	$P = 0.20$	NS
			Clutch initiation date	$F_{1,295} = 0.55$	$P = 0.46$	NS
			ULC × Year	$F_{4,295} = 0.65$	$P = 0.63$	NS
	GT	2000-04	ULC	$F_{1,209} = 0.00$	$P = 0.95$	NS

Table 6.1. continued

Breeding parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**Direction**
Brood size as a proportion of clutch size	GT	2000-04	BLC	$F_{1,209} = 0.08$	$P = 0.78$	NS
			Year	$F_{4,209} = 1.76$	$P = 0.14$	NS
			Northings	$F_{1,209} = 1.82$	$P = 0.18$	NS
			Eastings	$F_{1,209} = 1.47$	$P = 0.23$	NS
			Altitude	$F_{1,209} = 1.40$	$P = 0.24$	NS
			Clutch initiation date	$F_{1,209} = 2.05$	$P = 0.15$	NS
			ULC × Year	$F_{4,209} = 1.70$	$P = 0.15$	NS

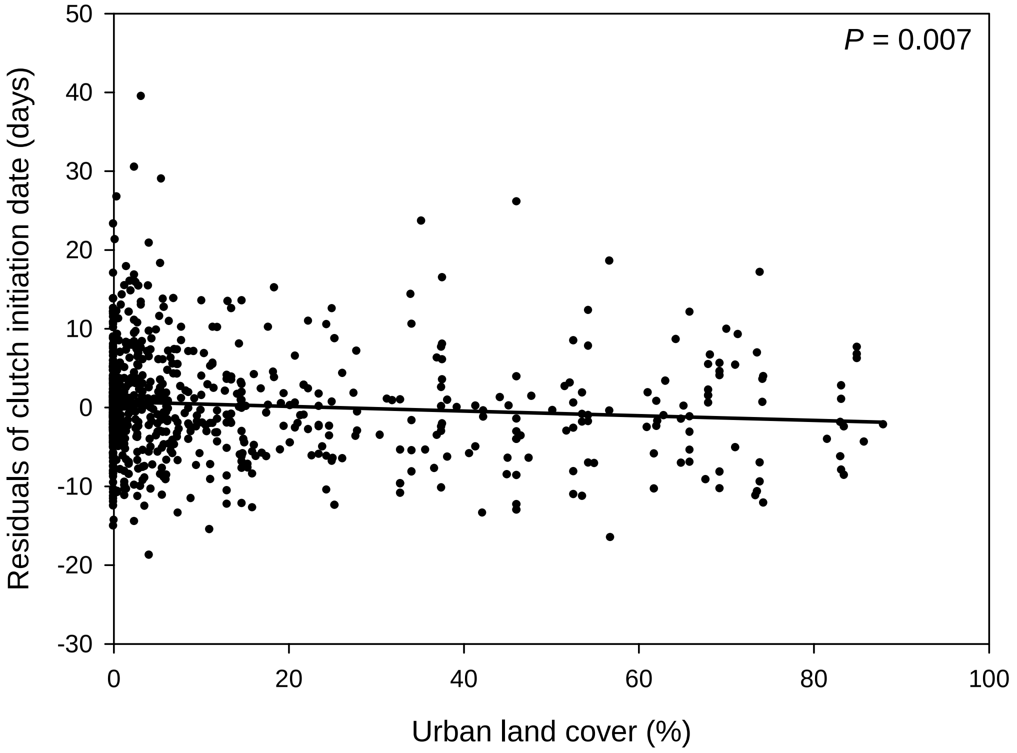

Figure 6.1. The relationship between urban land cover (percentage of land surface area per 1-km grid square) and clutch initiation date of blue tits in the UK in 2000-2004. Residuals of clutch initiation date were calculated after accounting for all predictors other than ULC in the final model (see Table 6.1). See text for details.

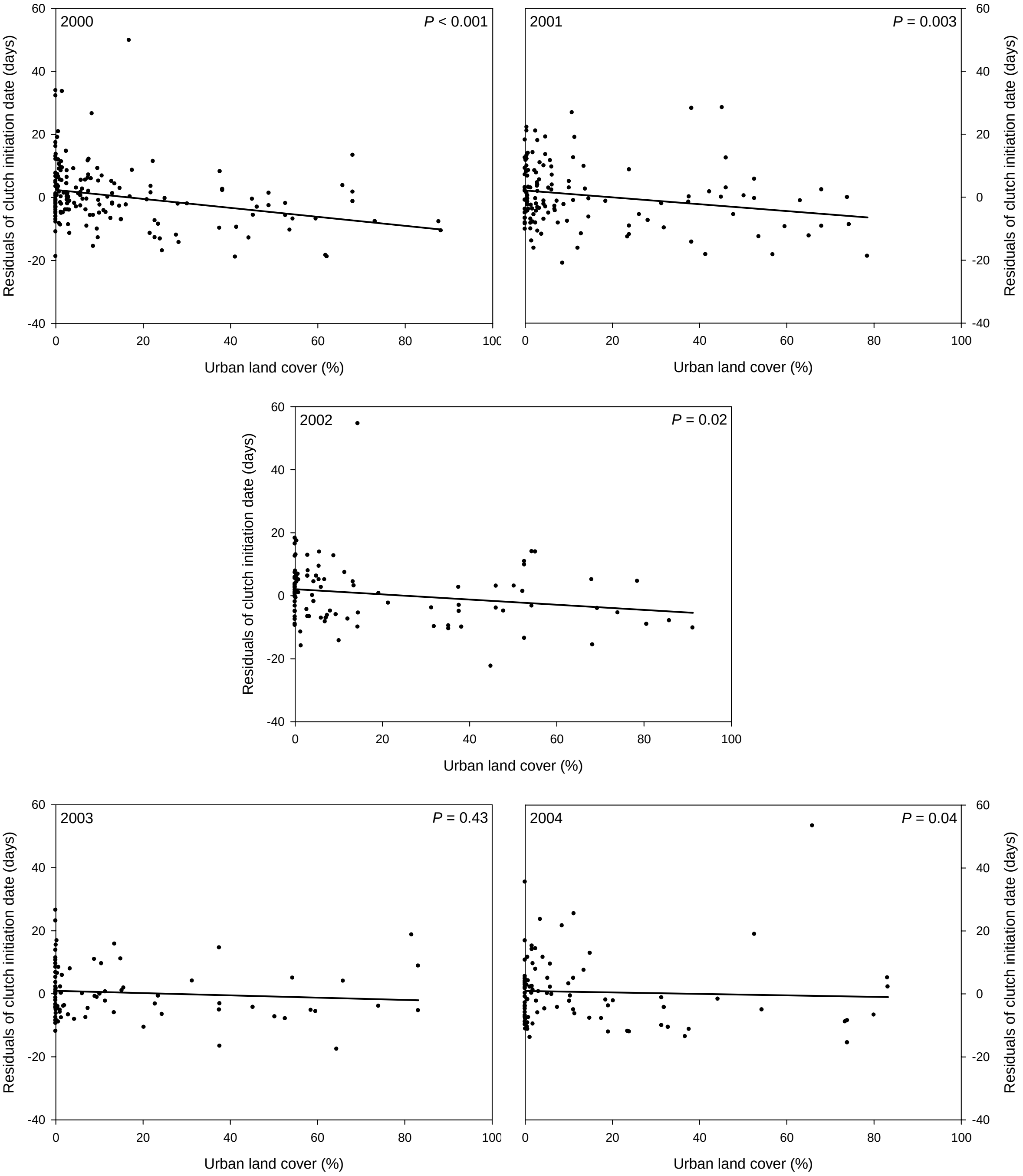

Figure 6.2. The relationship between urban land cover (percentage of land surface area per 1-km grid square) and clutch initiation date of great tits in the UK in 2000-2004. Separate years are presented due to a significant year × ULC interaction ($P = 0.04$). Residuals of clutch initiation date were calculated after accounting for all predictors other than ULC (and any ULC interaction terms) in the final models (see Table 6.1). See text for details.

5.93, $P = 0.02$), and 2004 ($F_{1,87} = 4.33$, $P = 0.04$), but not in 2003 ($F_{1,79} = 0.64$, $P = 0.43$) (Fig. 6.2) when earlier laying with increased ULC was only found at higher, not lower, altitudes (altitude × ULC: $F_{1,79} = 6.39$, $P = 0.01$). For every 10% increase in ULC great tits advanced laying by 1.4 days in 2000, 1.1 days in 2001, 0.8 days in 2002 and 0.2 days in 2004 (Fig. 6.2).

6.4.2. Productivity: clutch size, brood size, and brood size as a proportion of clutch size

Clutch size of blue tits did not differ significantly across an urban gradient ($F_{1,393} = 1.39$, $P = 0.24$) (Fig. 6.3), but was significantly larger with greater BLC ($F_{1,393} = 7.78$, $P = 0.006$). For every 10% increase in BLC clutch size of blue tits increased by 0.2 eggs. Clutch size of great tits declined significantly with increased ULC ($F_{1,273} = 6.25$, $P = 0.01$) (Fig. 6.3), but did not relate significantly to BLC ($F_{1,273} = 0.03$, $P = 0.86$). In great tits, clutch size decreased by 0.1 eggs for every 10% increase in ULC (Fig. 6.3).

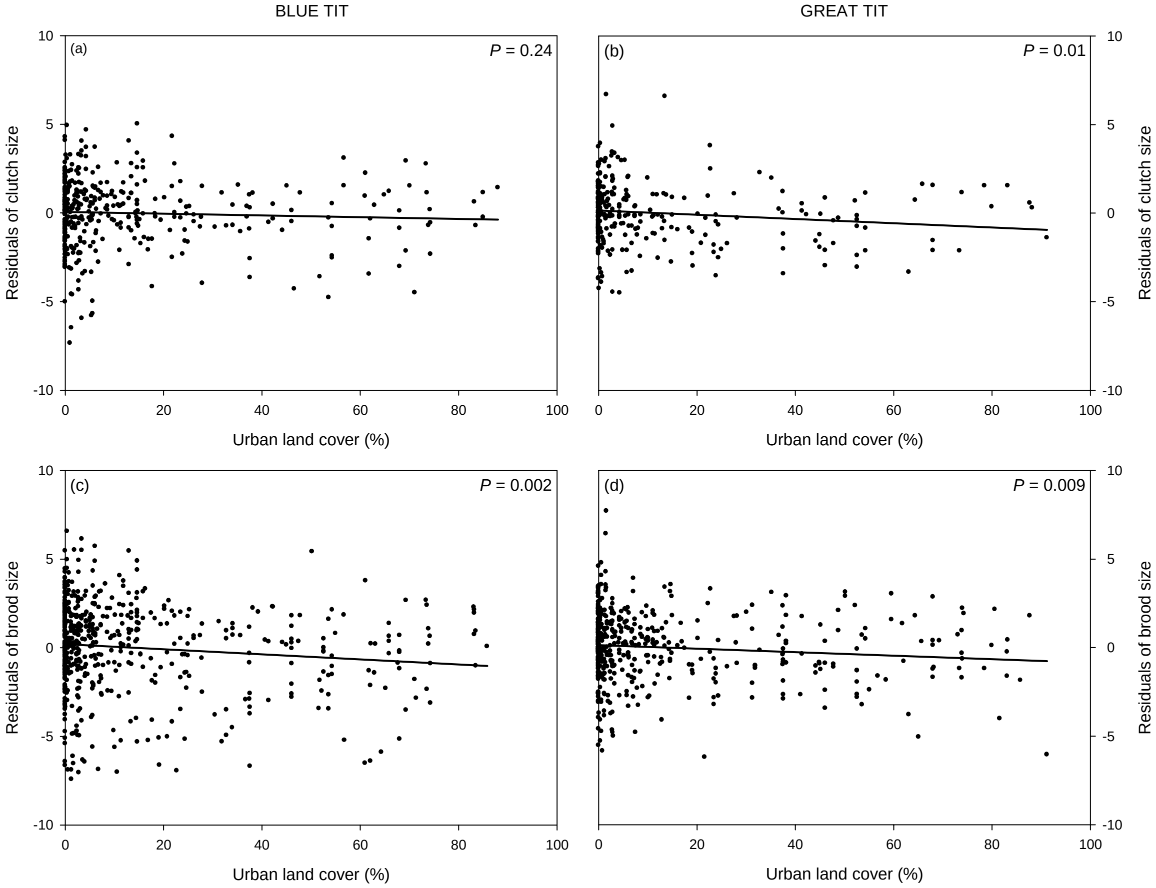

Figure 6.3. The relationship between urban land cover (percentage of land surface area per 1-km grid square) and clutch size of (a) blue and (b) great tits in the UK in 2000-2004. (c) and (d) represent the same comparison in blue and great tits, respectively, but for brood size. Residuals of clutch and brood size were calculated after accounting for all predictors other than ULC in the final models (see Table 6.1). See text for details.

Brood size of both species declined significantly with increased ULC (blue tits $F_{1,560} = 9.38$, $P = 0.002$; great tits $F_{1,472} = 6.86$, $P = 0.009$) (Fig. 6.3). In both species, brood size decreased by 0.1 nestlings for every 10% increase in ULC (Fig. 6.3). Increased BLC was associated with larger brood sizes in blue ($F_{1,560} = 3.72$, $P = 0.05$), but not in great ($F_{1,472} = 0.91$, $P = 0.34$), tits. In blue tits, broods increased by 0.1 nestlings for every 10% increase in BLC.

Brood size as a proportion of clutch size declined significantly with increased ULC in blue ($F_{1,295} = 3.83$, $P = 0.05$), but not in great ($F_{1,209} = 0.00$, $P = 0.95$), tits. For every 10% increase in ULC brood size as a proportion of clutch size of blue tits decreased by 0.02 (2%). BLC did not predict brood size as a proportion of clutch size significantly in blue ($F_{1,295} = 0.02$, $P = 0.88$), or in great ($F_{1,209} = 0.08$, $P = 0.78$), tits.

6.5. Discussion

Breeding phenology and productivity of blue and great tits varied significantly across an urban gradient. As hypothesised, increased ULC was associated with significantly earlier laying (both species, Figs 6.1 & 6.2) and reduced productivity (smaller clutch sizes – great tits, Fig. 6.3; and smaller brood sizes – both species, Fig. 6.3). Brood size as a proportion of clutch size declined significantly with increased ULC in blue, but not in great, tits (Table 6.1). As hypothesised, BLC was associated with increased productivity, but this was only true in blue, not in great, tits (Table 6.1).

6.5.1. Phenology: clutch initiation date

Previous studies of blue and great tits have reported earlier laying with increased urbanisation (e.g. Schmidt & Steinbach 1983; Dhondt *et al.* 1984). Early-breeding blue and great tits normally lay larger clutches (Lack 1966) and have more of their young recruited into the breeding population (Verhulst & Tinbergen 1991; Barba *et al.* 1995). However, typically, such findings have been made in non-urban habitats and comparative research in urban areas is lacking. Advanced laying with increased ULC might reflect an adaptive ‘tracking’ of peaks in natural food resources (e.g. caterpillars) that may be earlier due to warmer temperatures in urban areas (Perrins 1979; Haggard 1990). Alternatively, there could be a mis-match of timing across an urban gradient should clutch initiation date not shift in parallel with peaks in natural foods. These important possibilities require further investigation.

A number of factors might advance laying in urban areas (Figs 6.1 & 6.2). In the UK *c.* 40-50% of households provide food supplements for birds in their gardens (Davies *et al.* 2009; Fuller *et al.* In press) and such provision is likely to advance clutch initiation (reviewed in Arcese & Smith 1988; Meijer & Drent 1999; see Chapter Two). This might be particularly important in species such as blue and great tits that often feed on supplements in gardens (Chamberlain *et al.* 2005). In temperate climes, over-winter supplementary feeding may improve adult condition and provide a mechanism through which laying is advanced in the spring (e.g. Robb *et al.* 2008b). Increased food availability prior to laying could also act as a cue that seasonal peaks in natural food (e.g. caterpillars), upon which blue and great tits depend to raise their young (Perrins & McCleery 1989; Perrins 1991), are advanced and that laying should commence (Lack 1954; Perrins 1965). Alternatively, settlement on to breeding territories could be earlier in urban, compared with non-urban, areas due to the presence of food supplements (Kelly & Van Horne 1997).

Increased ULC is also likely to be associated with warmer temperatures (Haggard 1990) that can advance clutch initiation (Visser *et al.* 2009). Warmer temperatures might reduce energetic costs in breeding females and, thereby, alleviate constraints on laying

(Dhondt & Eyckerman 1979). Alternatively warmer conditions might advance the peak availability of cold-blooded invertebrates that are needed to raise young (Perrins 1979). Increased light levels in urban landscapes may also promote clutch initiation via a stimulatory effect on gonadal growth (see Partecke *et al.* 2004 and references therein).

6.5.2. Productivity: clutch size, brood size, and brood size as a proportion of clutch size

Smaller clutch and brood sizes of blue and great tits with increased urbanisation have been reported previously (e.g. Perrins 1965; Berressem *et al.* 1983; Schmidt & Einloft-Achenbach 1984; Schmidt & Steinbach 1983; Hamann *et al.* 1989; Solonen 2001). Reduced brood size as a proportion of clutch size in more urbanised habitats has also been found in both species (e.g. Schmidt & Einloft-Achenbach 1984; Solonen 2001). Reduced productivity (e.g. smaller clutch size) in urban habitats could represent an adaptive response to sub-optimal conditions when rearing nestlings (e.g. fewer natural food items – Perrins 1979; Schmidt & Steinbach 1983). Alternatively, reduced productivity might suggest poor adaptation to breeding in urban areas (see Section 6.5.3). Productivity increased in broadleaved habitats but, unexpectedly, this was only true in blue tits (Table 6.1). This suggests that the decline in breeding productivity of urban-breeding blue tits could be made less severe by the presence of broadleaved habitat. This possibility is considered further in Chapter Seven.

In urban, compared with rural (e.g. broadleaved), habitats natural food availability might be reduced perhaps driven by garden management practices (e.g. use of pesticides, planting of exotic flora – Schmidt 1988; Burghardt *et al.* 2009) and/or pollution that can reduce invertebrate availability or cause direct toxicity (Eeva *et al.* 1997, 2005). Solonen (2001) suggested that higher breeding densities in urban, compared with non-urban, habitats could increase competition for natural food, although Perrins (1965) reported lower breeding densities in urban habitats. Food supplementation might also reduce productivity (Chapters Two & Four). For example, food supplements could contribute to a poor-quality pre-breeding diet (Solonen 2001), increase the risk of disease (Pennycott *et al.* 2002), and might be fed to nestlings causing mortality (Cowie & Hinsley 1988a). Other factors that could reduce productivity in urban habitats include smaller body size of breeding adults (Liker *et al.* 2008), increased parasite infestation (Gregoire *et al.* 2002), and a mis-match in timing between the peak demands of young and the maximum availability of natural foods (e.g. due to advanced clutch initiation – Figs 6.1 & 6.2).

6.5.3. Urban breeding: adaptation or maladaptation?

Blue tits appeared less well adapted to urban breeding, and more reliant on BLC, than great tits. In the latter, the decline of clutch and brood size with increased ULC (Fig. 6.3), and the lack of an association between brood size as a proportion of clutch size and ULC (Table 6.1), suggest that great tits strategically manipulated their clutch size relative to a brood size that could be reared successfully (or with ‘acceptable’ losses) across an urban gradient. In blue tits, however, brood size declined significantly with increased ULC, despite no significant reduction in clutch size (Fig. 6.3), suggesting that clutches in urban habitats were sub-optimally large. This increased disparity between clutch and brood size with greater ULC (see brood size as a proportion of clutch size of blue tits – Table 6.1) was caused by increased hatching failure and/or partial brood mortality. Berressem *et al.* (1983) and Isaksson *et al.* (2008) did not find significant differences in hatching success between urban and non-urban populations of great tits. However, food supplementation is common in urban habitats and, as demonstrated in Chapter Two, hatching success of blue, but not of great, tits can be reduced as a result. Increased partial brood mortality in urban habitats is also possible (e.g. through a scarcity of natural foods and/or the feeding of unsuitable food supplements to nestlings). In Chapter Four I found that food supplementation increased partial brood mortality in great, but not in blue, tits. Therefore, there are parallels between these findings and those of my field study (Chapters Two-Five) but not consistently so. Interspecific differences in BLC *versus* clutch and brood size (see Table 6.1) suggested that blue tits were more specialised (i.e. experienced increased productivity) for reproduction in broadleaved, rather than in urban, habitats than were great tits. Lower habitat specialisation of great tits during reproduction may be because great tit nestlings are more general in their diet compared with blue tit contemporaries (Betts 1955; Török 1985, 1986) and might also be fed more anthropogenic foods (Cowie & Hinsley 1988a).

Species such as blue tits for which urban breeding is sub-optimal but common may succumb to an ecological trap (Robertson & Hutto 2006). This could occur because blue tits that fledge from urban (sink) habitats are likely to be fewer in number and of poorer quality (e.g. physically smaller) compared with conspecifics from non-urban (source) habitats (e.g. broadleaved woodland – Perrins 1965; Cowie & Hinsley 1987; Dhondt *et al.* 1990; Blondel *et al.* 1993). Consequently, a recruitment bias towards fledglings from source habitats might operate resulting in asymmetric gene flow across an urban gradient and in the retention of non-urban breeding traits (e.g. clutch sizes that are sub-optimally large in urban areas) in the population at large. Source fledglings might be 'enticed' to breed in urban habitats by characteristics such as the mass provision food supplements and artificial nest sites (e.g. nestboxes) in gardens across the UK (Davies *et al.* 2009). Therefore, since these cues might inflate birds' perception of habitat quality unreliably, they could form the basis of an ecological trap.

6.5.4. Broader considerations and conclusions

I found that breeding productivity of blue and great tits decreased across an urban gradient (Fig. 6.3). This might reduce lifetime reproductive success in these species since individuals are typically short-lived and, in the UK, single-brooded in each year (Perrins 1979). However, at a population-level productivity of blue and great tits probably increased as a result of utilising, rather than being excluded from, urban habitats. Indeed, greater breeding densities of both species in urban, compared with non-urban, habitats can result in increased productivity per km^2 (Solonen 2001). Survival rates can also be higher in more urban areas as a result of warmer temperatures and food supplementation (e.g. Hõrak & Lebreton 1998; McGowan 2001; Chapter Four; but see Leston & Rodewald 2006; Rodewald & Shustack 2008a,b). Ascertaining the extent to which breeding in urban habitats is adaptive (e.g. through increased survival) or maladaptive (e.g. through reduced nestling phase productivity – Fig. 6.3) in a range of different species is an important direction for future research.

Chapter Seven

NO COUNTRY-RETREAT FOR RURAL-BREEDING BIRDS?

7.1. Abstract

Breeding parameters of birds differ markedly between urban and non-urban habitats with the former characterised by advanced laying and decreased productivity. Such differences could be driven by habitat characteristics at a local scale (e.g. between nest site habitats – the immediate habitat in which nests are located) or at a landscape scale (e.g. habitat characteristics in the wider landscape surrounding each nest). Here, I investigate these possibilities by examining breeding parameters of blue tits and great tits across the UK. Breeding phenology (clutch initiation date) and productivity (clutch and brood size) showed some significant differences between urban and non-urban nest site habitats but differences were not widespread. However, in non-urban nest site habitats, increased ULC in the surrounding landscape associated negatively with: (i) clutch initiation date (both species); (ii) clutch size (great tits); (iii) brood size (both species); and (iv) brood size as a proportion of clutch size (blue tits). Conversely, increased BLC (the most productive breeding habitat of both species in the UK) in the surrounding landscape did not relate positively to productivity in non-broadleaved nest site habitats. These results suggest that landscape scale effects of urbanisation on avian reproduction may be additive in non-urban nest site habitats, but that landscape scale effects of non-urban habitat on reproduction in urban nest site habitats might be less pronounced. I discuss the importance of these findings with respect to habitat fragmentation caused by urbanisation, the value of resulting fragments to breeding birds, and mechanisms that underlie these results.

7.2. Introduction

Continued, rapid growth of the human population (UN 2008) will be associated with increased urbanisation that will influence avian populations. While characteristics such as warmer temperatures (Wilby & Perry 2006) and supplementary feeding (Jones & Reynolds 2008) may enhance survival rates of birds over winter in urban habitats, in some species urban breeding might represent a sub-optimal consequence of habitat loss (e.g. Baumann 2006), or an ecological trap (e.g. Boal & Mannan 1999). Urbanisation influences multiple aspects of avian reproduction, typically advancing laying and reducing productivity per breeding attempt (Chamberlain *et al.* 2009; Chapter Six). However, the scale at which urban habitat acts on avian reproduction is poorly understood. For example, differences in reproduction between urban and non-urban habitats could be driven by localised habitat differences (e.g. the immediate habitat in which each nest is located – hereafter 'nest site habitat'). However, it is also possible that urbanisation might act on reproduction at a landscape scale, perhaps being additive (i.e. stronger with increased ULC surrounding nests) and/or pervasive (i.e. influential in non-urban nest site habitats). With respect to the latter, previous research has demonstrated that laying can be advanced in non-urban nest site habitats with closer proximity to urban areas (Hedblom 2007), although the opposite has also been found (Rodewald & Shustack 2008b). Similarly, evidence regarding the influence of nearby urban habitat on clutch and brood size in non-urban nest site habitats is, currently, inconclusive (e.g. Morrison & Bolger 2002).

Here, using data from across the UK, I investigate differences in breeding phenology (defined by clutch initiation date) and productivity (defined by clutch and brood size) of blue and great tits at a localised scale, between urban and non-urban nest site habitats. I also examine within each nest site habitat category to test landscape scale associations between the quantity of ULC or BLC in landscape surrounding each nest, and breeding parameters therein. BLC was analysed in addition to ULC because breeding productivity of both species is greatest in this habitat in the UK, and close proximity to BLC might increase productivity in urban nest site habitats (Perrins 1965). Based on previous research (Chamberlain *et al.* 2009; Chapter Six), I hypothesised that breeding phenology would be advanced and productivity reduced in urban, compared with non-urban, nest site habitats. I hypothesised that increased ULC in the surrounding landscape would advance laying and reduce productivity, and that increased BLC would enhance productivity, in all nest site habitats.

7.3. Methods

7.3.1. Selection and filtering of nest records

Breeding data were obtained from the BTO’s NRS (Crick 1992). The same nest records were analysed in this study as in Chapter Six, but analyses were restricted to three nest site habitats (defined using standard NRS codes by each nest recorder): (i) broadleaved woodland (e.g. more than 10 trees generally greater than five metres tall) (hereafter ‘broadleaved’); (ii) rural human sites (e.g. those without buildings or containing only a few scattered houses) (hereafter ‘rural’); and (iii) urban/suburban human sites (e.g. densely built up inner city areas including large suburban gardens/green spaces) (hereafter ‘urban’). As in Chapter Six, each nest record was allocated to the 1-km grid square (Ordnance Survey) from which the record was obtained and was combined with land cover data (ULC and BLC), latitude (northings), longitude (eastings), and mean altitude within the corresponding 1-km grid square. Classification of nest site habitats (broadleaved, rural, or urban) by NRS participants was consistent with patterns in ULC and BLC from the corresponding 1-km grid square (Fig. 7.1), suggesting that these classifications were accurate. Nest records were obtained from throughout the UK (range:

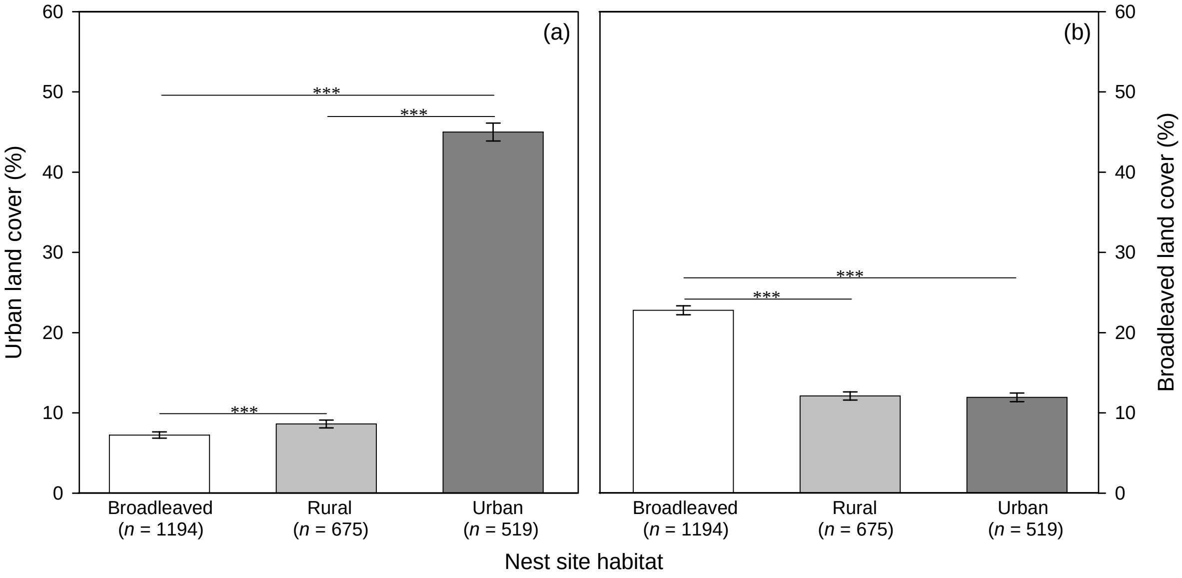

Figure 7.1. Nest site habitat, classified by Nest Record Scheme participants, *versus* percentage (a) urban and (b) broadleaved land cover (mean ± 1 SE) in the 1-km grid square from which each nest record was obtained. *** $P \leq 0.001$. Number of nest records in parentheses below nest site habitat. See text for details.

northings 34000-882000; eastings 161000-654000) (Universal Transverse Mercator grid system), but there was some variation in this range between analyses due to the inclusion or exclusion of nest records based on their suitability. Definitions of clutch initiation date, clutch size, brood size, and brood size as a proportion of clutch size (the latter providing a measure of hatching success and/or partial brood mortality) were provided in Chapter Six, as were details of the filtering of nest records.

7.3.2. Statistical analysis

Statistical analyses were conducted using PROC GLIMMIX in SAS (SAS Institute Inc. 2008) and MINITAB 15 (Minitab 2007). All predictors were specified as fixed factors. In analyses of breeding parameters between-nest site habitats, models included year, northings, eastings, altitude, and clutch initiation date (although the latter was only included in analyses of clutch and brood size, and brood size as a proportion of clutch size). The rationale regarding the use of these predictors was provided in Chapter Six. Nest site habitat × covariate interactions were of interest to test whether differences in reproduction between nest site habitats were consistent across different spatio-temporal scales. There was no *a priori* expectation that these interactions would be significant so these were removed if non-significant ($P > 0.05$) with changes in model deviance compared. Analyses within each nest site habitat category included the same predictors as above but also included ULC (in all analyses) and BLC (in analyses of clutch and brood size, and brood size as a proportion of clutch size). BLC was not included in analyses of clutch initiation date due to the absence of a clear hypothesis. Clutch initiation date analyses were fitted with a normal error structure after square root transformation. Clutch and brood size analyses were fitted with poisson errors, whereas binomial errors were specified when examining brood size as a proportion of clutch size.

As in previous chapters, full results for each model are tabulated. The magnitude of significant differences in the breeding parameters between nest site habitats are described by comparing means generated from statistical estimates (i.e. nest site habitat effects while accounting for all other predictors in the final model). The magnitude of significant associations between ULC or BLC and the breeding parameters are described from a linear regression equation of the residuals generated after accounting for all other predictors in the final model.

7.4. Results

7.4.1. Phenology: clutch initiation date

In blue tits, clutch initiation date did not differ significantly between nest site habitats ($F_{2,591} = 1.68$, $P = 0.19$) (Fig. 7.2; Table 7.1). However, in broadleaved nest site habitats, laying was significantly earlier with increased ULC in the surrounding habitat ($F_{1,316} = 3.86$, $P = 0.05$)

Table 7.1. Models of breeding parameters (F and associated P values) of blue (BT) and great (GT) tits in the UK in 2000-2004, recorded in three nest site habitats: broadleaved (B), rural (R), and urban (U). Combined-year analyses except BT clutch size (significant year × nest site habitat interaction: $P = 0.04$). Fixed factors in each model are given with significant P values in bold text. Least squares means tests (adjusted for multiple comparisons via the Tukey method) compare between nest site habitats where significant differences were found. Directions of significant effects are given: '+' and '-' denote significant positive and negative associations, respectively, and 'NS' denotes non-significance ($P > 0.05$). See text for details.

						Least squares means (P values)			
Breeding parameter	**Sp.**	**Year**	**Fixed factor**	F	P	**B *vs.* R**	**B *vs.* U**	**R *vs.* U**	**Direction**
Clutch initiation date	BT	2000-04	Nest site habitat	$F_{2,591} = 1.68$	$P = 0.19$				NS
			Year	$F_{4,591} = 43.92$	**$P < 0.001$**				2001 = latest; 2002 = earliest
			Northings	$F_{1,591} = 47.49$	**$P < 0.001$**				+
			Eastings	$F_{1,591} = 3.71$	**$P = 0.05$**				-
			Altitude	$F_{1,591} = 24.15$	**$P < 0.001$**				+
	GT	2000-04	Nest site habitat	$F_{2,477} = 13.37$	**$P < 0.001$**	**$P = 0.03$**	**$P < 0.001$**	**$P = 0.01$**	B = latest; U = earliest
			Year	$F_{4,477} = 18.27$	**$P < 0.001$**				2001 = latest; 2002 = earliest
			Northings	$F_{1,477} = 25.69$	**$P < 0.001$**				+
			Eastings	$F_{1,477} = 1.36$	$P = 0.25$				NS
			Altitude	$F_{1,477} = 4.61$	**$P = 0.03$**				+
			Northings × nest site habitat	$F_{2,477} = 3.67$	**$P = 0.03$**				R = more pronounced latitudinal variation than B and U
Clutch size	BT	2000	Nest site habitat	$F_{2,90} = 0.98$	$P = 0.38$				NS
			Northings	$F_{1,90} = 4.98$	**$P = 0.03$**				+
			Eastings	$F_{1,90} = 0.05$	$P = 0.83$				NS
			Altitude	$F_{1,90} = 1.19$	$P = 0.28$				NS
			Clutch initiation date	$F_{1,90} = 32.52$	**$P < 0.001$**				-
		2001	Nest site habitat	$F_{2,78} = 2.65$	$P = 0.08$				NS
			Northings	$F_{1,78} = 0.53$	$P = 0.47$				NS
			Eastings	$F_{1,78} = 0.76$	$P = 0.39$				NS
			Altitude	$F_{1,78} = 0.37$	$P = 0.54$				NS
			Clutch initiation date	$F_{1,78} = 8.90$	**$P = 0.004$**				-
		2002	Nest site habitat	$F_{2,41} = 8.30$	**$P = 0.001$**	**$P = 0.006$**	**$P = 0.02$**	$P = 0.68$	B = largest; R = smallest
			Northings	$F_{1,41} = 4.68$	**$P = 0.04$**				+
			Eastings	$F_{1,41} = 3.13$	$P = 0.08$				NS
			Altitude	$F_{1,41} = 2.39$	$P = 0.13$				NS
			Clutch initiation date	$F_{1,41} = 13.10$	**$P = 0.001$**				-
		2003	Nest site habitat	$F_{2,33} = 7.56$	**$P = 0.002$**	**$P = 0.002$**	$P = 0.16$	$P = 0.24$	B = largest; R = smallest
			Northings	$F_{1,33} = 0.48$	$P = 0.49$				NS

Table 7.1. continued

						Least squares means (P values)			
Breeding parameter	**Sp.**	**Year**	**Fixed factor**	F	P	**B *vs.* R**	**B *vs.* U**	**R *vs.* U**	**Direction**
Clutch size	BT	2003	Eastings	$F_{1,33} = 6.69$	**$P = 0.01$**				+
			Altitude	$F_{1,33} = 1.27$	$P = 0.27$				NS
			Clutch initiation date	$F_{1,33} = 0.25$	$P = 0.62$				NS
		2004	Nest site habitat	$F_{2,59} = 3.53$	**$P = 0.04$**	$P = 1.00$	**$P = 0.03$**	$P = 0.11$	R = largest; U = smallest
			Northings	$F_{1,59} = 2.49$	$P = 0.12$				NS
			Eastings	$F_{1,59} = 3.21$	$P = 0.08$				NS
			Altitude	$F_{1,59} = 0.65$	$P = 0.42$				NS
			Clutch initiation date	$F_{1,59} = 12.65$	**$P = 0.001$**				-
	GT	2000-04	Nest site habitat	$F_{2,209} = 1.83$	$P = 0.16$				NS
			Year	$F_{4,209} = 1.16$	$P = 0.33$				NS
			Northings	$F_{1,209} = 0.09$	$P = 0.76$				NS
			Eastings	$F_{1,209} = 3.51$	$P = 0.06$				NS
			Altitude	$F_{1,209} = 0.31$	$P = 0.58$				NS
			Clutch initiation date	$F_{1,209} = 4.82$	**$P = 0.03$**				-
			Altitude × nest site habitat	$F_{2,209} = 3.30$	**$P = 0.04$**				R = smaller with increased altitude; U = the opposite; B = little difference
Brood size	BT	2000-04	Nest site habitat	$F_{2,464} = 12.48$	**$P < 0.001$**	**$P < 0.001$**	**$P = 0.002$**	$P = 0.84$	B = largest; R =smallest
			Year	$F_{4,464} = 1.71$	$P = 0.15$				NS
			Northings	$F_{1,464} = 0.85$	$P = 0.36$				NS
			Eastings	$F_{1,464} = 0.11$	$P = 0.74$				NS
			Altitude	$F_{1,464} = 0.35$	$P = 0.56$				NS
			Clutch initiation date	$F_{1,464} = 13.89$	**$P < 0.001$**				-
	GT	2000-04	Nest site habitat	$F_{2,390} = 1.06$	$P = 0.35$				NS
			Year	$F_{4,390} = 5.32$	**$P < 0.001$**				2003 = smallest; 2004 = largest
			Northings	$F_{1,390} = 6.51$	**$P = 0.01$**				+
			Eastings	$F_{1,390} = 1.11$	$P = 0.29$				NS
			Altitude	$F_{1,390} = 4.17$	**$P = 0.04$**				+
			Clutch initiation date	$F_{1,390} = 11.12$	**$P = 0.001$**				-
Brood size as a proportion of clutch size	BT	2000-04	Nest site habitat	$F_{2,251} = 1.44$	$P = 0.24$				NS
			Year	$F_{4,251} = 1.51$	$P = 0.20$				NS
			Northings	$F_{1,251} = 0.13$	$P = 0.71$				NS
			Eastings	$F_{1,251} = 0.37$	$P = 0.55$				NS
			Altitude	$F_{1,251} = 3.56$	$P = 0.06$				NS
			Clutch initiation date	$F_{1,251} = 3.19$	$P = 0.08$				NS

Table 7.1. continued

						Least squares means (*P* values)			
Breeding parameter	**Sp.**	**Year**	**Fixed factor**	***F***	***P***	**B *vs.* R**	**B *vs.* U**	**R *vs.* U**	**Direction**
Brood size as a proportion of clutch size	GT	2000-04	Nest site habitat	$F_{2,168} = 1.10$	$P = 0.33$				NS
			Year	$F_{4,168} = 1.33$	$P = 0.26$				NS
			Northings	$F_{1,168} = 1.40$	$P = 0.24$				NS
			Eastings	$F_{1,168} = 1.21$	$P = 0.27$				NS
			Altitude	$F_{1,168} = 0.15$	$P = 0.70$				NS
			Clutch initiation date	$F_{1,168} = 3.28$	$P = 0.07$				NS

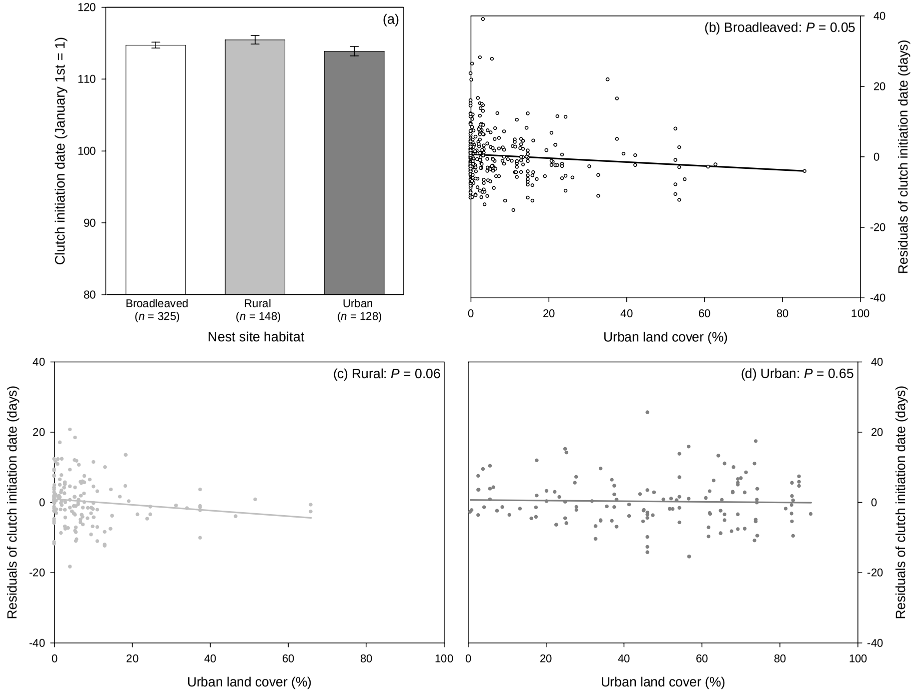

Figure 7.2. (a) The relationship between nest site habitat and clutch initiation date (mean ± 1 SE from statistical estimates) of blue tits in the UK in 2000-2004. Number of nest records is in parentheses below each nest site habitat. The relationship between urban land cover (percentage of land surface area per 1-km grid square) and clutch initiation date in (b) broadleaved, (c) rural, and (d) urban nest site habitats. Residuals were obtained after accounting for all other predictors in each model (see Table 7.2). See text for details.

(Fig. 7.2; Table 7.2), a tendency also found in rural nests ($F_{1,139} = 3.69$, $P = 0.06$) (Fig. 7.2; Table 7.2). Clutch initiation date did not vary significantly with increased ULC in urban nest site habitats ($F_{1,119} = 0.20$, $P = 0.65$) (Fig. 7.2; Table 7.2). In broadleaved nest site habitats for every 10% increase in ULC blue tits advanced laying by 0.6 days (Fig. 7.2). In great tits, laying was significantly earlier in urban, compared with broadleaved (mean: 6.5 days later; $P < 0.001$) and rural (mean: 3.8 days later; $P = 0.01$), nest site habitats (Fig. 7.3; Table 7.1). Laying was also significantly earlier in rural, compared with broadleaved (mean: 2.7 days later; $P = 0.03$), nest site habitats (Fig. 7.3; Table 7.1). In broadleaved ($F_{1,260} = 3.88$, $P = 0.05$) and rural ($F_{1,111} = 10.65$, $P = 0.002$), but not urban ($F_{1,91} = 0.26$, $P = 0.61$), nest site habitats clutch initiation of great tits advanced significantly with increased ULC in the surrounding

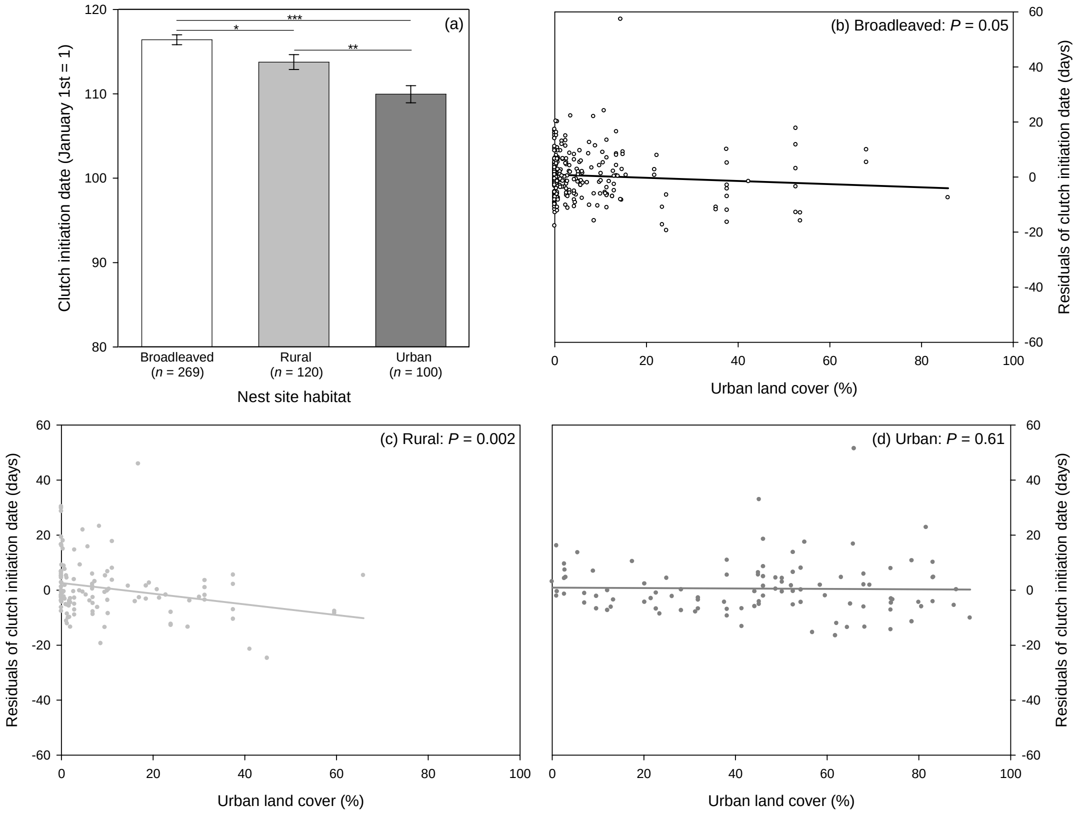

Figure 7.3. (a) The relationship between nest site habitat and clutch initiation date (mean ± 1 SE from statistical estimates) of great tits in the UK in 2000-2004 (*$P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$). Number of nest records is in parentheses below each nest site habitat. The relationship between urban land cover (percentage of land surface area per 1-km grid square) and clutch initiation date in (b) broadleaved, (c) rural, and (d) urban nest site habitats. Residuals were obtained after accounting for all other predictors in each model (see Table 7.2). See text for details.

Table 7.2. Models of breeding parameters (F and associated P values) of blue (BT) and great (GT) tits in the UK in 2000-2004, recorded in three nest site habitats: broadleaved, rural, and urban. Combined-year analyses conducted. Fixed factors in each model are given with significant P values in bold text. Urban land cover = ULC, broadleaved land cover = BLC. BLC was not included in analyses of clutch initiation date since there was no clear hypothesis to do so. Directions of significant effects are given: '+' and '-' denote significant positive and negative associations, respectively, and 'NS' denotes non-significance ($P > 0.05$). See text for details.

Breeding parameter	**Sp.**	**Nest site habitat**	**Fixed factor**	**F**	**P**	**Direction**
Clutch initiation date	BT	Broadleaved	ULC	$F_{1,316} = 3.86$	**P = 0.05**	-
			Year	$F_{4,316} = 31.26$	**P < 0.001**	2001 = latest; 2002 = earliest
			Northings	$F_{1,316} = 18.08$	**P < 0.001**	+
			Eastings	$F_{1,316} = 3.97$	**P = 0.05**	-
			Altitude	$F_{1,316} = 4.30$	**P = 0.04**	+
		Rural	ULC	$F_{1,139} = 3.69$	$P = 0.06$	NS
			Year	$F_{4,139} = 9.87$	**P < 0.001**	2001 = latest; 2002 = earliest
			Northings	$F_{1,139} = 17.74$	**P < 0.001**	+
			Eastings	$F_{1,139} = 1.46$	$P = 0.23$	NS
			Altitude	$F_{1,139} = 9.06$	**P = 0.003**	+
		Urban	ULC	$F_{1,119} = 0.20$	$P = 0.65$	NS
			Year	$F_{4,119} = 6.22$	**P < 0.001**	2001 = latest; 2002 = earliest
			Northings	$F_{1,119} = 4.59$	**P = 0.03**	+
			Eastings	$F_{1,119} = 1.99$	$P = 0.16$	NS
			Altitude	$F_{1,119} = 9.88$	**P = 0.002**	+
	GT	Broadleaved	ULC	$F_{1,260} = 3.88$	**P = 0.05**	-
			Year	$F_{4,260} = 16.32$	**P < 0.001**	2001 = latest; 2002 = earliest
			Northings	$F_{1,260} = 10.07$	**P = 0.002**	+
			Eastings	$F_{1,260} = 1.65$	$P = 0.20$	NS
			Altitude	$F_{1,260} = 3.55$	$P = 0.06$	NS
		Rural	ULC	$F_{1,111} = 10.65$	**P = 0.002**	-
			Year	$F_{4,111} = 2.70$	**P = 0.03**	2000 = latest; 2002 = earliest
			Northings	$F_{1,111} = 18.13$	**P < 0.001**	+
			Eastings	$F_{1,111} = 0.78$	$P = 0.38$	NS
			Altitude	$F_{1,111} = 0.10$	$P = 0.76$	NS
		Urban	ULC	$F_{1,91} = 0.26$	$P = 0.61$	NS
			Year	$F_{4,91} = 3.21$	**P = 0.02**	2002 = earliest; 2004 = latest
			Northings	$F_{1,91} = 5.19$	**P = 0.03**	+
			Eastings	$F_{1,91} = 3.59$	$P = 0.06$	NS
			Altitude	$F_{1,91} = 3.18$	$P = 0.08$	NS
Clutch size	BT	Broadleaved	ULC	$F_{1,188} = 0.64$	$P = 0.43$	NS

Table 7.2. continued

Breeding parameter	**Sp.**	**Nest site habitat**	**Fixed factor**	***F***	***P***	**Direction**
Clutch size	BT	Broadleaved	BLC	$F_{1,188} = 5.11$	**P = 0.03**	+
			Year	$F_{4,188} = 2.39$	**P = 0.05**	2001 = largest; 2003 = smallest
			Northings	$F_{1,188} = 9.00$	**P = 0.003**	+
			Eastings	$F_{1,188} = 1.31$	$P = 0.25$	NS
			Altitude	$F_{1,188} = 0.00$	$P = 0.99$	NS
			Clutch initiation date	$F_{1,188} = 46.91$	**P < 0.001**	-
		Rural	ULC	$F_{1,69} = 0.35$	$P = 0.56$	NS
			BLC	$F_{1,69} = 0.04$	$P = 0.85$	NS
			Year	$F_{4,69} = 2.68$	**P = 0.04**	2002 = smallest; 2004 = largest
			Northings	$F_{1,69} = 0.21$	$P = 0.65$	NS
			Eastings	$F_{1,69} = 0.04$	$P = 0.83$	NS
			Altitude	$F_{1,69} = 3.80$	$P = 0.06$	NS
			Clutch initiation date	$F_{1,69} = 8.53$	**P = 0.005**	-
		Urban	ULC	$F_{1,46} = 0.00$	$P = 0.95$	NS
			BLC	$F_{1,46} = 0.09$	$P = 0.76$	NS
			Year	$F_{4,46} = 1.56$	$P = 0.20$	NS
			Northings	$F_{1,46} = 0.23$	$P = 0.63$	NS
			Eastings	$F_{1,46} = 1.53$	$P = 0.22$	NS
			Altitude	$F_{1,46} = 0.02$	$P = 0.90$	NS
			Clutch initiation date	$F_{1,46} = 4.92$	**P = 0.03**	-
	GT	Broadleaved	ULC	$F_{1,120} = 7.51$	**P = 0.007**	-
			BLC	$F_{1,120} = 0.71$	$P = 0.40$	NS
			Year	$F_{4,120} = 1.00$	$P = 0.41$	NS
			Northings	$F_{1,120} = 0.22$	$P = 0.64$	NS
			Eastings	$F_{1,120} = 6.39$	**P = 0.01**	+
			Altitude	$F_{1,120} = 0.01$	$P = 0.91$	NS
			Clutch initiation date	$F_{1,120} = 0.04$	$P = 0.83$	NS
		Rural	ULC	$F_{1,39} = 0.09$	$P = 0.77$	NS
			BLC	$F_{1,39} = 1.11$	$P = 0.30$	NS
			Year	$F_{4,39} = 0.91$	$P = 0.47$	NS
			Northings	$F_{1,39} = 0.31$	$P = 0.58$	NS
			Eastings	$F_{1,39} = 0.28$	$P = 0.60$	NS
			Altitude	$F_{1,39} = 4.02$	**P = 0.05**	-
			Clutch initiation date	$F_{1,39} = 3.89$	$P = 0.06$	NS
		Urban	ULC	$F_{1,30} = 0.25$	$P = 0.62$	NS

Table 7.2. continued

Breeding parameter	**Sp.**	**Nest site habitat**	**Fixed factor**	***F***	***P***	**Direction**
Clutch size	GT	Urban	BLC	$F_{1,30} = 0.75$	$P = 0.39$	NS
			Year	$F_{4,30} = 2.63$	$\boldsymbol{P = 0.05}$	2000 = largest; 2003 = smallest
			Northings	$F_{1,30} = 1.04$	$P = 0.32$	NS
			Eastings	$F_{1,30} = 0.14$	$P = 0.71$	NS
			Altitude	$F_{1,30} = 2.59$	$P = 0.12$	NS
			Clutch initiation date	$F_{1,30} = 3.01$	$P = 0.09$	NS
Brood size	BT	Broadleaved	ULC	$F_{1,251} = 6.76$	$\boldsymbol{P = 0.01}$	-
			BLC	$F_{1,251} = 2.22$	$P = 0.14$	NS
			Year	$F_{4,251} = 0.77$	$P = 0.54$	NS
			Northings	$F_{1,251} = 0.69$	$P = 0.41$	NS
			Eastings	$F_{1,251} = 0.27$	$P = 0.61$	NS
			Altitude	$F_{1,251} = 1.05$	$P = 0.31$	NS
			Clutch initiation date	$F_{1,251} = 9.36$	$\boldsymbol{P = 0.003}$	-
		Rural	ULC	$F_{1,106} = 0.02$	$P = 0.88$	NS
			BLC	$F_{1,106} = 2.33$	$P = 0.13$	NS
			Year	$F_{4,106} = 1.11$	$P = 0.36$	NS
			Northings	$F_{1,106} = 0.20$	$P = 0.65$	NS
			Eastings	$F_{1,106} = 0.02$	$P = 0.90$	NS
			Altitude	$F_{1,106} = 0.00$	$P = 0.95$	NS
			Clutch initiation date	$F_{1,106} = 2.86$	$P = 0.09$	NS
		Urban	ULC	$F_{1,85} = 0.23$	$P = 0.63$	NS
			BLC	$F_{1,85} = 0.01$	$P = 0.93$	NS
			Year	$F_{4,85} = 2.10$	$P = 0.09$	NS
			Northings	$F_{1,85} = 1.16$	$P = 0.28$	NS
			Eastings	$F_{1,85} = 0.98$	$P = 0.33$	NS
			Altitude	$F_{1,85} = 0.54$	$P = 0.46$	NS
			Clutch initiation date	$F_{1,85} = 1.19$	$P = 0.28$	NS
	GT	Broadleaved	ULC	$F_{1,207} = 3.89$	$\boldsymbol{P = 0.05}$	-
			BLC	$F_{1,207} = 0.21$	$P = 0.64$	NS
			Year	$F_{4,207} = 4.55$	$\boldsymbol{P = 0.002}$	2003 = smallest; 2004 = largest
			Northings	$F_{1,207} = 3.35$	$P = 0.07$	NS
			Eastings	$F_{1,207} = 0.33$	$P = 0.57$	NS
			Altitude	$F_{1,207} = 0.92$	$P = 0.34$	NS
			Clutch initiation date	$F_{1,207} = 4.89$	$\boldsymbol{P = 0.03}$	-
		Rural	ULC	$F_{1,90} = 0.19$	$P = 0.66$	NS

Table 7.2. continued

Breeding parameter	**Sp.**	**Nest site habitat**	**Fixed factor**	***F***	***P***	**Direction**
Brood size	GT	Rural	BLC	$F_{1,90} = 1.46$	$P = 0.23$	NS
			Year	$F_{4,90} = 0.87$	$P = 0.49$	NS
			Northings	$F_{1,90} = 1.06$	$P = 0.31$	NS
			Eastings	$F_{1,90} = 0.52$	$P = 0.47$	NS
			Altitude	$F_{1,90} = 0.64$	$P = 0.43$	NS
			Clutch initiation date	$F_{1,90} = 2.38$	$P = 0.13$	NS
		Urban	ULC	$F_{1,71} = 0.40$	$P = 0.53$	NS
			BLC	$F_{1,71} = 3.33$	$P = 0.07$	NS
			Year	$F_{4,71} = 2.55$	$\mathbf{P = 0.05}$	2001 = smallest; 2004 = largest
			Northings	$F_{1,71} = 0.54$	$P = 0.47$	NS
			Eastings	$F_{1,71} = 2.86$	$P = 0.10$	NS
			Altitude	$F_{1,71} = 3.37$	$P = 0.07$	NS
			Clutch initiation date	$F_{1,71} = 4.53$	$\mathbf{P = 0.04}$	-
Brood size as a proportion of clutch size	BT	Broadleaved	ULC	$F_{1,150} = 10.70$	$\mathbf{P = 0.001}$	-
			BLC	$F_{1,150} = 0.31$	$P = 0.58$	NS
			Year	$F_{4,150} = 0.89$	$P = 0.47$	NS
			Northings	$F_{1,150} = 0.36$	$P = 0.55$	NS
			Eastings	$F_{1,150} = 0.00$	$P = 1.00$	NS
			Altitude	$F_{1,150} = 2.10$	$P = 0.15$	NS
			Clutch initiation date	$F_{1,150} = 1.36$	$P = 0.24$	NS
		Rural	ULC	$F_{1,52} = 0.53$	$P = 0.47$	NS
			BLC	$F_{1,52} = 2.16$	$P = 0.15$	NS
			Year	$F_{4,52} = 2.36$	$P = 0.07$	NS
			Northings	$F_{1,52} = 0.25$	$P = 0.62$	NS
			Eastings	$F_{1,52} = 0.07$	$P = 0.79$	NS
			Altitude	$F_{1,52} = 1.65$	$P = 0.20$	NS
			Clutch initiation date	$F_{1,52} = 0.80$	$P = 0.37$	NS
		Urban	ULC	$F_{1,27} = 0.23$	$P = 0.63$	NS
			BLC	$F_{1,27} = 0.04$	$P = 0.85$	NS
			Year	$F_{4,27} = 1.04$	$P = 0.40$	NS
			Northings	$F_{1,27} = 3.93$	$P = 0.06$	NS
			Eastings	$F_{1,27} = 3.73$	$P = 0.06$	NS
			Altitude	$F_{1,27} = 0.77$	$P = 0.39$	NS
			Clutch initiation date	$F_{1,27} = 4.58$	$\mathbf{P = 0.04}$	+
	GT	Broadleaved	ULC	$F_{1,96} = 2.07$	$P = 0.15$	NS

Table 7.2. continued

Breeding parameter	**Sp.**	**Nest site habitat**	**Fixed factor**	***F***	***P***	**Direction**
Brood size as a proportion of clutch size	GT	Broadleaved	BLC	$F_{1,96} = 0.23$	$P = 0.63$	NS
			Year	$F_{4,96} = 1.03$	$P = 0.40$	NS
			Northings	$F_{1,96} = 3.80$	$\mathbf{P = 0.05}$	+
			Eastings	$F_{1,96} = 1.36$	$P = 0.25$	NS
			Altitude	$F_{1,96} = 0.28$	$P = 0.60$	NS
			Clutch initiation date	$F_{1,96} = 1.18$	$P = 0.28$	NS
		Rural	ULC	$F_{1,30} = 2.20$	$P = 0.15$	NS
			BLC	$F_{1,30} = 0.73$	$P = 0.40$	NS
			Year	$F_{4,30} = 1.53$	$P = 0.22$	NS
			Northings	$F_{1,30} = 0.44$	$P = 0.51$	NS
			Eastings	$F_{1,30} = 0.02$	$P = 0.90$	NS
			Altitude	$F_{1,30} = 0.13$	$P = 0.72$	NS
			Clutch initiation date	$F_{1,30} = 0.00$	$P = 0.95$	NS
		Urban	ULC	$F_{1,20} = 0.95$	$P = 0.34$	NS
			BLC	$F_{1,20} = 0.20$	$P = 0.66$	NS
			Year	$F_{4,20} = 1.53$	$P = 0.23$	NS
			Northings	$F_{1,20} = 2.82$	$P = 0.11$	NS
			Eastings	$F_{1,20} = 0.20$	$P = 0.66$	NS
			Altitude	$F_{1,20} = 2.49$	$P = 0.13$	NS
			Clutch initiation date	$F_{1,20} = 0.34$	$P = 0.57$	NS

landscape (Fig. 7.3; Table 7.2). Laying advanced by 0.6 and 1.9 days, respectively, for every 10% increase in ULC in broadleaved and rural nest site habitats (Fig. 7.3).

7.4.2. Productivity: clutch size, brood size, and brood size as a proportion of clutch size

Clutch size of blue tits was usually largest in broadleaved, and smallest in rural, nest site habitats but these differences varied between years (year × nest site habitat: $F_{8,317} = 2.02$, $P = 0.04$), and within-year analyses revealed few consistent patterns in clutch size between nest site habitats (Table 7.1). Clutch size of blue tits was not predicted significantly by ULC in any nest site habitat (all *P*s > 0.05) (Table 7.2) but a positive association between clutch size and BLC was found in broadleaved ($F_{1,188} = 5.11$, $P = 0.03$), but not rural ($F_{1,69} = 0.04$, $P = 0.85$) or urban ($F_{1,46} = 0.09$, $P = 0.76$), nest site habitats (Table 7.2). In broadleaved nest site habitats, clutch size of blue tits increased by 0.1 eggs for every 10% increase in BLC. In great tits, clutch size did not differ significantly between nest site habitats ($F_{2,209} = 1.83$, $P = 0.16$) (Table 7.1). Clutch size of great tits decreased with increased ULC in broadleaved ($F_{1,120} = 7.51$, $P = 0.007$), but not rural ($F_{1,39} = 0.09$, $P = 0.77$) or urban ($F_{1,30} = 0.25$, $P = 0.62$), nest site habitats (Table 7.2). In broadleaved nest site habitats, clutch size of great tits decreased by 0.3 eggs for every 10% increase in ULC. BLC did not predict clutch size of great tits significantly in any nest site habitat (all *P*s > 0.05) (Table 7.2).

Brood size of blue tits was significantly larger in broadleaved, compared with rural (mean: 1.2 fewer nestlings; $P < 0.001$) and urban (mean: 1.1 fewer nestlings; $P = 0.002$), nest site habitats (Fig. 7.4; Table 7.1). Brood size of blue tits also decreased with increased ULC in broadleaved ($F_{1,251} = 6.76$, $P = 0.01$), but not rural ($F_{1,106} = 0.02$, $P = 0.88$) or urban ($F_{1,85} = 0.23$, $P = 0.63$), nest site habitats (Fig. 7.4; Table 7.2). In broadleaved nest site habitats, brood size of blue tits decreased by 0.3 nestlings for every 10% increase in ULC (Fig. 7.4). In great

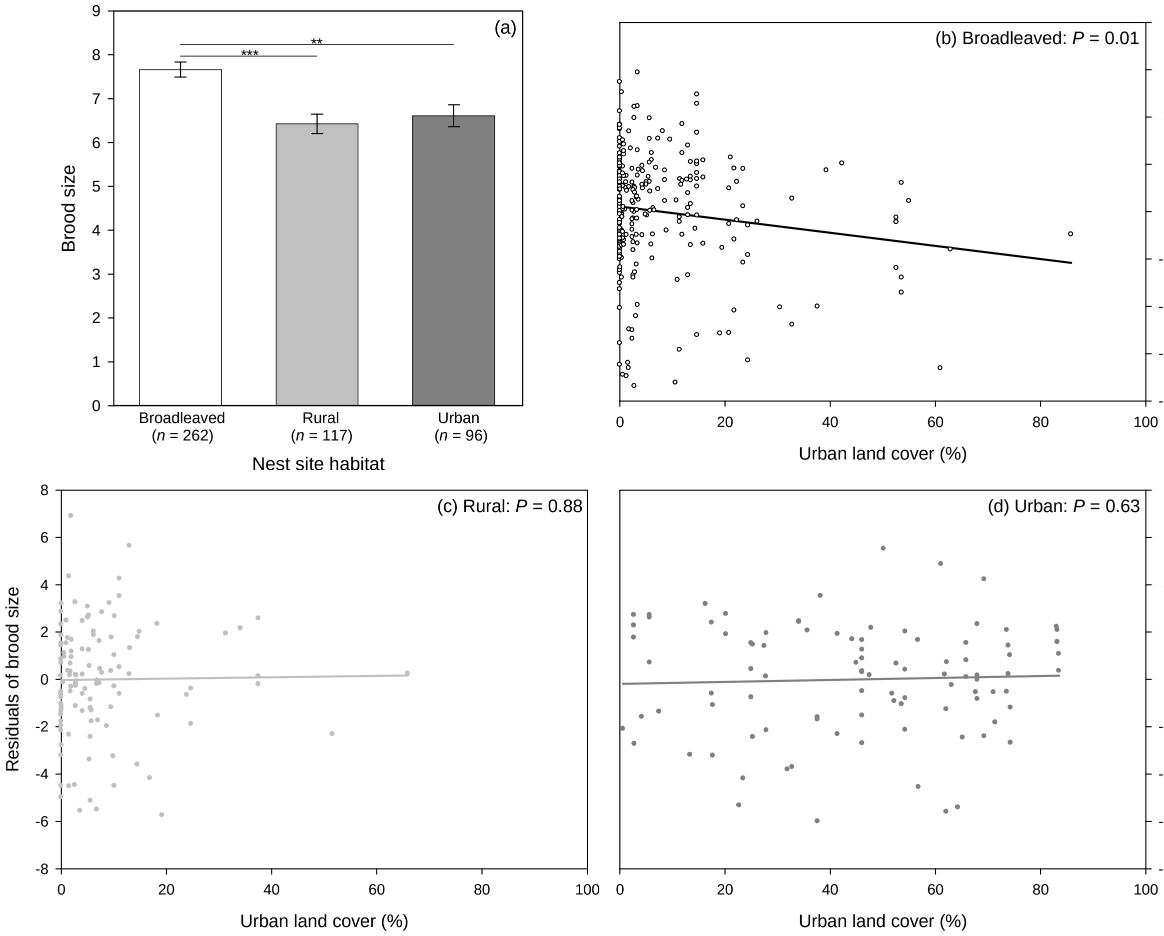

Figure 7.4. (a) The relationship between nest site habitat and brood size (mean ± 1 SE from statistical estimates) of blue tits in the UK in 2000-2004 (** $P \leq 0.01$; *** $P \leq 0.001$). Number of nest records is in parentheses below each nest site habitat. The relationship between urban land cover (percentage of land surface area per 1-km grid square) and brood size in (b) broadleaved, (c) rural, and (d) urban nest site habitats. Residuals were obtained after accounting for all other predictors in each model (see Table 7.2). See text for details.

tits, brood size did not differ significantly between nest site habitats ($F_{2,390} = 1.06$, $P = 0.35$) (Fig. 7.5; Table 7.1). However, increased ULC was associated with smaller broods in broadleaved ($F_{1,207} = 3.89$, $P = 0.05$), but not rural ($F_{1,90} = 0.19$, $P = 0.66$) or urban ($F_{1,71} = 0.40$, $P = 0.53$), nest site habitats (Fig. 7.5; Table 7.2). In broadleaved nest site habitats, brood size of great tits decreased by 0.2 nestlings for every 10% increase in ULC (Fig. 7.5). BLC did not predict brood size of either species significantly in any nest site habitat (all Ps > 0.05) (Table 7.2).

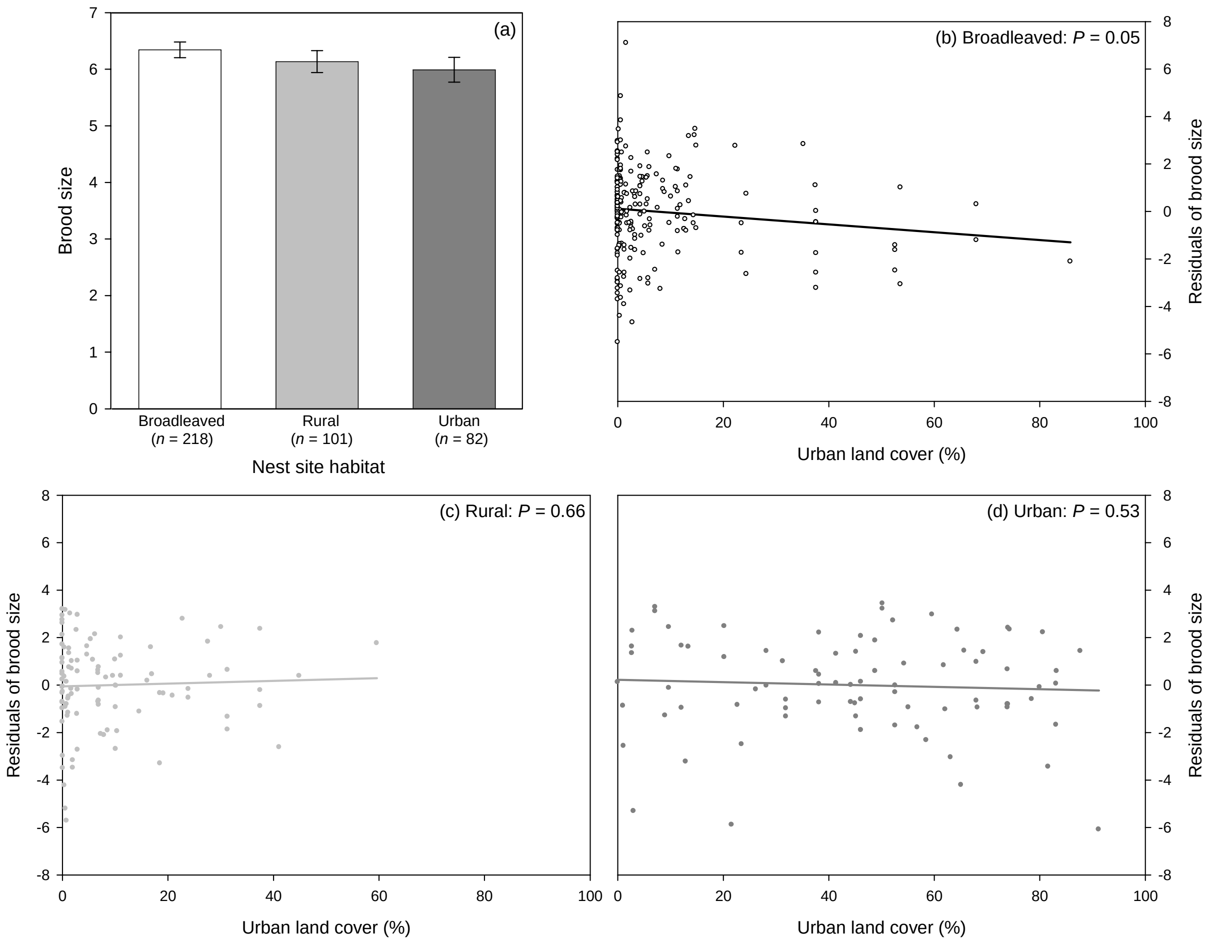

Figure 7.5. (a) The relationship between nest site habitat and brood size (mean ± 1 SE from statistical estimates) of great tits in the UK in 2000-2004. Number of nest records is in parentheses below each nest site habitat. The relationship between urban land cover (percentage of land surface area per 1-km grid square) and brood size in (b) broadleaved, (c) rural, and (d) urban nest site habitats. Residuals were obtained after accounting for all other predictors in each model (see Table 7.2). See text for details.

Brood size as a proportion of clutch size did not differ significantly between nest site habitats in blue ($F_{2,251} = 1.44$, $P = 0.24$), or great ($F_{2,168} = 1.10$, $P = 0.33$), tits (Table 7.1). In blue tits, brood size as a proportion of clutch size decreased with increased ULC in broadleaved ($F_{1,150} = 10.70$, $P = 0.001$), but not rural ($F_{1,52} = 0.53$, $P = 0.47$) or urban ($F_{1,27} = 0.23$, $P = 0.63$), nest site habitats (Table 7.2). In broadleaved nest site habitats, brood size as a proportion of clutch size in blue tits declined by 0.04 (4%) for every 10% increase in ULC. In great tits, ULC did not predict brood size as a proportion of clutch size significantly in any nest site habitat (all Ps > 0.05) (Table 7.2). BLC did not predict brood size as a proportion of clutch size significantly in either species and in any nest site habitat (all *P*s > 0.05) (Table 7.2).

7.5. Discussion

Significant differences were found in breeding parameters between nest site habitats, but numerous non-significant differences were also found (Figs 7.2-7.5; Table 7.1). This suggests that local habitat differences between urban and non-urban nests can cause significant variation in breeding parameters, but that these effects are not always influential. Importantly, my research demonstrates that avian reproduction might be influenced by landscape scale habitat characteristics, particularly with respect to ULC in non-urban (especially broadleaved) nest site habitats (Figs 7.2-7.5; Table 7.2). Increased BLC was only associated significantly with larger clutches of blue tits in broadleaved nest site habitats (Table 7.2), suggesting a less pronounced landscape scale influence than for ULC. These findings partially support my hypotheses.

7.5.1. Phenology: clutch initiation date

Advanced laying in urban nest site habitats was predicted in both species, but a more significant effect in great (Fig. 7.3), rather than blue (Fig. 7.2), tits supports the findings of previous studies. Dhondt *et al.* (1984) found that great tits advanced laying significantly with increased urbanisation, but found a less clear effect in blue tits. Perrins (1965) also reported similar patterns. These interspecific differences are difficult to explain but might be driven by blue tits having a narrower temporal window within which clutches are initiated than great tits (Perrins 1979) thereby causing less intraspecific variation in breeding phenology.

In both species, increased ULC was associated with advanced laying in non-urban (broadleaved and rural), but not urban, nest site habitats (Figs 7.2 & 7.3). This suggests that ULC could influence breeding phenology of birds breeding beyond its physical boundary. For this to occur, blue and great tits in non-urban nest site habitats in highly-urbanised landscapes must have: (i) utilised urban habitats directly (e.g. obtaining food supplements that may advance laying – Nager *et al.* 1997; Ramsay & Houston 1997; Chapter Two); (ii) experienced pervasive effects of increased ULC without utilising urban habitats directly (e.g. warmer temperatures/advanced availability of cold-blooded invertebrates – Haggard 1990; Perrins 1979); and/or (iii) had an unusually high proportion of 'urban birds' in the breeding population (that might be genetically predisposed to early laying – van Noordwijk 1987). ULC did not predict breeding phenology in urban nest site habitats and, in great tits at least, this could be because laying was already advanced compared with rural and broadleaved nest site habitats (Fig. 7.3).

Very few studies have demonstrated an association between urbanisation and breeding phenology in non-urban habitats, and certainly none on this spatial scale. Dhondt *et al.* (1984) found that great tits in small urban parks laid earlier than in a large urban park, probably because of greater access to supplementary food in gardens. Hedblom (2007) demonstrated that great tits hatched progressively later along transects that started in urban habitats and penetrated 150 m into woodland. Rodewald and Shustack (2008b) found that Acadian flycatchers *Empidonax virescens* initiated nests later in urban, compared with non-urban, forests, but this species is migratory unlike blue and great tits.

7.5.2. Productivity: clutch size, brood size, and brood size as a proportion of clutch size

Reduced productivity was predicted in urban nest site habitats, particularly when compared with nests in broadleaved habitats. In blue tits, there was evidence that this occurred (clutch and brood size – Fig. 7.4; Table 7.1). However, in great tits, productivity did not differ significantly between nest site habitats (Fig. 7.5; Table 7.1). These interspecific differences suggest that great tits are: (i) better adapted to urban-breeding than are blue tits (e.g. perhaps due to the more general diet of great tit nestlings – Betts 1955; Török 1985, 1986); (ii) similarly productive across habitats due to the mixing of urban (perhaps genetically predisposed to laying smaller clutches) and non-urban (perhaps genetically predisposed to laying larger clutches) recruits, causing a homogenisation of productivity across habitats; and/or (iii) less dependent on broadleaved habitat than are blue tits to breed successfully (Gibb and Betts 1963).

Increased ULC was associated with reduced clutch and brood sizes of great tits in broadleaved nest site habitats (Fig. 7.5; Table 7.2). For this to occur, great tits in broadleaved habitats in highly-urbanised landscapes must have: (i) utilised urban habitats directly (e.g. fed on poor-quality foods/unsuitable food supplements – Cowie & Hinsley 1988a; Solonen 2001; Chapters Two & Four, but see Chapter Five); (ii) experienced pervasive effects of increased ULC without utilising urban habitats directly (e.g. pollution, warmer temperatures resulting in mis-timed breeding attempts – Eeva *et al.* 1997; Visser & Both 2005); and/or (iii) had an unusually high proportion of ‘urban birds’ in the breeding population (that might be genetically predisposed to smaller clutches – Perrins & Jones 1974). These mechanisms could also explain reduced brood size of blue tits in broadleaved nest site habitats with increased ULC in the surrounding landscape (Fig. 7.4; Table 7.2). ULC did not predict clutch or brood sizes of either species significantly in rural or urban nest site habitats (Figs 7.4 & 7.5; Table

7.2). This might be because productivity was lower in these, compared with broadleaved, nest site habitats (e.g. see blue tits – Fig. 7.4; Table 7.1). Indeed, advanced breeding phenology and reduced productivity through increased urbanisation on a landscape scale might be diluted by the influence of increased urbanisation on a local scale on these parameters.

In great tits, brood size as a proportion of clutch size did not differ significantly with changes in ULC, suggesting that investment in clutch size matched brood sizes reared. In blue tits, however, brood size as a proportion of clutch size declined significantly with increased ULC in broadleaved nest site habitats (Table 7.2), suggesting that investment in clutch size was disproportionately large relative to brood sizes reared. This discrepancy was caused by increased hatching failure and/or partial brood mortality. Although I cannot dissociate these possibilities here, either are of note given that all nests were situated in similar (i.e. broadleaved) habitat so that little variation in breeding parameters might be expected.

In Chapter Six I proposed that broadleaved habitat might ameliorate some of the adverse effects of urbanisation on productivity of blue and great tits. Indeed, Perrins (1965) suggested that close proximity to woodland may decrease brood mortality of tits breeding in urban areas. Here, however, I found no evidence that increased BLC enhanced productivity in rural and urban nest site habitats (Table 7.2). BLC was only associated significantly with clutch size of blue tits in broadleaved nest site habitats (a positive relationship – Table 7.2), again indicating that blue tits are most productive in large broadleaved woodlands, away from ULC. Overall, relationships between BLC and reproduction in non-broadleaved nest site habitats were much weaker than those between ULC and reproduction in non-urban nest site habitats (Table 7.2). To my knowledge, no previous study of blue or great tits has found an association between urbanisation and clutch or brood size, or brood size as a proportion of clutch size, in non-urban nest site habitats. In the only comparable study, clutch and brood sizes of rufous-crowned sparrows *Aimophila ruficeps* nesting in sage scrub habitat (in California, USA) did not differ significantly with closer proximity to urban development (although brood size showed some decline – Morrison & Bolger 2002).

7.5.3. General discussion and conclusions

Urbanisation can fragment habitats (Sallabanks 2002; Thorington & Bowman 2003) with undeveloped areas (e.g. remnant ‘natural’ habitats such as urban woodlands) promoted as important areas of biodiversity and conservation (e.g. Fernández-Juricic & Jokimäki 2001; Atchison & Rodewald 2006; Croci *et al.* 2008). Therefore, an influence of ULC in non-urban habitats raises concern regarding the value of set-aside habitats and ‘ecologically-sensitive’ urban development. Future research should examine the sensitivity of more species to changes in ULC (and other key habitats – e.g. BLC in this study) on a landscape scale. NRS data provide an ideal approach for exploring this further.

Significant associations between ULC or BLC and breeding phenology and productivity might have been caused by erroneous classification of nest site habitats across urban and broadleaved habitat gradients. However, Figure 7.1 indicates that classification was generally accurate. Moreover, significant ULC or BLC associations were usually found in broadleaved, but not rural or urban, nest site habitats (Figs 7.2-7.5; Table 7.2), the former being relatively unambiguous to define (five other woodland classifications were available, and municipal parks/recreation areas had a different NRS habitat code). Despite this, broadleaved woodland management might differ in more urbanised landscapes (e.g. more exotic vegetation that may support fewer caterpillars – Borgmann & Rodewald 2004; Burghardt *et al.* 2009), although vegetation structure (Croci *et al.* 2008) and tree-species composition (Isaksson & Andersson 2007) might be similar.

As discussed, a number of urban-specific factors might influence reproduction in non-urban habitats. First, breeding pairs could utilise urban habitats directly (e.g. feed on supplements in gardens). For example, the foraging ranges of blue and great tits can exceed *c.* 300 m during reproduction (Wilkin *et al.* 2009). Second, particular characteristics of ULC (e.g. heat – Wilby & Perry 2006; pollution – Eeva *et al.* 1997; light – Partecke *et al.* 2004; noise – Slabbekoorn & Peet 2003) might spread beyond its physical boundaries. Such pervasive characteristics are unlikely to be common with other habitats (e.g. BLC; Table 7.2). Lastly, pairs that are most adapted to breeding in urban habitats might advance laying and reduce productivity (e.g. clutch size) adaptively to optimise reproductive effort. Therefore, a greater representation of 'urban birds' in non-urban nest site habitats in more urbanised landscapes might also account for some of the ULC associations recorded (Figs 7.2-7.5; Table 7.2). These intriguing possibilities require experimental separation and should form the basis of new, and important, research.

Chapter Eight

GENERAL DISCUSSION

8.1. Summary of findings

In my field study, supplemented pairs of blue and great tits fledged significantly fewer young than did control conspecifics (Chapter Four). This occurred due to a significant decrease in clutch size of both species and, in blue tits, a significant reduction in hatching success (Chapter Two). Moreover, in both species, fledging success was greatest in the control treatment (Chapter Four), despite differences in nestling growth (Chapter Three) and synchrony of reproduction with peak caterpillar abundances (Chapter Four) not being pronounced between dietary treatments. I did not hypothesise that food supplementation would reduce pre-fledging productivity of blue or great tits. In support of my hypotheses, however, food supplementation advanced clutch initiation and shortened incubation periods of both species significantly (Chapter Two). Furthermore, apparent survival of fledglings increased through the provision of mealworms (Chapter Four). Intriguingly, these multiple significant effects occurred without either supplement forming a substantial component of the diet and with supplement use showing few significant differences between dietary treatments (Chapter Five).

In my NRS research, I found that increased ULC was associated negatively with clutch initiation date (both species), clutch size (great tits), brood size (both species), and brood size as a proportion of clutch size (blue tits) (Chapter Six). I also found that characteristics of the ULC might influence breeding phenology and productivity of blue and great tits breeding in non-urban habitats (Chapter Seven). The associations between ULC and breeding parameters of both species as presented in Chapters Six and Seven could be influenced by food supplementation in urban habitats.

The significance of my field and NRS findings with respect to the recommendation to supplement birds throughout the spring and summer in UK gardens (e.g. RSPB 2006; Toms & Sterry 2008; BTO 2009) is discussed below. The wider applicability of the findings from my field study with respect to other incidents in which free-living birds are exposed to long-term supplementation during reproduction is also discussed below.

8.2. Food supplementation in gardens

8.2.1. Synthesis of field and NRS findings

Many avian species experience advanced breeding phenology and reduced productivity in urban, compared with rural, habitats (reviewed in Chamberlain *et al.* 2009). In Chapters Six and Seven I demonstrated these effects in blue and great tits across the UK. Importantly, however, these patterns in reproduction in urban habitats (Chapters Six & Seven) were remarkably similar to the effects of food supplementation in my field study (Chapters Two & Four). Given the prevalence of food supplementation across the UK (*c.* 40-50% of households provide food – Davies *et al.* 2009; Fuller *et al.* In press) detection of effects of supplementation, such as those demonstrated in my field study, in urban habitats could well be expected.

Clutch initiation advanced significantly as a result of food supplementation in both species (Chapter Two), indicating that supplementation might also be important in causing advanced laying in urban habitats (Chamberlain *et al.* 2009; Chapters Six & Seven). Similarly, reduced productivity (e.g. brood size, number fledged), as is common in urban habitats (Chamberlain *et al.* 2009; Chapters Six & Seven), was also found as a consequence of food supplementation in my field study. Moreover, the specific details of this reduced productivity are interesting to consider. For example, brood size as a proportion of clutch size decreased significantly with increased ULC in blue, but not in great, tits (Chapter Six) due to increased hatching failure and/or partial brood mortality. In my field study I found that supplementation with peanut cake reduced hatching success of blue, but not great, tits (Chapter Two), suggesting that increased hatching failure might have occurred at increased ULC due to food supplementation. Finally, post-fledging survival is important to consider. Survival rates of birds are often higher in urban, compared with rural, habitats (Hõrak & Lebreton 1998; McGowan 2001). In my field study I found that supplementation with mealworms increased apparent survival of fledglings of both species (Chapter Four). This indicates that some forms of food supplementation could result in enhanced survival in urban habitats.

However, caution should be ascribed to direct comparisons between my field and NRS results. Principally, it is impossible to attribute patterns in breeding parameters with changes in ULC in Chapters Six and Seven directly to food supplementation. Temporal patterns in food supplementation are unknown on a national scale in my NRS work, and spatial distributions can only be approximated from the literature (e.g. Davies *et al.* 2009; Fuller *et al.* In press). Effects of food supplementation are also likely to be confounded by other variables. For example, although supplementation advanced clutch initiation in my field study (Chapter Two), advanced laying in urban habitats (Chapters Six & Seven) could be caused by warmer temperatures (Haggard 1990; Visser *et al.* 2009). Similarly, while food supplementation decreased breeding productivity in my field study (Chapters Two & Four), reduced productivity in urban habitats could be due to factors such as lower natural food availability (Perrins 1979), increased pollution (Eeva *et al.* 1997), or greater parasite infestation (Gregoire *et al.* 2002). It is also important to note that advanced breeding phenology and reduced productivity of blue and great tits in urban, compared with rural, habitats is not a new phenomenon (Perrins 1965), despite the popularity of food supplementation in gardens increasing dramatically over the last few decades (Chamberlain *et al.* 2005; Jones & Reynolds 2008).

Potential habitat-specific differences in the effect of food supplementation on avian reproduction also restrict comparisons between my field and NRS work. For example, my field study was conducted in broadleaved oak woodland, the most productive breeding habitat of blue and great tits in the UK (Perrins 1965). Therefore, it is possible that food supplementation conferred few fitness benefits in this habitat but, instead, had more of a disruptive influence. In gardens, invertebrate foods that are important to rear young are usually scarcer than in non-urban habitats (Perrins 1979), so almost any form of food supplementation might enhance breeding productivity.

8.2.2. Recommendations and future directions

My study provides little evidence to endorse the recommendation to supplement birds in gardens throughout the spring and summer (e.g. RSPB 2006; Toms & Sterry 2008). My field study demonstrated that food supplementation during this period reduced the number of young fledged significantly and, although supplementation with mealworms increased apparent survival of juveniles, the significance of this result was diluted by my lack of knowledge about post-fledging dispersal between dietary treatments (Chapter Four). My NRS findings concur broadly with those of my field study and, therefore, also fail to provide support for food supplementation in gardens during the spring and summer.

However, there are considerable gaps in our knowledge that require bridging. For example, as discussed, habitat-specific differences in the influence of food supplementation might be pronounced. Therefore, it is essential that future research into the influence of food supplementation in gardens is conducted in urban, preferably garden, habitats. The logistical challenges of working in gardens (e.g. access to private property, controlling the amount and type of foods provided – see Chapter One) will require considerable management but are not insurmountable. For example, research focused within small, relatively isolated, urban areas (e.g. housing estates on the periphery of an urban centre) in which discrete food supplementation treatments could be established would offer experimental control and an area small enough to generate sufficient public support. However, such initiatives will require considerable time to initiate and sustain, and researchers must be prepared to manage high levels of interaction with the public above and beyond those experienced in most areas of ecological research (Jones & Reynolds 2008).

Within urban study sites, attention should be focused on a number of key areas concerning the influence of food supplementation on avian reproduction and survival. These areas include ascertaining: (i) the effects of food supplementation during winter compared with throughout the year; (ii) the influence of specific food supplements (e.g. live invertebrates) at different times of the year; (iii) the influence of the predictability (e.g. daily, weekly, monthly, the time of day provided – Howard & Jones 2004; Gaston *et al.* 2007) of food supplementation; (iv) the importance of food supplements in the diet (supplements might only provide a ‘snacking’ resource – O'Leary & Jones 2006; Jones 2008; Chapter Five); and (v) the role of food supplementation in influencing gene flow between urban and rural populations (see Chapters Six & Seven). Much of the above contribute to the wider debate about whether food supplementation in gardens can create an ecological trap (e.g. through cues regarding habitat quality being inflated unreliably – also discussed in Robb *et al.* 2008a). The findings in my NRS research suggest that the extent to which breeding in urban habitats might represent an ecological trap (potentially caused by food supplementation) varies interspecifically, perhaps driven by intraspecific habitat specialisation (see comparisons between blue and great tits in Chapters Six & Seven). Future research should examine the possibility of supplement-induced ecological traps in gardens (see Robertson & Hutto 2006 for guidelines).

In addition to the experimental work as suggested above, my NRS findings could be made more relevant to food supplementation and perhaps even, more specifically, to food supplementation during the spring and summer. For example, information regarding supplement availability could be obtained via direct liaison with NRS nest recorders and/or by using an index of the likelihood of supplements being provided based on housing density and socioeconomic status (e.g. as described in Fuller *et al.* 2008, In press). Expansion of my NRS work to encompass a greater range of species would also broaden its context.

In Chapter Seven, I found associations between breeding parameters of blue and great tits in non-urban nest site habitats and the amount of ULC in the surrounding landscape. Future research should dissociate potential characteristics of the urban environment that might cause these effects (discussed in Chapter Seven) experimentally. For example, regarding food supplementation, a simple experiment would be to use a non-urban study site (e.g. a rural woodland) along one edge of which food supplements would be provided at a similar spacing to that found between gardens (assuming that *c.* 40-50% of householders provide food for birds – Davies *et al.* 2009; Fuller *et al.* In press). On an opposite edge (with considerable spatial separation from the ‘supplemented edge’) no food would be provided as a control treatment. By monitoring nests within the study site at varying distances from the supplemented or control edge, breeding parameters (e.g. phenology, productivity) could be compared. Dietary treatments should be switched between edges between years.

Much remains unknown about the effects of providing food to birds in gardens, not least during the spring and summer. However, it is clear that research is needed to establish guidelines for ‘best practice’ regarding food supplementation in gardens (also suggested in Howard & Jones 2004). These guidelines should be based on evidence collected in urban habitats and be made in collaboration with other garden bird initiatives. For example, the BTO’s Garden Bird Feeding Survey (BTO 2006a) could be used to identify species that use food supplements most frequently on a national scale (e.g. to attempt to reduce supplement use by exotic species – Howard & Jones 2004; Daniels & Kirkpatrick 2006). The findings of the BTO’s Garden Bird Health initiative, that examines factors that affect the risk of disease at garden feeding stations across the UK (BTO 2005a), should also be incorporated into future guidelines.

8.3. Relevance of my field study to food supplementation in non-garden habitats

Further to having implications in gardens, the findings of my field study are also relevant to food supplementation of birds during reproduction in non-urban habitats. In particular this extends to food supplementation as part of conservation initiatives and in pure scientific research (see Chapter One). To a lesser extent, my findings might also be relevant to ‘unintentional’ food supplementation of birds during reproduction (e.g. foraging on landfill, fisheries’ discards – see Chapter One).

8.3.1. Conservation initiatives

8.3.1.1. Applicability of the findings from my field study

Food supplementation is commonly used to decelerate population decline or enhance population growth of endangered species of birds. In many cases food supplements are provided over protracted periods, often during reproduction, and within the natural or semi-natural habitat of passerine species (e.g. stitchbird – Castro *et al.* 2003; Florida scrub jay – Schoech *et al.* 2008). Consequently, the findings of my field study are broadly transferable to such research. In this regard, despite some evidence of increased survival as a result of supplementation with mealworms (Chapter Four), many of my findings are of concern. Food supplementation reduced clutch size (both species), hatching success (blue tits), brood size (both species), fledging success (both species) and the number of young fledged (both species) (Chapters Two & Four). These findings should be considered closely by conservation ecologists in future.

8.3.1.2. Recommendations

I recommend that initiatives wishing to use food supplementation as a conservation tool consider several key issues. Importantly, the influence of food supplementation can vary intraspecifically and geographically (discussed in Chapter Two), so supplementation should not be considered a ‘silver bullet’. Moreover, a host of concerns (e.g. increased survival of poor quality individuals, male-biased brood sex ratios – see Chapter One) have been raised regarding food supplementation of endangered species in recent years. Therefore, conservationists wishing to use food supplementation should undertake a number of important steps to minimise the risk of adverse effects. First, researchers should ensure that the basic ecology (e.g. breeding habitat preferences to ensure that supplements do not encourage reproduction in sub-optimal habitats) of the target species is characterised thoroughly, that nutritional shortfalls are identified (if indeed they exist – e.g. Jamieson 2004), and that researchers are familiar with previous food supplementation initiatives, particularly of the same, or closely-related, species. Second, if it appears that food supplementation will be a valuable tool, small-scale feeding trials should be implemented to examine the influence of carefully-chosen supplements on a wide range of demographic parameters (e.g. breeding productivity, annual survival rates of adults and juveniles). Third, if small-scale trials stimulate population growth with no obvious costs (both intraspecific or interspecific), large-scale initiatives should commence with demographic parameters monitored over multiple years (effects of supplementation can vary annually and there is concern that fitness benefits might decrease over time – Schoech *et al.* 2008). Similar steps have been recommended regarding supplementation of birds with calcium (Reynolds *et al.* 2004). The rationale behind these steps is that populations of endangered species are too fragile for food supplementation to be implemented rashly and to increase extinction risk as a result.

8.3.2. Pure scientific research

8.3.2.1. Applicability of the findings from my field study

The findings in my field study contribute to a large body of pure scientific research that has examined the influence of food supplementation on aspects of avian reproduction (e.g. see reviews in Boutin 1990; Meijer & Drent 1999; Robb *et al.* 2008a; Chapter One). Further to being highly applicable in this regard, my study is also better placed than most to examine the impacts of long-term food supplementation on avian reproduction. First, I supplemented for more than 20 weeks, longer than most previous studies (mean of less than seven weeks calculated from 34 studies reviewed in Meijer & Drent 1999). Second, my study was conducted over several years with dietary treatments rotated between treatment blocks, and with natural food availability recorded (Fig. 4.5; Appendix Four). Poor quality years (Nager *et al.* 1997) and/or territories (Svensson & Nilsson 1995) usually enhance the effects of food supplementation. Therefore, these requirements are essential, but have been overlooked either partially or completely in most previous studies. Third, a comparative two-species approach is unusual in food supplementation research and is helpful because the effects of food supplementation can vary interspecifically (e.g. see Meijer & Drent 1999), and because supplements may be accessible to multiple species, especially in urban habitats (e.g. Cowie & Hinsley 1988b). Finally, unlike most previous studies, I examined the effects of food supplementation beyond the nestling period. Energy demands of young may peak post-fledging (Martin 1987) and survival during this period has a great bearing on population size (Perrins 1979). Therefore, long-term measures of breeding success better reflect the ultimate consequences of food supplementation.

8.3.2.2. Recommendations

My research has revealed two principal considerations regarding the use of food supplementation in pure scientific research. First, food supplementation can have pronounced effects on reproduction without supplements constituting a large proportion of the diet (Chapter Five). Therefore, all studies should quantify supplement use before assuming that effects are necessarily mediated nutritionally (see also Section 8.4.4). Second, one of the main advantages of food supplementation over studies that assess the effects of variations in natural food abundance is that the role of food supply is isolated experimentally. However, if the method with which food supplements are provided elicits influence beyond that of increased food availability (e.g. reproductive costs through the defence of a concentrated, but spatially disparate, resource – e.g. peanut cake in my study) that is not found during periods of high natural food abundance (e.g. that might be distributed with greater uniformity across a habitat), effects of food supplementation could be misinterpreted. To this end, experiments that examine whether the influence of high natural food availability on avian reproduction is equivalent to that of food supplementation (e.g. see example in Section 8.3.3.2), would be especially valuable.

8.3.3. Unintentional food supplementation

8.3.3.1. Applicability of the findings from my field study

The transferability of my findings to birds exposed to food supplementation unintentionally (e.g. through foraging on landfill and fisheries' discards) during reproduction is interesting to consider, but might be limited. For example, the breeding ecology of blue and great tits is quite different from that of species exposed to supplementation unintentionally (e.g. many seabird species that forage on landfill and fisheries' discards rely on endogenous nutrient reserves during reproduction and also nest in colonies – Meijer & Drent 1999; Nager 2006). Moreover, since food supplementation is unintentional it offers less experimental control of supplement type and schedule than studies in which supplementation is intentional (such as my own).

8.3.3.2. Recommendations

The effects of food supplementation as a result of waste disposal and fisheries' discards on avian reproduction are broadly positive and, as such, contrast with the concerns raised by my field study (e.g. Chapters Two & Four). Refuse and fisheries' discards can support large populations of birds (Garthe *et al.* 1996; Ramos *et al.* 2009) and breeding productivity is reduced when either resource is unavailable (Pons 1992; Oro *et al.* 1996). However, there is evidence that specialising on refuse at the expense of feeding on natural foods can reduce breeding productivity (e.g. clutch size, hatching success, and number of young fledged – Pierotti & Annett 1991), demonstrating parallels with my findings (Chapters Two & Four). I recommend that research continues into the dependence on, and potential adverse consequences of, refuse and fisheries' discards in the diet of breeding birds. Such research will enable current policies aimed at reducing landfill waste and fisheries' discards to be viewed within the context of population dependence, and current and future breeding success. In this respect, further investigation into the influence of unintentional food supplementation on predator-prey interactions is also important. For example, nest depredation by avian predators occurs more frequently with closer proximity to landfill (Husby 2006). Therefore, reduced landfill waste on which predatory species forage could increase predation rates on nearby nests. Similarly, if fisheries' discards are reduced then predatory species of seabird such as great skuas *Stercorarius skua* that feed on discards could increase the extent to which they predate other seabird species (Votier *et al.* 2004).

Finally, it is interesting to consider that some birds might be obligate scavengers on fisheries' discards due to reduced natural fish stocks as a result of over-fishing (Thompson 1992; Thompson & Riddy 1995). This raises an interesting broader issue concerning the value of food supplementation *versus* the sustainable management of natural systems. For example, in conservation initiatives, the value of habitat management to increase the availability of important natural foods during reproduction, rather than using food supplementation, could be considered. In gardens, invertebrate (e.g. caterpillar) availability would increase through decreased application of pesticides (Schmidt 1988) and through the planting of native flora (Burghardt *et al.* 2009). These possibilities could offer an alternative to food supplementation of birds in gardens during the spring and summer. Therefore, an exciting avenue of research would be to examine the role of sustainable habitat management instead of, or in addition to, food supplementation. For example, natural food availability could be reduced experimentally (e.g. Marshall *et al.* 2002) and avian reproduction studied on ‘degraded’ *versus* un-manipulated (control) plots, while concurrently examining the influence of food supplementation (i.e. supplemented *versus* non-supplemented [control]) in replicate ‘degraded’ or un-manipulated plots. This would be of conservation value and would enhance our understanding of the influences of changes in natural food availability on reproduction, as opposed to the influences of food supplementation (see also Section 8.3.2.2).

8.4. Recommendations for future research at Chaddesley Woods NNR

8.4.1. Mechanisms

Although many of the results of my field study are striking, the mechanisms with which food supplementation influenced these findings are almost entirely unknown. In each chapter I have proposed mechanisms that now serve as a framework upon which future studies can be built. The probability of each mechanism suggested (Chapters Two-Four) has been focused by my findings in Chapter Five, in which it was shown that supplement use was not considerable and was similar between treatments. Therefore, research into mechanisms that are contingent on direct supplement use (e.g. through nutritional effects) or on feeder visitation (e.g. through pathogenic infection) should not be prioritised. Instead, behaviourally-based mechanisms should be favoured. For example, supplemented pairs might have incurred reproductive costs (culminating in reduced nestling phase productivity – Chapter Four) through increased territorial behaviour, intrusion, and confrontation (Ewald & Rohwer 1982; Schoech *et al.* 2008; discussed in Chapters Four & Five). As discussed previously, the provision of peanut cake potentially on the boundaries of adjacent breeding territories might have been important in these respects if supplemented pairs defended this concentrated, but spatially disparate, ‘insurance’ (i.e. not heavily utilised – Chapter Five) food resource.

Examination of the influence of food supplementation on other aspects of reproductive behaviour (e.g. onset of territoriality, incubation behaviour, provisioning rates, prey selectivity) could also shed light on the effects of food supplementation on breeding parameters (Chapters Two-Four). For example, advanced onset of incubation relative to the laying sequence of supplemented, compared with control, females could reduce incubation period (Chapter Two) and cause hatching asynchrony, leading to reduced hatching (Chapter Two) and/or fledging (Chapter Four) success (e.g. Perrins 1979; Nilsson 1993). The low intake of supplements (Chapter Five) might also be explained by behavioural observations. For example, mealworms might have been avoided in feeders at ground-level because they did not fall within the ‘search image’ of adults that forage predominantly in the canopy during the nestling period (Gibb 1954; TJEH pers. obs.). This could be investigated through comparing mealworm use from trays at ground-level *versus* use from trays hoisted into the canopy. Indeed, encouragingly, many of the mechanisms proposed in my study could be addressed using relatively simple, well-designed experimental approaches.

8.4.2. Breeding adults

An important omission from my study has been an examination of the effects of food supplementation on breeding adults (e.g. physiological condition, apparent survival). A subset of the breeding population was caught in 2007 and 2008, but very few adults were caught in 2006 (due to a shortage of field personnel). In future the breeding population should be characterised thoroughly in each year. Building upon ideas presented in Chapters Two-Five, this information would reveal treatment effects: (i) *within-years*: demographics of adult quality (e.g. body condition) and age, partition of reproductive costs between adults and young; and (ii) *between-years*: recruitment of fledglings from the previous year, adult survival and long-term reproductive strategies, and carry-over effects of supplementation. Measures of juvenile recruitment, adult survival, and long-term reproductive strategies will provide key information as to the extent to which advanced breeding phenology and reduced productivity of supplemented pairs are adaptive or otherwise (Chapters Two & Four).

8.4.3. Survival and dispersal

In both adults and fledglings, the effects of food supplementation on rates of survival and dispersal are unknown. This presents a promising area of future research given the strong effects of dietary treatment on the apparent survival of fledglings (Chapter Four), including interesting sex-specific patterns in great tits (Chapter Four). As recommended (see Chapter Four), a number of expermimental methods would help to disentangle survival and dispersal between treatments and sexes (e.g. mist-netting in nearby habitats, radio telemetry – Dhondt 1979; Naef-Daenzer *et al.* 2001). If survival is estimated over longer periods of time in future research, with a greater number of sampling events (e.g. apparent survival of fledglings to autumn, recruitment into the breeding population the following spring, and subsequent survival as breeding adults), specialist mark-recapture analyses (e.g. Program MARK – White & Burnham 1999) will be required.

8.4.4. Supplement use

The use of SIA to examine supplement use has clear advantages over other techniques (e.g. examination supplement and natural food use, potentially revealing direct and indirect nutritional effects of supplementation – see other benefits in Chapter Five). However, to maximise the potential of this technique, I have outlined a number of recommendations for future research (e.g. a tracer to improve the isotopic separation of peanut cake – see other suggestions in Chapter Five). Apparent survival of juveniles was greatest from the PCMW treatment, despite mealworm intake not differing significantly between treatments and also not being substantial (Chapter Five). A possible explanation is that mealworms were provided to nestlings in the PCMW treatment following tissue sampling 12 days post-hatch but before fledging, causing enhanced fledgling condition and subsequent survival (Chapters Four & Five). To investigate this, tissue samples could be collected from nestlings later in the nestling period (but no later than *c.* 15 days post-hatch to avoid force-fledging). However, a more productive approach might be to capture (e.g. mist-net) and tissue sample (as described in Chapter Five) young *c.* 2 weeks post-fledging, thereby obtaining information on supplement use late in the nestling period and also gaining valuable information on post-fledging dispersal between treatments (e.g. see Section 8.4.3). In combination, these steps would reveal the most likely mechanisms with which mealworm supplementation during the nestling period had a carry-over effect on apparent survival (Chapter Four).

8.5. Final recommendation: nomenclature

Prior to my concluding comments, I would like to finish by considering the appropriateness of the term ‘supplementation’. In food supplementation studies, a supplement is usually characterised as a human-provided food whose type or quantity is not available naturally. However, this does not follow the precise definition of a ‘supplement’ that is:

“something that is added to make something else complete or that makes up a deficiency” (Chambers Dictionary 2009).

Therefore, for the term ‘supplementation’ to be used appropriately researchers should ascertain whether the foraging environment in which a food is provided is otherwise incomplete/deficient. For example, my field study was conducted in broadleaved woodland – the most productive breeding habitat of blue and great tits in the UK, in large part due to substantial natural invertebrate abundance (Perrins 1965, 1979). Therefore, in my study, the term food ‘supplementation’ might not be especially instructive. Indeed, perhaps only when supplements are provided in nutrient-poor environments, so that birds are dependent on supplements, does ‘true’ food supplementation occur. In some instances, such as in gardens, dependence on food supplements has not been shown (e.g. O'Leary & Jones 2006). In others, however, for example birds feeding on refuse and fisheries’ discards, population declines that have followed the removal of these resources suggest dependence (Oro *et al.* 2004; Ramos *et al.* 2009). It is perhaps for these instances that the term food ‘supplementation’ should be reserved.

The word ‘supplementation’ should also be treated with caution with respect to what exactly is being supplemented. For example, in Chapter Five I demonstrated that food supplementation can have pronounced effects on reproduction while forming only a subsidiary part of the diet. In this instance, food supplementation might enrich an environment with entities other than nutrients, such as time (e.g. as a result of increased foraging efficiency – Davies & Lundberg 1985) or territorial intrusion/confrontation (e.g. Ewald & Rohwer 1982; Schoech *et al.* 2008). Therefore, in addition to examining whether ‘true’ food supplementation occurs, I recommend that future studies use the word ‘supplementation’ more specifically regarding the most important currencies (e.g. nutrition, time, intrusion pressure) being provided. In general, I think that the term ‘food addition’ is more appropriate than ‘food supplementation’ because food is, indubitably, added but there is not the supposition that the foraging environment is otherwise incomplete/deficient as is implied with ‘supplementation’.

8.6. Conclusions

The results of my field study reveal considerable concerns (e.g. fewer fledged young), and potential long-term benefits (e.g. increased apparent survival of fledglings), regarding food supplementation of birds during reproduction. The applicability of these findings to urban habitats (e.g. gardens) is supported by their pronounced similarities to the findings of my NRS research. However, linking the findings of my field and NRS work directly is, currently, impossible. To this end, conclusive recommendations regarding food supplementation of birds in gardens during the spring and summer are difficult to make. Indeed, my most fervent recommendation is that future research into all aspects of food supplementation of birds in gardens should be conducted within urban habitats. To date, very little research has fulfilled this requirement due to the considerable logistical difficulties often posed. However, these difficulties are not insurmountable and such research will generate novel findings that will shine light on what has become, in effect, a massive food supplementation experiment across much of the world (Jones & Reynolds 2008). The widespread interest generated by such work could also inspire greater engagement of the general public with the natural world and with scientific research.

Although the effects of food supplementation of birds in gardens remain relatively unknown, the influence on householders has become increasingly apparent. Feeding birds in gardens provides great pleasure and is likely to improve quality of life (Howard & Jones 2004). Indeed, urbanisation of human populations will probably cause increased dissociation from nature (Fuller *et al.* 2007), so regular interactions with wildlife, such as feeding birds in gardens, might be especially valuable. While these reasons are compelling, however, they do not represent a *carte blanche* for food supplementation of birds in gardens. Recommendations in this respect should be based on the influence of food supplementation on birds and/or on the wider ecological community. Best practice guidelines for food supplementation are required urgently, and should be formulated through research in urban habitats. However, in the absence of such research, the clear benefits to humans of providing food for birds in gardens is a tangible reason as to why food supplementation during the spring and summer should not, currently, be discouraged.

Finally, and more broadly, my study contributes to an array of research that has examined the influence of food supplementation during avian reproduction. The circumstances in which birds are exposed to intentional and unintentional forms of food supplementation are numerous (e.g. as discussed in this Chapter). My findings are applicable to each to a greater or lesser extent. Most pertinently, however, my findings have implications for food supplementation of birds in gardens, as part of conservation initiatives, and in pure scientific research. Recommendations that I have made with respect to each have been outlined to reduce the risk of food supplementation being used inappropriately (e.g. in gardens and conservation initiatives), and to ensure that the effects of food supplementation are not misinterpreted (e.g. in pure scientific research). It is my hope that my findings and recommendations will provide a catalyst for future research activities. Indeed, understanding the extent to which food supplementation of birds represents a curate’s egg (i.e. one that is, in fact, rotten in all parts) or one that is rotten only in some, or is not rotten at all, remains an exciting challenge for future research.

APPENDIX ONE

Figure 1.1.A. The location of Chaddesley Woods National Nature Reserve (denoted by a green circle) located on the south west of Birmingham in central England.

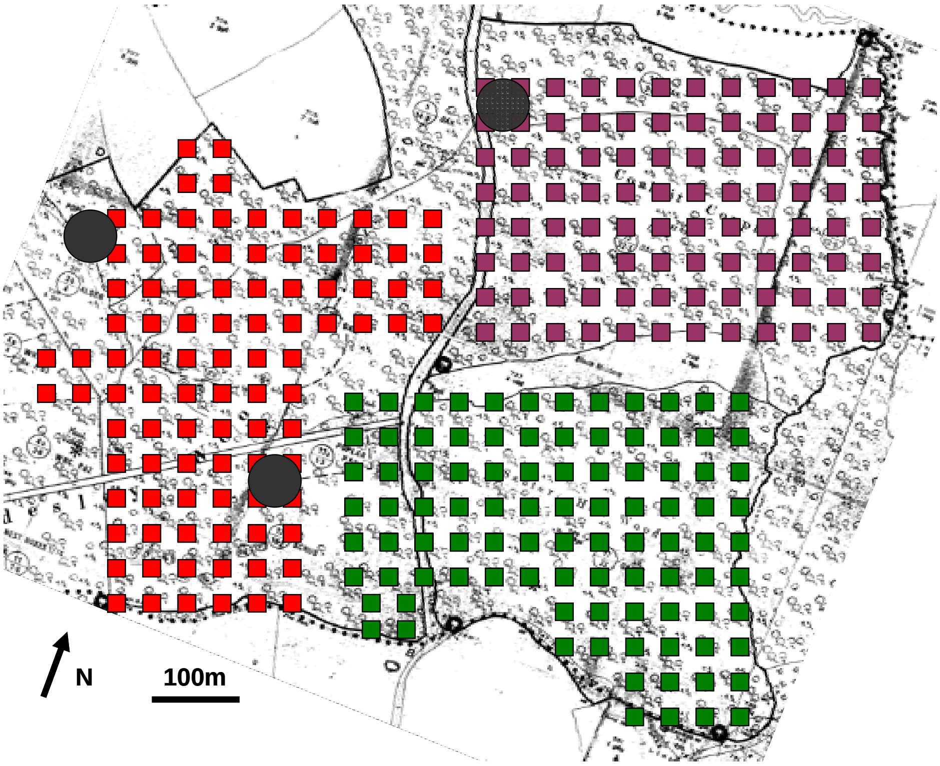

Figure 1.2.A Map of the study area at Chaddesley Woods National Nature Reserve in 2006-08. Each square denotes a nestbox: purple denotes treatment block one; red denotes treatment block two; green denotes treatment block three. Treatment block one was supplemented with peanut cake and mealworms in 2006, was the control (non-supplemented) in 2007, and was supplemented with peanut cake in 2008. Treatment block two was the control in 2006, was supplemented with peanut cake in 2007, and was supplemented with peanut cake and mealworms in 2008. Treatment block three was supplemented with peanut cake in 2006, was supplemented with peanut cake and mealworms in 2007, and was the control in 2008. Grey circles denote the three mist-net sites. See Chapters Two-Four for details.

Species	Year	Dietary treatment	Treatment block	Number of nestboxes occupied
BT	2006	C	Two	50
		PC	Three	50
		PCMW	One	50
	2007	C	One	53
		PC	Two	55
		PCMW	Three	57
	2008	C	Three	48
		PC	One	40
		PCMW	Two	42
GT	2006	C	Two	25
		PC	Three	24
		PCMW	One	26
	2007	C	One	37
		PC	Two	23
		PCMW	Three	23
	2008	C	Three	34
		PC	One	45
		PCMW	Two	38
Not BT or GT	2006	C	Two	21
		PC	Three	22
		PCMW	One	20
	2007	C	One	6
		PC	Two	18
		PCMW	Three	16
	2008	C	Three	14
		PC	One	11
		PCMW	Two	16

Table 1.1.A The number of nestboxes occupied by blue (BT) and great (GT) tits at Chaddesley Woods National Nature Reserve in 2006-2008. Occupancy was determined when laying occurred and only considered first clutches. See Figure 1.2.A for details of treatment block numbers, see Figures 1.3.A-1.5.A for maps of occupancy, and see Chapters Two and Three for details.

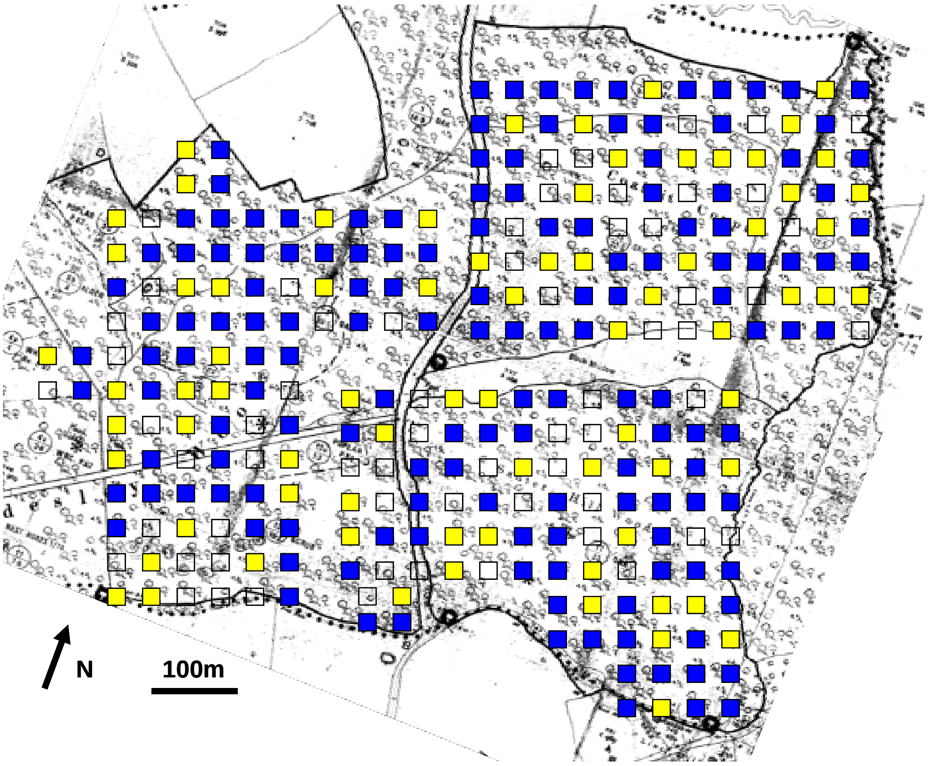

Figure 1.3.A Map of the study area at Chaddesley Woods National Nature Reserve in 2006. A blue square denotes a nestbox that was occupied by a blue tit, a yellow square denotes a nestbox that was occupied by a great tit, and a colourless square denotes a nestbox that was not occupied by a blue or a great tit. Occupancy was determined when laying occurred and only considered first clutches. See Figure 1.2.A for details of dietary treatments and treatment blocks, see Table 1.1.A for total occupancy, and see Chapter Two for details.

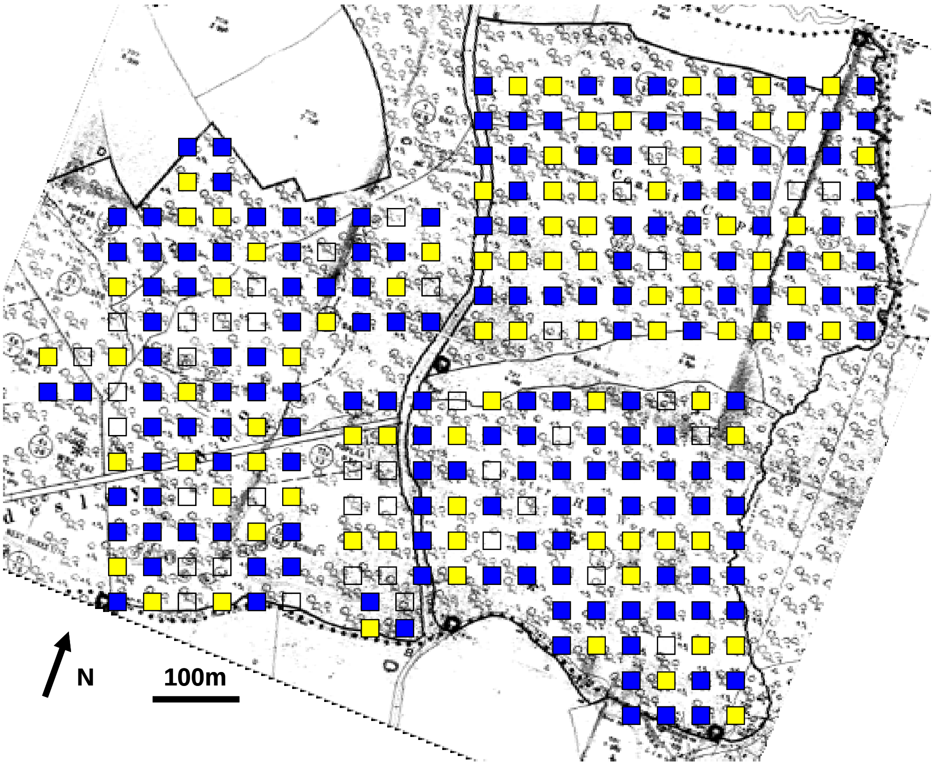

Figure 1.4.A Map of the study area at Chaddesley Woods National Nature Reserve in 2007. See Figure 1.3.A for explanations of nestbox occupancy. See Figure 1.2.A for details of dietary treatments and treatment blocks, see Table 1.1.A for total occupancy, and see Chapter Two for details.

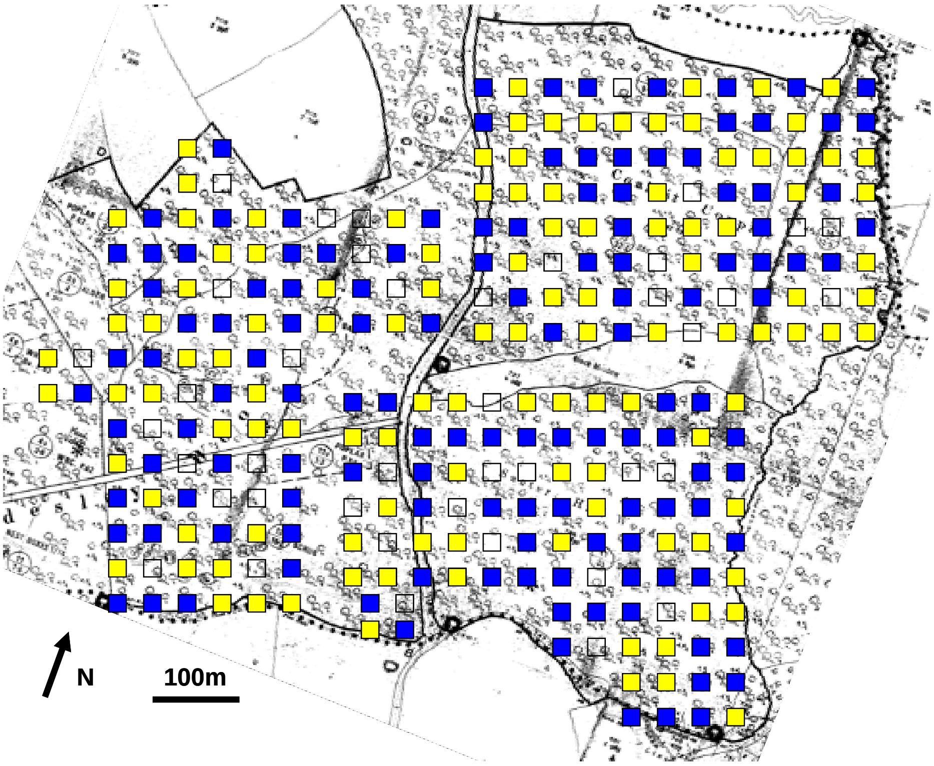

Figure 1.5.A Map of the study area at Chaddesley Woods National Nature Reserve in 2008. See Figure 1.3.A for explanations of nestbox occupancy. See Figure 1.2.A for details of dietary treatments and treatment blocks, see Table 1.1.A for total occupancy, and see Chapter Two for details.

APPENDIX TWO

The relationship between egg weight and volume

In addition to egg weight, I also investigated the influence of food supplementation on egg volume. After weighing the eggs (see Chapter Three), the clutch was placed on a horizontally-aligned black board (with dimples for the eggs) to be photographed (Fig. 2.1.A). Eggs were arranged so that their horizontal and vertical axes lay parallel to the board. The board was placed on the foot of a clamp-stand, directly below a digital camera (Goodman's five mega-pixel camera in 2006 and 2007; Kodak 7.1 mega pixel camera in 2008). Pictures were taken from a standard height and in the shade to avoid shadows. The board was numbered so that each egg had a corresponding number. One egg was chosen at random and had its maximum vertical and horizontal axes measured to the nearest 0.01 mm using callipers (Faithfull digital callipers – unless conditions were very wet when dial callipers were used). The calliper

Figure 2.1.A. A great tit clutch photographed in the control treatment block in 2006 from which egg volume measurements were made. See text for details.

measurements were used to calibrate the size of the image (e.g. Fig. 2.1.A) for later analysis of egg volume. Egg volume was calculated from each image as in Bridge *et al.* (2007). This process was labour-intensive so only three eggs (selected at random) per clutch were measured in this way. On rare occasions, the image-quality was poor so only one or two eggs were measured.

The relationship between egg volume and egg weight differed significantly between treatments in blue tits (egg weight × dietary treatment: $F_{1,33} = 5.20$, $P = 0.03$) (Fig. 2.2.A), but weight predicted volume significantly in both species and across treatments (blue tit control: $F_{1,60} = 159.42$, $P < 0.001$; blue tit PC: $F_{1,14} = 320.47$, $P < 0.001$; great tit control and PC: $F_{1,42} = 340.13$, $P < 0.001$) (Fig. 2.2.A). Owing to this close relationship, and because all eggs in a clutch were weighed but only a subset of eggs per clutch was selected to calculate volume, I have only presented findings for egg weight, rather than volume, in Chapter Three.

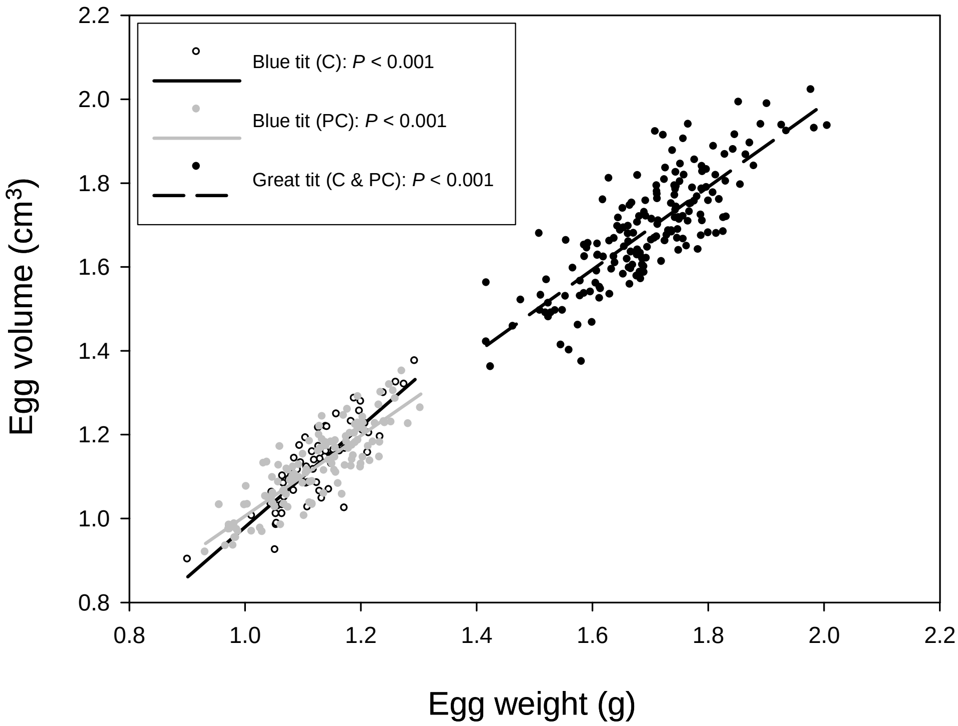

Figure 2.2.A. The relationship between egg volume and egg weight of blue and great tits at Chaddesley Woods National Nature Reserve in 2006-2008. Dietary treatments: C = control (non-supplemented); PC = peanut cake. C and PC are presented separately in blue tits because of a significant egg weight × dietary treatment interaction ($P = 0.03$). See text for details.

The significant egg weight × dietary treatment interaction with respect to egg volume in blue tits (Fig. 2.2.A) was perhaps caused by differences in egg composition between dietary treatments (see Chapter Three). Indeed, differences in egg composition could also account for the ‘noise’ around the regression lines in Figure 2.2.A. However, comparisons were based on clutch means for egg weight, and *c.* three randomly selected eggs per clutch for egg volume. Therefore, this could explain the noise around the regression lines and, potentially, the egg weight × dietary treatment interaction in blue tits (i.e. an erroneous statistical finding).

A high correlation between egg weight and volume has been reported in previous studies (reviewed in Williams 1994; Christians 2002). Both authors used the term ‘egg size’ as a surrogate for egg weight or volume. Correspondingly, I have used this nomenclature in Chapter Three.

APPENDIX THREE

Nestling growth curve analyses

In addition to the analyses of nestling growth presented in Chapter Three, I also tested for differences in growth curves (i.e. trajectories of nestling growth) between dietary treatments with respect to nestling weight, tarsus length, and total head length. Growth curve analyses followed the same repeated-measures design as outlined in Reynolds *et al.* (2003a). Growth curves used the same time-points presented Chapter Three, but the repeated-measures design meant that data were restricted to ‘complete records’ (i.e. broods for which measures were recorded at all four time-points). In addition to dietary treatment, I specified hatching date and brood size in all models (Perrins 1965). There were no significant differences (all *P*s > 0.05) in the growth curves of either species between dietary treatments, consistent with the results described in Chapter Three.

While examination of growth curves provided a different aspect of nestling development (i.e. growth trajectories) compared with analyses in Chapter Three, there were advantages to focusing on data presented in Chapter Three. First, analyses in Chapter Three were conducted on the full, rather than the reduced, dataset. Indeed, growth curves could not be compared between dietary treatments in blue tits in 2006 due to a small number of complete records. Second, random factors (e.g. nestbox and treatment block) could not be specified in these growth curve analyses so less powerful within-year analyses were conducted (unlike in Chapter Three). Third, subtleties in growth trajectories might not be detected through only a small number of time-points (i.e. four). Finally, any differences in growth trajectories between dietary treatments were not significant and did not amount to significant differences in growth measures at any of the four time-points considered independently in Chapter Three.

APPENDIX FOUR

Caterpillar sampling method

Ten oak trees were selected at random across each treatment block. Oaks are preferred over other tree species by breeding blue and great tits owing to their greater caterpillar abundance (Naef-Daenzer & Keller 1999). To sample geometridae (‘looper’) caterpillars (e.g. winter moth *Operophtera brumata*), two pairs of *c.* 1200 cm^2 plastic trays were placed under each focal tree and filled with water (*sensu* Perrins 1991; Chamberlain *et al.* 1999). To control for canopy size, trays were placed halfway between the trunk and the outermost branch and, where possible, in a north-south direction (caterpillars on the south-side of the trunk may hatch before those on the north, so 180° separation seemed appropriate – Buse *et al.* 1999). The same trees were studied in each year. Trays were covered in wire mesh (*c.* 25 mm diameter holes) and were emptied every *c*. three days. Collected among leaf litter in trays were geometer caterpillars that had descended from the canopy to pupate in the ground and drowned.

Caterpillars were sampled in this way in 2007 and 2008. In 2008, half the number of trays was used compared with 2007 to ensure that the collection and processing of samples was less labour intensive. However, I still monitored the same trees and with the same 180° separation of trays where possible. Dry caterpillar biomass was multiplied by two in 2008 to make the data comparable with that of 2007. Geometer caterpillars were separated in the laboratory and oven-dried to constant weight. Dry biomass / day was calculated for the period between caterpillar collections (Fig. 4.5).

APPENDIX FIVE

$\delta^{13}C$ and $\delta^{15}N$ of peanut cake before and after fat-extraction

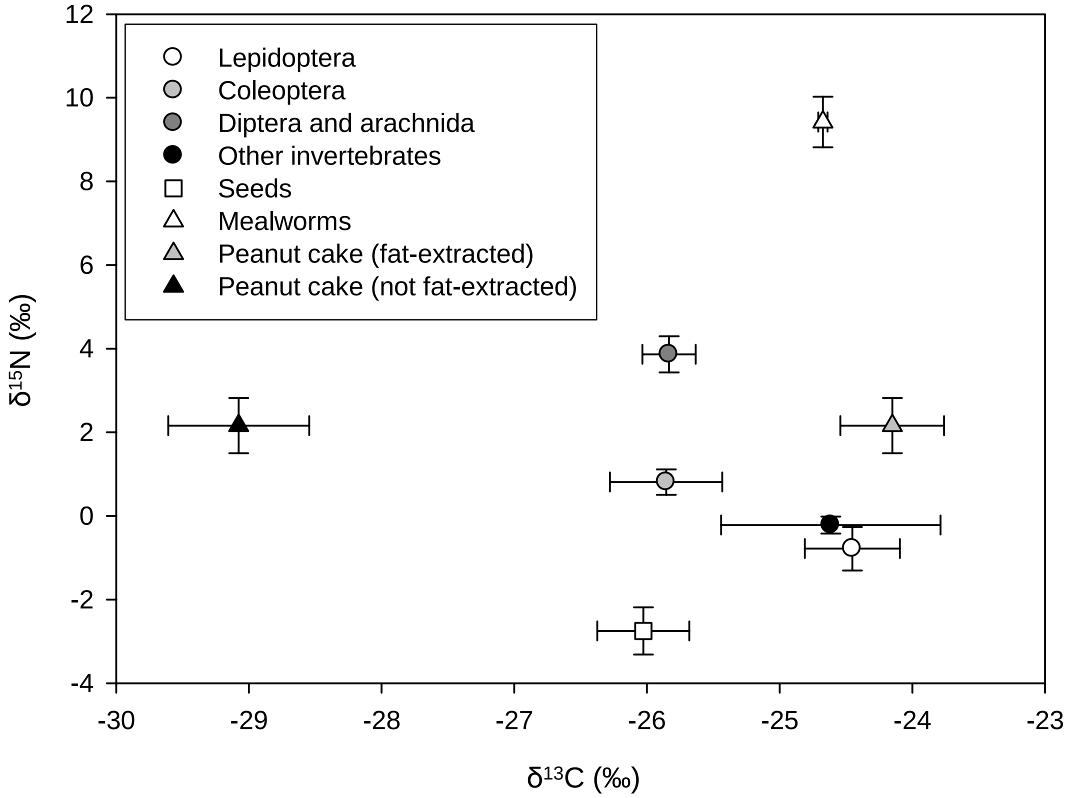

Figure 5.1.A. $\delta^{13}C$ and $\delta^{15}N$ (mean ± 1 SD) of non fat-extracted peanut cake presented alongside the food groups illustrated in Figure 5.1 (see main text for details). The graph and legend details are otherwise identical to Figure 5.1. Fat extraction of peanut cake caused the mean $\delta^{13}C$ value to be enriched by 4.9 ‰.

APPENDIX SIX

Species	Year	Number of nest records
BT	2000	356
	2001	356
	2002	261
	2003	219
	2004	283
GT	2000	368
	2001	328
	2002	256
	2003	236
	2004	243

Table 6.1.A The number of nest records of blue (BT) and great (GT) tits derived from the British Trust for Ornithology’s Nest Record Scheme in 2000-2004. The number of nest records used in analyses of each breeding parameter varied depending upon suitability of the data contained within each nest record. See Figures 6.1.A-6.5.A for associated maps and see Chapter Six for details.

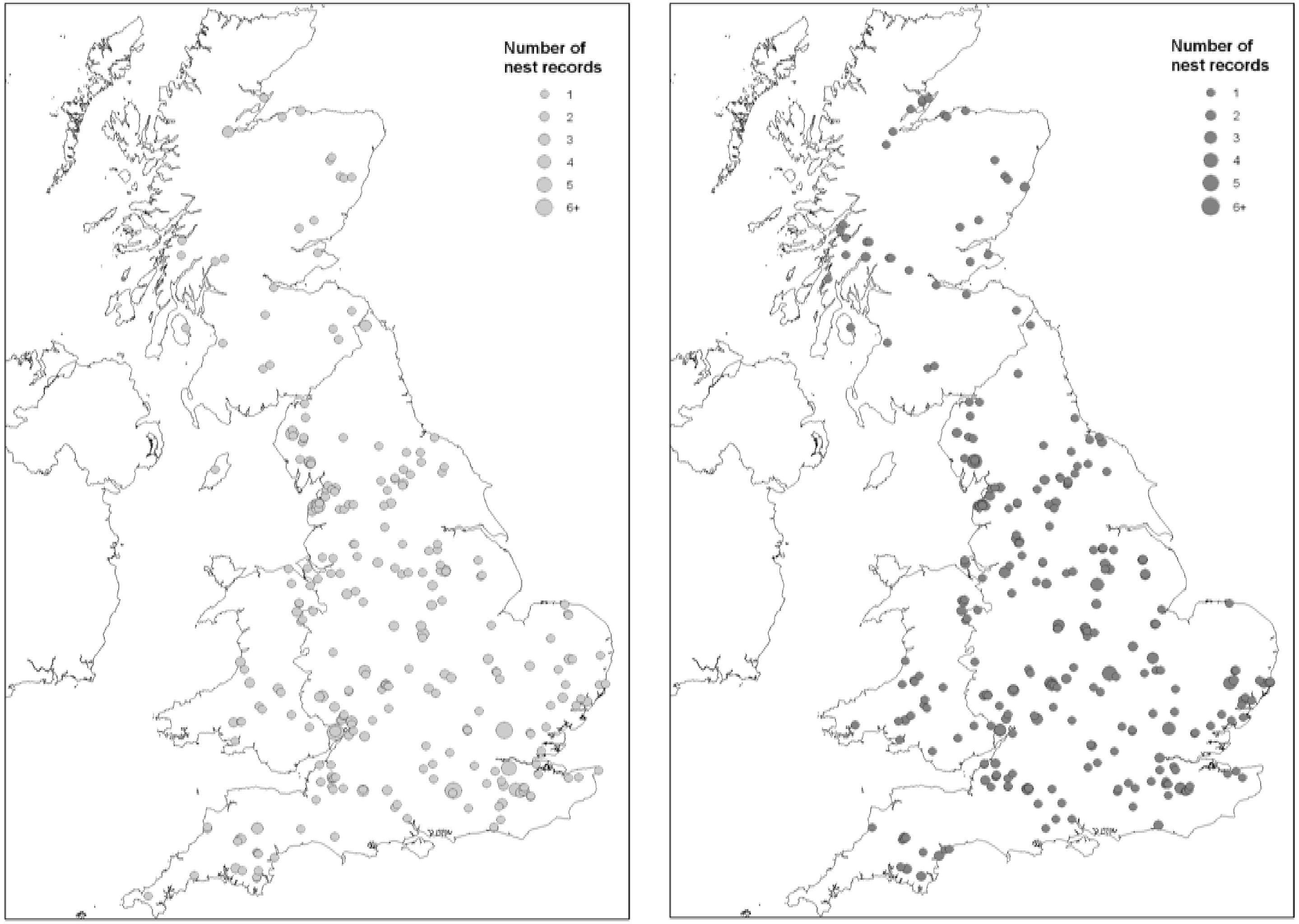

Figure 6.1.A. Distribution of nest records of blue (light grey dots) and great (dark grey dots) tits as derived from the British Trust for Ornithology’s Nest Record Scheme in 2000. The number of nest records used in analyses of each breeding parameter varied depending upon suitability of the data contained within each nest record. See Table 6.1.A for the total number of nest records and see Chapter Six for details.

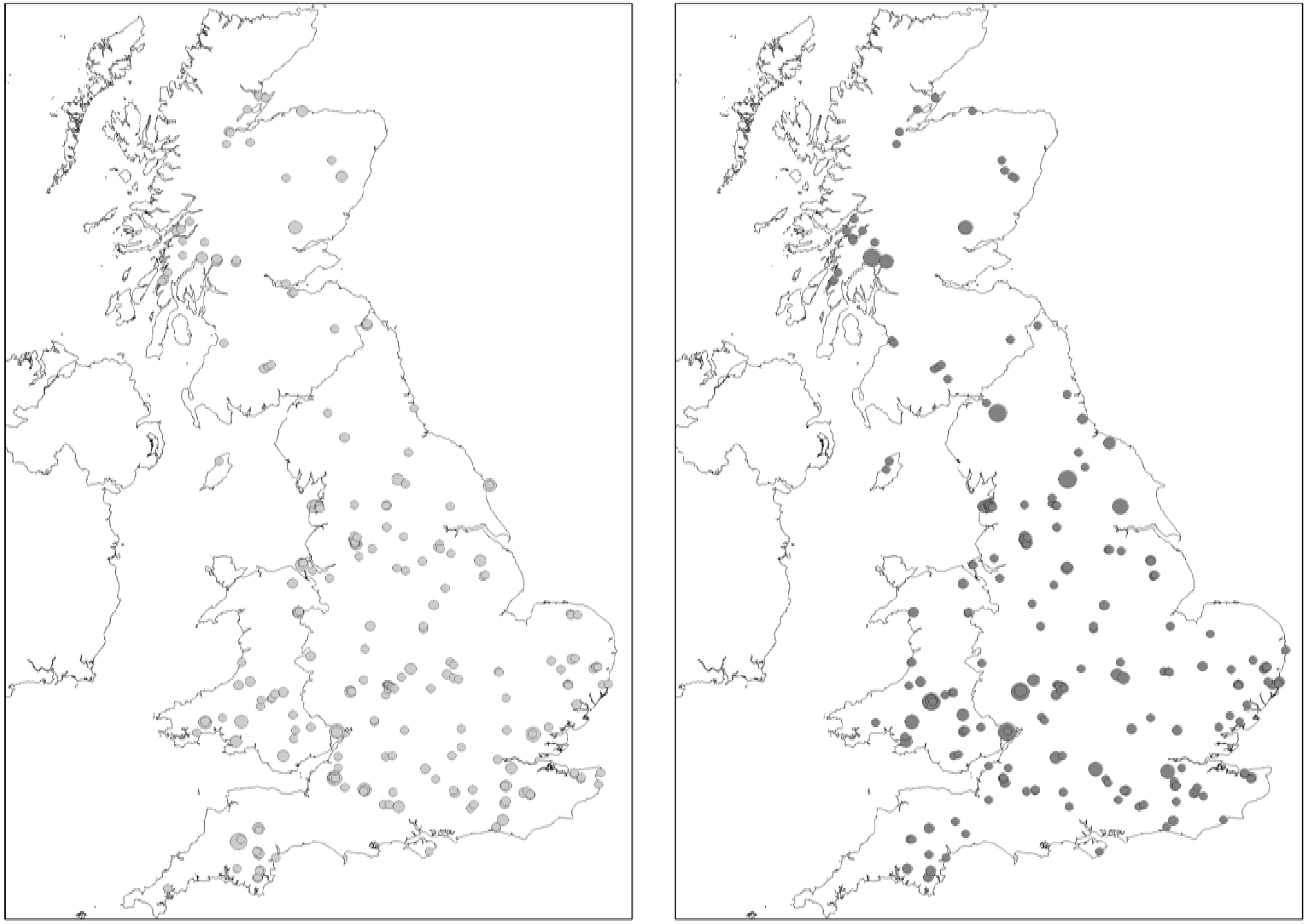

Figure 6.2.A. Distribution of nest records of blue (light grey dots) and great (dark grey dots) tits as derived from the British Trust for Ornithology’s Nest Record Scheme in 2001. The number of nest records used in analyses of each breeding parameter varied depending upon suitability of the data contained within each nest record. See Figure 6.1.A for the key regarding symbol size, see Table 6.1.A for the total number of nest records, and see Chapter Six for details.

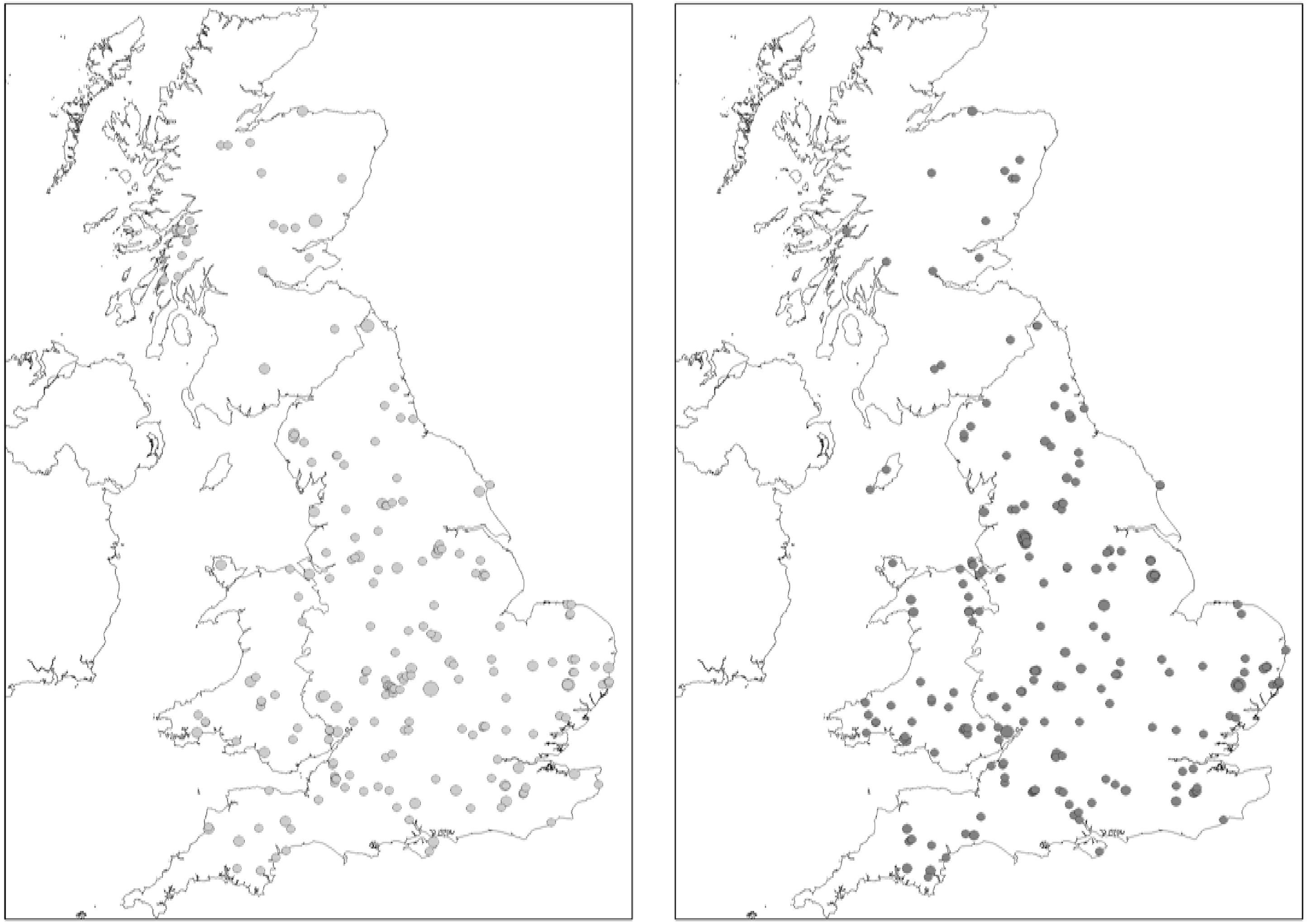

Figure 6.3.A. Distribution of nest records of blue (light grey dots) and great (dark grey dots) tits as derived from the British Trust for Ornithology's Nest Record Scheme in 2002. The number of nest records used in analyses of each breeding parameter varied depending upon suitability of the data contained within each nest record. See Figure 6.1.A for the key regarding symbol size, see Table 6.1.A for the total number of nest records, and see Chapter Six for details.

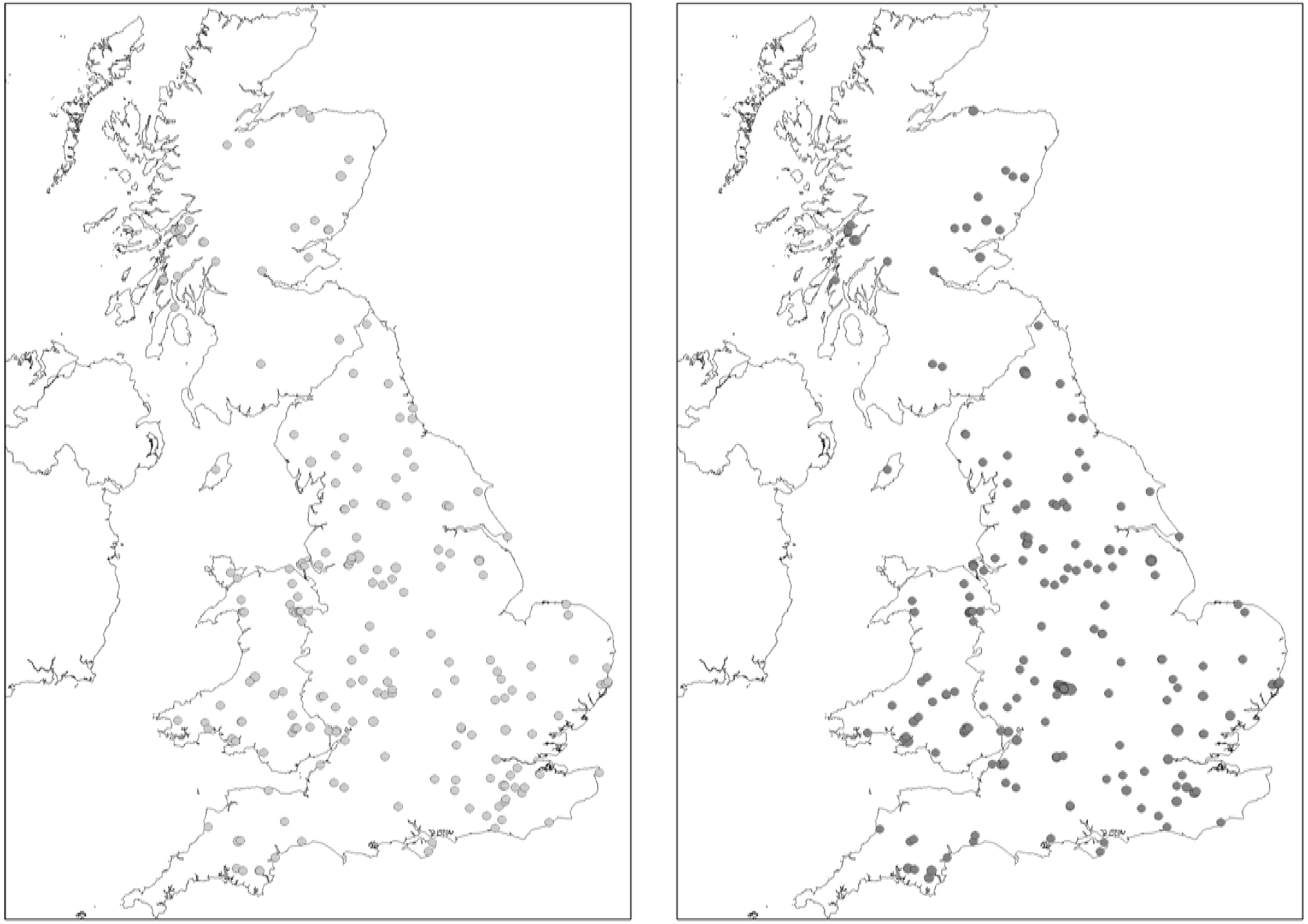

Figure 6.4.A. Distribution of nest records of blue (light grey dots) and great (dark grey dots) tits as derived from the British Trust for Ornithology’s Nest Record Scheme in 2003. The number of nest records used in analyses of each breeding parameter varied depending upon suitability of the data contained within each nest record. See Figure 6.1.A for the key regarding symbol size, see Table 6.1.A for the total number of nest records, and see Chapter Six for details.

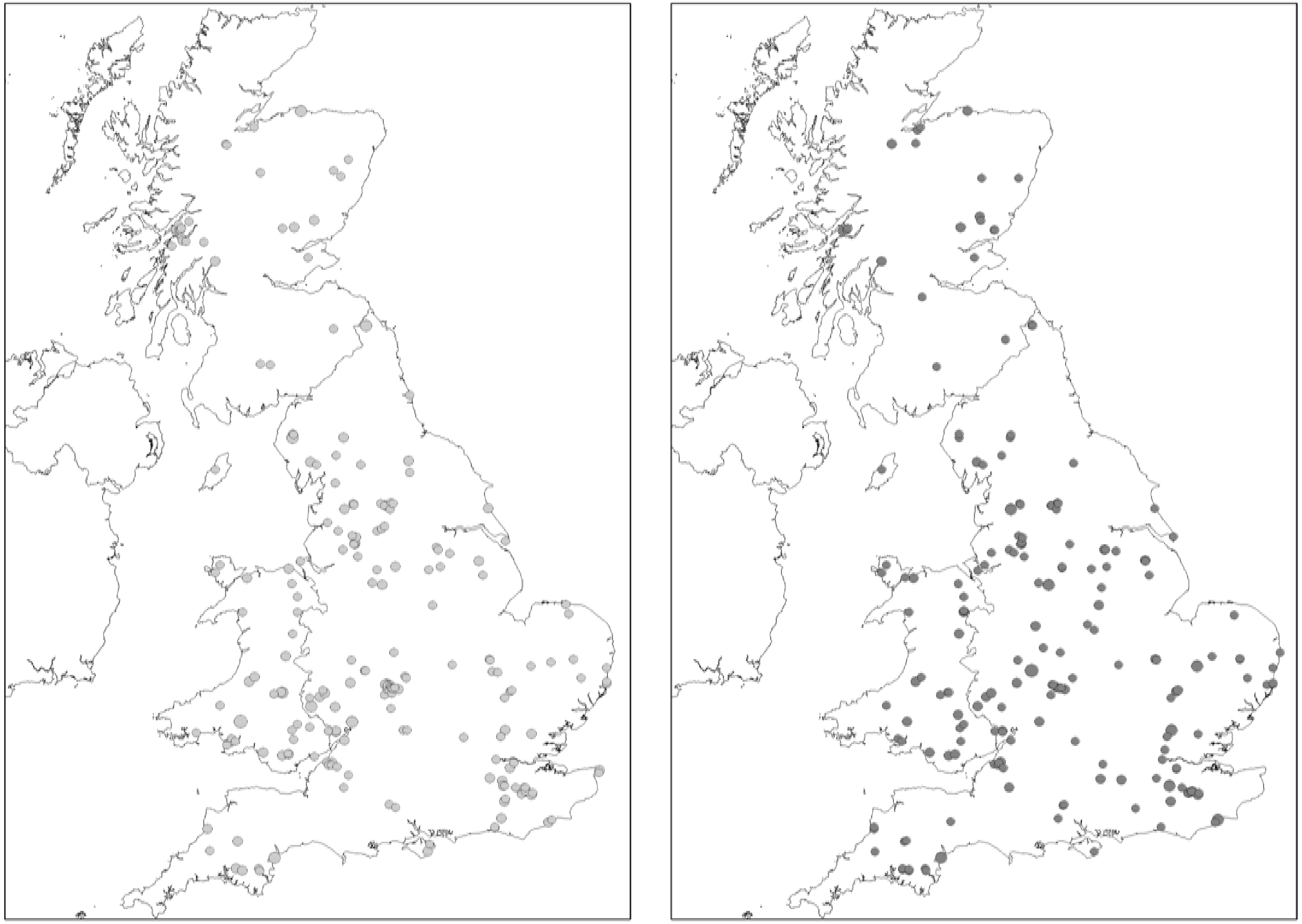

Figure 6.5.A. Distribution of nest records of blue (light grey dots) and great (dark grey dots) tits as derived from the British Trust for Ornithology's Nest Record Scheme in 2004. The number of nest records used in analyses of each breeding parameter varied depending upon suitability of the data contained within each nest record. See Figure 6.1.A for the key regarding symbol size, see Table 6.1.A for the total number of nest records, and see Chapter Six for details.

PUBLICATIONS

Bridge, E. S., R. K. Boughton, R. A. Aldredge, T. J. E. Harrison, R. Bowman & S. J. Schoech (2007). Measuring egg size using digital photography: testing Hoyt's method using Florida scrub-jay eggs. *Journal of Field Ornithology* **78**(1): 109–116.

Robb, G. N., R. A. McDonald, D. E. Chamberlain, S. J. Reynolds, T. J. E. Harrison & S. Bearhop (2008). Winter feeding of birds increases productivity in the subsequent breeding season. *Biology Letters* **4**(2): 220–223.

Robb G. N., R. A. McDonald, R. Inger, J. Newton, R. A. R. McGill, D. E. Chamberlain, S. J. Reynolds, T. J. E. Harrison & S. Bearhop (In review). Using stable isotope analysis as a technique for determining individual use of supplementary food in birds. *Journal of Field Ornithology*.

I am also the first author of a manuscript (based on Chapter Two) that has been provisionally accepted by *Oecologia*.

REFERENCES

Aparicio, J. M. (1994). The seasonal decline in clutch size: an experiment with supplementary food in the kestrel, *Falco tinnunculus*. *Oikos* **71**(3): 451–458.

Arcese, P. & J. N. M. Smith (1988). Effects of population-density and supplemental food on reproduction in song sparrows. *Journal of Animal Ecology* **57**(1): 119–136.

Arcos, J. M., X. Ruiz, S. Bearhop & R. W. Furness (2002). Mercury levels in seabirds and their fish prey at the Ebro Delta (NW Mediterranean): the role of trawler discards as a source of contamination. *Marine Ecology-Progress Series* **232**: 281–290.

Armstrong, D. P., I. Castro & R. Griffiths (2007). Using adaptive management to determine requirements of re-introduced populations: the case of the New Zealand hihi. *Journal of Applied Ecology* **44**(5): 953–962.

Arnold, T. W. (1994). Effects of supplemental food on egg production in American coots. *Auk* **111**(2): 337–350.

Arnold, T. W., R. T. Alisauskas & C. D. Ankney (1991). Egg composition of American coots in relation to habitat, year, laying date, clutch size, and supplemental feeding. *Auk* **108**(3): 532–547.

Atchison, K. A. & A. D. Rodewald (2006). The value of urban forests to wintering birds. *Natural Areas Journal* **26**(3): 280–288.

Barba, E., J. A. Gil-Delgado & J. S. Monrós (1995). The costs of being late: consequences of delaying great tit *Parus major* first clutches. *Journal of Animal Ecology* **64**(5): 642–651.

Baumann, N. (2006). Ground-nesting birds on green roofs in Switzerland: preliminary observations. *Urban Habitats* **4**: (no page numbers).

Baxter, A. T. & A. P. Robinson (2007). A comparison of scavenging bird deterrence techniques at UK landfill sites. *International Journal of Pest Management* **53**(4): 347–356.

Bearhop, S., D. R. Thompson, S. Waldron, I. C. Russell, G. Alexander & R. W. Furness (1999). Stable isotopes indicate the extent of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. *Journal of Applied Ecology* **36**(1): 75–84.

Bearhop, S., S. Waldron, S. C. Votier & R. W. Furness (2002). Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* **75**(5): 451–458.

Bearhop, S., R. W. Furness, G. M. Hilton, S. C. Votier & S. Waldron (2003). A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. *Functional Ecology* **17**(2): 270–275.

Beldal, E. J., E. Barba, J. A. Gil-delgado, D. J. Iglesias, G. M. Lopez & J. S. Monros (1998). Laying date and clutch size of great tits (*Parus major*) in the Mediterranean region: a comparison of four habitat types. *Journal Für Ornithologie* **139**(3): 269–276.

Berressem, K. G., H. Berressem & K. -H. Schmidt (1983). Comparative studies of the breeding biology of hole-nesting passerines in urban and rural habitats. *Journal Für Ornithologie* **124**(4): 431–445.

Betts, M. M. (1955). The food of titmice in oak woodland. *Journal of Animal Ecology* **24**(2): 282–323.

Blanco, G. (2006). Natural selection and the risks of artificial selection in the wild: nestling quality or quantity from supplementary feeding in the Spanish imperial eagle. *Ardeola* **53**(2): 341–351.

Blanco, G. & J. Marchamalo (1999). Pest-breeding inland movements and use of refuse dumps by Audouin's gulls in Spain. *Waterbirds* **22**(2): 307–309.

Bland, R. L., J. Tully & J. J. D. Greenwood (2004). Birds breeding in British gardens: an underestimated population? *Bird Study* **51**(2): 97–106.

Blomqvist, D., O. C. Johansson & F. Gotmark (1997). Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. *Oecologia* **110**(1): 18–24.

Blondel, J., P. C. Dias, M. Maistre & P. Perret (1993). Habitat heterogeneity and life-history variation of Mediterranean blue tits (*Parus caeruleus*). *Auk* **110**(3): 511–520.

Blondel, J., M. Maistre, P. Perret, S. Hurtrez-Bousses & M. M. Lambrechts (1998). Is the small clutch size of a Corsican blue tit population optimal? *Oecologia* **117**(1–2): 80–89.

Boal, C. W. & R. W. Mannan (1999). Comparative breeding ecology of Cooper's hawks in urban and exurban areas of southeastern Arizona. *Journal of Wildlife Management* **63**(1): 77–84.

Bolton, M. (1991). Determinants of chick survival in the lesser black-backed gull: relative contributions of egg size and parental quality. *Journal of Animal Ecology* **60**(3): 949–960.

Bolton, M., D. Houston & P. Monaghan (1992). Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. *Journal of Animal Ecology* **61**(3): 521–532.

Borgmann, K. L. & A. D. Rodewald (2004). Nest predation in an urbanizing landscape: the role of exotic shrubs. *Ecological Applications* **14**(6): 1757–1765.

Bosque, C. & M. T. Bosque (1995). Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *American Naturalist* **145**(2): 234–260.

Bourgault, P., D. W. Thomas, J. Blondel, P. Perret & M. M. Lambrechts (2007). Between-population differences in egg composition in blue tits (*Cyanistes caeruleus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **85**(1): 71–80.

Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **68**(2): 203–220.

Boyce, M. S. & C. M. Perrins (1987). Optimizing great tit clutch size in a fluctuating environment. *Ecology* **68**(1): 142–153.

Bridge, E. S., R. K. Boughton, R. A. Aldredge, T. J. E. Harrison, R. Bowman & S. J. Schoech (2007). Measuring egg size using digital photography: testing Hoyt's method using Florida scrub-jay eggs. *Journal of Field Ornithology* **78**(1): 109–116.

British Trust for Ornithology (2005a). http://www.bto.org/gbw/hygiene/GBHi/

British Trust for Ornithology (2005b). *The Nest Record Scheme Handbook.* Thetford, British Trust for Ornithology.

British Trust for Ornithology (2006a). http://www.bto.org/survey/gbfs.htm

British Trust for Ornithology (2006b). We spend £200 million a year on wild bird food. BTO Press Release No. 2006/12/76, December 2006. Thetford.

British Trust for Ornithology (2009). http://www.bto.org/gbw/BIRDS_FEEDING_HOME.htm

Brommer, J. E., P. Karell & H. Pietiainen (2004). Supplementary fed Ural owls increase their reproductive output with a one year time lag. *Oecologia* **139**(3): 354–358.

Burghardt, K. T., D. W. Tallamy & W. G. Shriver (2009). Impact of native plants on bird and butterfly biodiversity in suburban landscapes. *Conservation Biology* **23**(1): 219–224.

Buse, A., S. J. Dury, R. J. W. Woodburn, C. M. Perrins & J. E. G. Good (1999). Effects of elevated temperature on multi-species interactions: the case of pedunculate oak, winter moth and tits. *Functional Ecology* **13**(suppl.): 74–82.

Cannon, A. R., D. E. Chamberlain, M. P. Toms, B. J. Hatchwell & K. J. Gaston (2005). Trends in the use of private gardens by wild birds in Great Britain 1995-2002. *Journal of Applied Ecology* **42**(4): 659–671.

Castro, I., D. H. Brunton, K. M. Mason, B. Ebert & R. Griffiths (2003). Life history traits and food supplementation affect productivity in a translocated population of the endangered hihi (stitchbird, *Notiomystis cincta*). *Biological Conservation* **114**(2): 271–280.

Caut, S., E. Angulo & F. Courchamp (2009). Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology* **46**(2): 443–453.

Centre for Ecology and Hydrology (2009). http://www.ceh.ac.uk/sci_programmes/BioGeoChem/LandCoverMap2000.html

Chamberlain, D. E., B. J. Hatchwell & C. M. Perrins (1999). Importance of feeding ecology to the reproductive success of blackbirds *Turdus merula* nesting in rural habitats. *Ibis* **141**(3): 415–427.

Chamberlain, D. E., J. A. Vickery, D. E. Glue, R. A. Robinson, G. J. Conway, R. J. W. Woodburn & A. R. Cannon (2005). Annual and seasonal trends in the use of garden feeders by birds in winter. *Ibis* **147**(3): 563–575.

Chamberlain, D. E., S. Gough, H. Vaughan, J. A. Vickery & G. F. Appleton (2007). Determinants of bird species richness in public green spaces. *Bird Study* **54**(1): 87–97.

Chamberlain, D. E., A. R. Cannon, M. P. Toms, D. I. Leech, B. J. Hatchwell & K. J. Gaston (2009). Avian productivity in urban landscapes: a review and meta-analysis. *Ibis* **151**(1): 1–18.

Chambers Dictionary (2009). http://www.chambersharrap.co.uk/search

Charnov, E. L. & J. R. Krebs (1974). Clutch-size and fitness. *Ibis* **116**(2): 217–219.

Christians, J. K. (2002). Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews* **77**(1): 1–26.

CJ Wildlife (2009). http://www.birdfood.co.uk/products.php?area_id=2&nav_id=29

Clamens, A. & P. Isenmann (1989). Effect of supplemental food on the breeding of blue and great tits in Mediterranean habitats. *Ornis Scandinavica* **20**(1): 36-42.

Clout, M. N., G. P. Elliott & B. C. Robertson (2002). Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. *Biological Conservation* **107**(1): 13–18.

Cowie, R. J. & S. A. Hinsley (1987). Breeding success of blue tits and great tits in suburban gardens. *Ardea* **75**(1): 81–90.

Cowie, R. J. & S. A. Hinsley (1988a). Feeding ecology of great tits (*Parus major*) and blue tits (*Parus caeruleus*), breeding in suburban gardens. *Journal of Animal Ecology* **57**(2): 611–626.

Cowie, R. J. & S. A. Hinsley (1988b). The provision of food and the use of bird feeders in suburban gardens. *Bird Study* **35**(3): 163–168.

Cramp, S. & C. M. Perrins (1993a). Blue tit. In Cramp, S. & C. M. Perrins (eds) *The Birds of the Western Palearctic*. Oxford, Oxford University Press. **7**: 225–248.

Cramp, S. & C. M. Perrins (1993b). Great tit. In Cramp, S. & C. M. Perrins (eds) *The Birds of the Western Palearctic*. Oxford, Oxford University Press. **7**: 255–281.

Cresswell, W. & R. McCleery (2003). How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology* **72**(2): 356–366.

Crick, H. Q. P. (1992). A bird-habitat coding system for use in Britain and Ireland incorporating aspects of land-management and human activity. *Bird Study* **39**(1): 1–12.

Crick, H. Q. P., S. R. Baillie & D. I. Leech (2003). The UK Nest Record Scheme: its value for science and conservation. *Bird Study* **50**(3): 254–270.

Croci, S., A. Butet, A. Georges, R. Aguejdad & P. Clergeau (2008). Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. *Landscape Ecology* **23**(10): 1171–1186.

Crossner, K. A. (1977). Natural selection and clutch size in European starling. *Ecology* **58**(4): 885–892.

Daniels, G. D. & J. B. Kirkpatrick (2006). Does variation in garden characteristics influence the conservation of birds in suburbia? *Biological Conservation* **133**(3): 326–335.

Davies, N. B. & A. Lundberg (1985). The influence of food on time budgets and timing of breeding of the dunnock *Prunella modularis*. *Ibis* **127**(1): 100–110.

Davies, Z. G., R. A. Fuller, A. Loram, K. N. Irvine, V. Sims & K. J. Gaston (2009). A national scale inventory of resource provision for biodiversity within domestic gardens. *Biological Conservation* **142**(4): 761–771.

Davis, S. E., R. G. Nager & R. W. Furness (2005). Food availability affects adult survival as well as breeding success of parasitic jaegers. *Ecology* **86**(4): 1047–1056.

De Giacomo, U. & G. Guerrieri (2008). The feeding behavior of the black kite (*Milvus migrans*) in the rubbish dump of Rome. *Journal of Raptor Research* **42**(2): 110–118.

de Neve, L., J. J. Soler, M. Ruiz-Rodriguez, D. Martin-Galvez, T. Perez-Contreras & M. Soler (2007). Habitat-specific effects of a food supplementation experiment on immunocompetence in Eurasian magpie *Pica pica* nestlings. *Ibis* **149**(4): 763–773.

Deeming, D. C. (2002). *Avian Incubation: Behaviour, Environment, and Evolution*. Oxford, Oxford University Press.

DeNiro, M. J. & S. Epstein (1978). Influence of diet on distribution of carbon isotopes in animals. *Geochimica Et Cosmochimica Acta* **42**(5): 495–506.

DeNiro, M. J. & S. Epstein (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica Et Cosmochimica Acta* **45**(3): 341–351.

Department for Environment, Food and Rural Affairs (2008). *A Biodiversity Strategy for England. Measuring Progress: Baseline Assessment*. London, Department for Environment, Food and Rural Affairs.

Dewey, S. R. & P. L. Kennedy (2001). Effects of supplemental food on parental-care strategies and juvenile survival of northern goshawks. *Auk* **118**(2): 352–365.

Dhondt, A. A. (1979). Summer dispersal and survival of juvenile great tits in southern Sweden. *Oecologia* **42**(2): 139–157.

Dhondt, A. A. & R. Eyckerman (1979). Temperature and date of laying by tits *Parus* spp. *Ibis* **121**(3): 329–331.

Dhondt, A. A., R. Eyckerman, R. Moermans & J. Huble (1984). Habitat and laying date of great and blue tit *Parus major* and *Parus caeruleus*. *Ibis* **126**(3): 388–397.

Dhondt, A. A., F. Adriaensen, E. Matthysen & B. Kempenaers (1990). Nonadaptive clutch sizes in tits. *Nature* **348**(6303): 723–725.

Dijkstra, C., L. Vuursteen, S. Daan & D. Masman (1982). Clutch size and laying date in the kestrel *Falco tinnunculus*: effect of supplementary food. *Ibis* **124**(2): 210–213.

Drent, R. H. & S. Daan (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**(1–4): 225–252.

Duhem, C., E. Vidal, P. Roche & J. Legrand (2003). Island breeding and continental feeding: how are diet patterns in adult yellow-legged gulls influenced by landfill accessibility and breeding stages? *Ecoscience* **10**(4): 502–508.

Duncan, D. C. (1988). Body reserves of neonate northern pintails (*Anas acuta*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **66**(4): 811–816.

Eeva, T., E. Lehikoinen & T. Pohjalainen (1997). Pollution-related variation in food supply and breeding success in two hole-nesting passerines. *Ecology* **78**(4): 1120–1131.

Eeva, T., M. Ryoma & J. Riihimaki (2005). Pollution-related changes in diets of two insectivorous passerines. *Oecologia* **145**(4): 629–639.

Eikenaar, C., M. L. Berg & J. Komdeur (2003). Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian reed warbler *Acrocephalus australis*. *Journal of Avian Biology* **34**(4): 419–427.

Eldridge, J. L. & G. L. Krapu (1988). The influence of diet quality on clutch size and laying pattern in mallards. *Auk* **105**(1): 102–110.

Elliott, K. H., J. Duffe, S. L. Lee, P. Mineau & J. E. Elliott (2006). Foraging ecology of bald eagles at an urban landfill. *Wilson Journal of Ornithology* **118**(3): 380–390.

Elvidge, C. D., B. T. Tuttle, P. S. Sutton, K. E. Baugh, A. T. Howard, C. Milesi, B. L. Bhaduri & R. Nemani (2007). Global distribution and density of constructed impervious surfaces. *Sensors* **7**(9): 1962–1979.

European Environment Agency (2006). *Urban Sprawl in Europe. The Ignored Challenge*. Copenhagen, European Environment Agency.

Evans, K. L., K. J. Gaston, S. P. Sharp, A. McGowan & B. J. Hatchwell (2009). The effect of urbanisation on avian morphology and latitudinal gradients in body size. *Oikos* **118**(2): 251–259.

Ewald, P. W. & S. Rohwer (1982). Effects of supplemental feeding on timing of breeding, clutch-size and polygyny in red-winged blackbirds *Agelaius phoeniceus*. *Journal of Animal Ecology* **51**(2): 429–450.

Ewen, J. G., R. Thorogood, F. Karadas & P. Cassey (2008). Condition dependence of nestling mouth colour and the effect of supplementing carotenoids on parental behaviour in the hihi (*Notiomystis cincta*). *Oecologia* **157**(2): 361–368.

Fargallo, J. A. (2004). Latitudinal trends of reproductive traits in the blue tit *Parus caeruleus*. *Ardeola* **51**(1): 177–190.

Fernández-Juricic, E. & J. Jokimäki (2001). A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. *Biodiversity and Conservation* **10**(12): 2023–2043.

Flint, P. L. & J. B. Grand (1999). Patterns of variation in size and composition of greater scaup eggs: are they related? *Wilson Bulletin* **111**(4): 465–471.

Foote, J. R., L. P. Fitzsimmons, D. J. Mennill & L. M. Ratcliffe (2008). Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis. *Behavioral Ecology* **19**(6): 1192–1199.

Fuller, R. A., K. N. Irvine, P. Devine-Wright, P. H. Warren & K. J. Gaston (2007). Psychological benefits of greenspace increase with biodiversity. *Biology Letters* **3**(4): 390–394.

Fuller, R. A., P. H. Warren, P. R. Armsworth, O. Barbosa & K. J. Gaston (2008). Garden bird feeding predicts the structure of urban avian assemblages. *Diversity and Distributions* **14**(1): 131–137.

Fuller, R. A., K. N. Irvine, Z. G. Davies, P. R. Armsworth & K. J. Gaston (In press). Interactions between people and birds in urban landscapes. *Studies in Avian Biology*.

Fuller, R. M., G. M. Smith, J. M. Sanderson, R. A. Hill, A. G. Thomson, R. Cox, N. J. Brown & F. F. Gerard (2002). *Countryside Survey 2000 Module 7. Land Cover Map 2000. Final Report.* Abbots Ripton, Centre for Ecology and Hydrology.

Furness, R. W., K. Ensor & A. V. Hudson (1992). The use of fishery waste by gull populations around the British-Isles. *Ardea* **80**(1): 105–113.

Garthe, S., C. J. Camphuysen & R. W. Furness (1996). Amounts of discards by commercial fisheries and their significance as food for seabirds in the North Sea. *Marine Ecology-Progress Series* **136**(1–3): 1–11.

Gaston, K. J., R. A. Fuller, A. Loram, C. MacDonald, S. Power & N. Dempsey (2007). Urban domestic gardens (XI): variation in urban wildlife gardening in the United Kingdom. *Biodiversity and Conservation* **16**(11): 3227–3238.

Gibb, J. A. (1954). The feeding ecology of tits, with notes on the treecreeper and goldcrest. *Ibis* **96**(4): 513–543.

Gibb, J. A. & M. M. Betts (1963). Food and food supply of nestling tits (paridae) in Breckland pine. *Journal of Animal Ecology* **32**(3): 489–533.

Gill, V. A. & S. A. Hatch (2002). Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. *Journal of Avian Biology* **33**(2): 113–126.

Gill, V. A., S. A. Hatch & R. B. Lanctot (2002). Sensitivity of breeding parameters to food supply in black-legged kittiwakes *Rissa tridactyla*. *Ibis* **144**(2): 268–283.

Gloutney, M. L., R. T. Alisauskas, K. A. Hobson & A. D. Afton (1999). Use of supplemental food by breeding Ross's geese and lesser snow geese: evidence for variable anorexia. *Auk* **116**(1): 97–108.

Glue, D. (2006). Variety at winter bird tables. *Bird Populations* **7**: 212–215.

Gosler, A. G. (1993). *The Great Tit*. London, Hamlyn.

Gosler, A. G. (1996). Environmental and social determinants of winter fat storage in the great tit *Parus major*. *Journal of Animal Ecology* **65**(1): 1–17.

Gregoire, A., B. Faivre, P. Heeb & F. Cezilly (2002). A comparison of infestation patterns by *Ixodes* ticks in urban and rural populations of the common blackbird *Turdus merula*. *Ibis* **144**(4): 640–645.

Gregory, R. D. & S. R. Baillie (1998). Large-scale habitat use of some declining British birds. *Journal of Applied Ecology* **35**(5): 785–799.

Grieco, F. (2001). Short-term regulation of food-provisioning rate and effect on prey size in blue tits, *Parus caeruleus*. *Animal Behaviour* **62**(1): 107–116.

Grieco, F. (2002). How different provisioning strategies result in equal rates of food delivery: an experimental study of blue tits *Parus caeruleus*. *Journal of Avian Biology* **33**(4): 331–341.

Grieco, F. (2003). Greater food availability reduces tarsus asymmetry in nestling blue tits. *Condor* **105**(3): 599–603.

Grieco, F., A. J. van Noordwijk & M. E. Visser (2002). Evidence for the effect of learning on timing of reproduction in blue tits. *Science* **296**(5565): 136–138.

Gustafsson, L. & W. J. Sutherland (1988). The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature* **335**(6193): 813–815.

Haggard, W. H. (1990). Urban weather. *International Journal of Environmental Studies* **36**(1): 73–82.

Hamann, H. J., K. -H. Schmidt & S. Simonis (1989). Altitude and size of eggs and clutch in the great tit (*Parus major*). *Journal Für Ornithologie* **130**(1): 69–74.

Heath, S. R., E. L. Kershner, D. M. Cooper, S. Lynn, J. M. Turner, N. Warnock, S. Farabaugh, K. Brock & D. K. Garcelon (2008). Rodent control and food supplementation increase productivity of endangered San Clemente loggerhead shrikes (*Lanius ludovicianus mearnsi*). *Biological Conservation* **141**(10): 2506–2515.

Hedblom, M. (2007). *Birds and Butterflies in Swedish Urban and Peri-urban Habitats: a Landscape Perspective.* Doctoral thesis. Uppsala, Swedish University of Agricultural Sciences**:** 1–37.

Helm, B., T. Piersma & H. Van der Jeug (2006). Sociable schedules: interplay between avian seasonal and social behaviour. *Animal Behaviour* **72**(2): 245–262.

Hill, W. L. (1988). The effect of food abundance on the reproductive patterns of coots. *Condor* **90**(2): 324–331.

Hiom, L., M. Bolton, P. Monaghan & D. Worrall (1991). Experimental evidence for food limitation of egg production in gulls. *Ornis Scandinavica* **22**(2): 94–97.

Hobson, K. A. (1995). Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. *Condor* **97**(3): 752–762.

Hobson, K. A. & F. Bairlein (2003). Isotopic fractionation and turnover in captive garden warblers (*Sylvia borin*): implications for delineating dietary and migratory associations in wild passerines. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **81**(9): 1630–1635.

Hochachka, W. M. & D. A. Boag (1987). Food shortage for breeding black-billed magpies (*Pica pica*): an experiment using supplemental food. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **65**(5): 1270–1274.

Högstedt, G. (1981). Effect of additional food on reproductive success in the magpie (*Pica pica*). *Journal of Animal Ecology* **50**(1): 219–229.

Hõrak, P. (1993). Low fledging success of urban great tits. *Ornis Fennica* **70**(3): 168–172.

Hõrak, P. & J. D. Lebreton (1998). Survival of adult great tits *Parus major* in relation to sex and habitat; a comparison of urban and rural populations. *Ibis* **140**(2): 205–209.

Houston, D. C., D. Donnan & P. J. Jones (1995). The source of the nutrients required for egg production in zebra finches *Poephila guttata*. *Journal of Zoology* **235**(3): 469–483.

Houston, D. C., K. McInnes, G. Elliott, D. Eason, R. Moorhouse & J. Cockrem (2007). The use of a nutritional supplement to improve egg production in the endangered kakapo. *Biological Conservation* **138**(1–2): 248–255.

Howard, P. & D. N. Jones (2004). A qualitative study of wildlife feeding in south-east Queensland. In Burger, S. K. & D. Lunney (eds) *Urban Wildlife: More than Meets the Eye*. Sydney, Royal Zoological Society of New South Wales: 55–62.

Husby, M. (2006). Predation rates on bird nests by predatory birds and mammals around refuse dumps. *Journal of Ornithology* **147**(5): 184–185.

Inger, R. & S. Bearhop (2008). Applications of stable isotope analyses to avian ecology. *Ibis* **150**(3): 447–461.

Isaksson, C. & S. Andersson (2007). Carotenoid diet and nestling provisioning in urban and rural great tits *Parus major*. *Journal of Avian Biology* **38**(5): 564–572.

Isaksson, C., A. Johansson & S. Andersson (2008). Egg yolk carotenoids in relation to habitat and reproductive investment in the great tit *Parus major*. *Physiological and Biochemical Zoology* **81**(1): 112–118.

Jacobs, S. R., K. H. Elliott, A. J. Gaston & J. M. Weber (2009). Fatty acid signatures of female Brunnich's guillemots *Uria lomvia* suggests reliance on local prey for replacement egg production. *Journal of Avian Biology* **40**(3): 327–336.

Jamieson, I. G. (2004). No evidence that dietary nutrient deficiency is related to poor reproductive success of translocated takahe. *Biological Conservation* **115**(1): 165–170.

Jansson, C., J. Ekman & A. Von Brömssen (1981). Winter mortality and food-supply in tits *Parus*-spp. *Oikos* **37**(3): 313–322.

Jones, D. N. (2008). *Feed the Birds?* Wingspan (magazine) **18**: 16–19.

Jones, D. N. & S. J. Reynolds (2008). Feeding birds in our towns and cities: a global research opportunity. *Journal of Avian Biology* **39**(3): 265–271.

Jones, P. J. & P. Ward (1976). Level of reserve protein as proximate factor controlling timing of breeding and clutch-size in red-billed quelea *Quelea quelea*. *Ibis* **118**(4): 547–574.

Källander, H. (1974). Advancement of laying of great tits by the provision of food. *Ibis* **116**(3): 365–367.

Källander, H. & J. Karlsson (1993). Supplemental food and laying date in the European starling. *Condor* **95**(4): 1031–1034.

Kelly, J. F. & B. Van Horne (1997). Effects of food supplementation on the timing of nest initiation in belted kingfishers. *Ecology* **78**(8): 2504–2511.

Kempenaers, B., F. Adriaensen, A. J. van Noordwijk & A. A. Dhondt (1996). Genetic similarity, inbreeding and hatching failure in blue tits: are unhatched eggs infertile? *Proceedings of the Royal Society of London Series B-Biological Sciences* **263**(1367): 179–185.

Kempenaers, B., F. Adriaensen & A. A. Dhondt (1998). Inbreeding and divorce in blue and great tits. *Animal Behaviour* **56**(3): 737–740.

Kilpi, M. & M. Ost (1998). Reduced availability of refuse and breeding output in a herring gull (*Larus argentatus*) colony. *Annales Zoologici Fennici* **35**(1): 37–42.

Komdeur, J. (1996). Breeding of the Seychelles magpie robin *Copsychus sechellarum* and implications for its conservation. *Ibis* **138**(3): 485–498.

Korpimäki, E. (1989). Breeding performance of Tengmalm's owl *Aegolius funereus*: effects of supplementary feeding in a peak vole year. *Ibis* **131**(1): 51–56.

Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Oxford, Oxford University Press.

Lack, D. (1966). *Population Studies of Birds*. Oxford, Clarendon Press.

Lessells, C. M. (1986). Brood size in Canada geese: a manipulation experiment. *Journal of Animal Ecology* **55**(2): 669–689.

Leston, L. F. V. & A. D. Rodewald (2006). Are urban forests ecological traps for understory birds? An examination using northern cardinals. *Biological Conservation* **131**(4): 566–574.

Liker, A., Z. Papp, V. Bokony & A. Z. Lendvai (2008). Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. *Journal of Animal Ecology* **77**(4): 789–795.

Lin, E. (2005). *Production and Processing of Small Seeds for Birds*. Rome, Food and Agriculture Organization of the United Nations.

Louzao, M., J. M. Igual, M. McMinn, J. S. Aguilar, R. Triay & D. Oro (2006). Small pelagic fish, trawling discards and breeding performance of the critically endangered Balearic shearwater: improving conservation diagnosis. *Marine Ecology-Progress Series* **318**: 247–254.

Lyon, B. E. & R. D. Montgomerie (1985). Incubation feeding in snow buntings: female manipulation or indirect male parental care. *Behavioral Ecology and Sociobiology* **17**(3): 279–284.

Magrath, R. D. (1992). The effect of egg mass on the growth and survival of blackbirds: a field experiment. *Journal of Zoology* **227**(4): 639–653.

Mänd, R., V. Tilgar, A. Lohmus & A. Leivits (2005). Providing nest boxes for hole-nesting birds – does habitat matter? *Biodiversity and Conservation* **14**(8): 1823–1840.

Marshall, M. R., R. J. Cooper, J. A. DeCecco, J. Strazanac & L. Butler (2002). Effects of experimentally reduced prey abundance on the breeding ecology of the red-eyed vireo. *Ecological Applications* **12**(1): 261–280.

Martin, T. E. (1987). Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* **18**: 453–487.

Mason, C. F. (2000). Thrushes now largely restricted to the built environment in eastern England. *Diversity and Distributions* **6**(4): 189–194.

McGowan, K. J. (2001). Demographic and behavioural comparisons of suburban and rural American crows. In Marzluff, J. M., R. Bowman & R. Donnelly (eds) *Avian Ecology and Conservation in an Urbanizing World*. New York, Kluwer Academic Publishers: 365–381.

Meijer, T. & R. Drent (1999). Re-examination of the capital and income dichotomy in breeding birds. *Ibis* **141**(3): 399–414.

Minitab (2007). *Meet Minitab 15 for Windows.* State College, PA, USA, Minitab Inc..

Minot, E. O. & C. M. Perrins (1986). Interspecific interference competition – nest sites for blue and great tits. *Journal of Animal Ecology* **55**(1): 331–350.

Monrós, J. S., E. J. Belda & E. Barba (2002). Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* **99**(3): 481–488.

Morrison, S. A. & D. T. Bolger (2002). Lack of an urban edge effect on reproduction in a fragmentation-sensitive sparrow. *Ecological Applications* **12**(2): 398–411.

Naef-Daenzer, B. (1994). Radiotracking of great and blue tits: new tools to assess territoriality, home-range use and resource distribution. *Ardea* **82**(2): 335–347.

Naef-Daenzer, B. & L. F. Keller (1999). The foraging performance of great and blue tits (*Parus major* and *P. caeruleus)* in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology* **68**(4): 708–718.

Naef-Daenzer, B., F. Widmer & M. Nuber (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* **70**(5): 730–738.

Nager, R. G. (2006). The challenges of making eggs. *Ardea* **94**(3): 323–346.

Nager, R. G. & A. J. van Noordwijk (1995). Proximate and ultimate aspects of phenotypic plasticity in timing of great tit breeding in a heterogeneous environment. *American Naturalist* **146**(3): 454–474.

Nager, R. G., C. Ruegger & A. J. van Noordwijk (1997). Nutrient or energy limitation on egg formation: a feeding experiment in great tits. *Journal of Animal Ecology* **66**(4): 495–507.

Nager, R. G., P. Monaghan, R. Griffiths, D. C. Houston & R. Dawson (1999). Experimental demonstration that offspring sex ratio varies with maternal condition. *PNAS* **96**(2): 570–573.

Nelson, M., S. H. Jones, C. Edwards & J. C. Ellis (2008). Characterization of *Escherichia coli* populations from gulls, landfill trash, and wastewater using ribotyping. *Diseases of Aquatic Organisms* **81**(1): 53–63.

Nilsson, J. Å. (1991). Clutch size determination in the marsh tit (*Parus palustris*). *Ecology* **72**(5): 1757–1762.

Nilsson, J. Å. (1993). Energetic constraints on hatching asynchrony. *American Naturalist* **141**(1): 158–166.

Nilsson, J. Å. (1994). Energetic bottle-necks during breeding and the reproductive cost of being too early. *Journal of Animal Ecology* **63**(1): 200–208.

Nilsson, J. Å. (2000). Time-dependent reproductive decisions in the blue tit. *Oikos* **88**(2): 351–361.

Nilsson, J. Å. & H. G. Smith (1988). Incubation feeding as a male tactic for early hatching. *Animal Behaviour* **36**(3): 641–647.

Nilsson, J. Å. & E. Svensson (1993a). Causes and consequences of egg mass variation between and within blue tit clutches. *Journal of Zoology* **230**(3): 469–481.

Nilsson, J. Å. & E. Svensson (1993b). Energy constraints and ultimate decisions during egg-laying in the blue tit. *Ecology* **74**(1): 244–251.

Nisbet, I. C. T. (1978). Dependence of fledging success on egg-size, parental performance and egg-composition among common and roseate terns, *Sterna hirundo* and *S. Dougallii*. *Ibis* **120**(2): 207–215.

Norris, K. (1993). Seasonal-variation in the reproductive success of blue tits: an experimental-study. *Journal of Animal Ecology* **62**(2): 287–294.

Nur, N. (1984). The consequences of brood size for breeding blue tits. 2. Nestling weight, offspring survival and optimal brood size. *Journal of Animal Ecology* **53**(2): 497–517.

Ojanen, M. (1983). Composition of the eggs of the great tit (*Parus major*) and the pied flycatcher (*Ficedula hypoleuca*). *Annales Zoologici Fennici* **20**(1): 57–63.

Olea, P. P. & V. Baglione (2008). Population trends of rooks *Corvus frugilegus* in Spain and the importance of refuse tips. *Ibis* **150**(1): 98–109.

O'Leary, R. & D. N. Jones (2006). The use of supplementary foods by Australian magpies *Gymnorhina tibicen*: implications for wildlife feeding in suburban environments. *Austral Ecology* **31**(2): 208–216.

Oro, D. & X. Ruiz (1997). Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands areas. *Ices Journal of Marine Science* **54**(4): 695–707.

Oro, D., X. Genovart, X. Ruiz, J. Jimenez & J. García-Gans (1996). Differences in diet, population size and reproductive performance between two colonies of Audouin's gull *Larus audouinii* affected by a trawling moratorium. *Journal of Avian Biology* **27**(3): 245–251.

Oro, D., X. Ruiz, L. Jover, V. Pedrocchi & J. González-Solís (1997). Diet and adult time budgets of Audouin's gull *Larus audouinii* in response to changes in commercial fisheries. *Ibis* **139**(4): 631–637.

Oro, D., E. Cam, R. Pradel & A. Martínez-Abraín (2004). Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**(1537): 387–396.

Parnell, A. & A. Jackson (2008). SIAR: Stable Isotope Analysis in R. Available from: http://cran.r-project.org/web/packages/siar/index.html

Partecke, J., T. Van't Hof & E. Gwinner (2004). Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**(1552): 1995–2001.

Payevsky, V. A. (2006). Mortality rate and population density regulation in the great tit, *Parus major* L.: a review. *Russian Journal of Ecology* **37**(3): 180–187.

Pearson, S. F., D. J. Levey, C. H. Greenberg & C. M. del Rio (2003). Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Oecologia* **135**(4): 516–523.

Pennycott, T. W., R. N. Cinderey, A. Park, H. A. Mather & G. Foster (2002). *Salmonella enterica* subspecies enterica serotype *Typhimurium* and *Escherichia coli* O86 in wild birds at two garden sites in south-west Scotland. *Veterinary Record* **151**(19): 563–567.

Perrins, C. M. (1965). Population fluctuations and clutch-size in the great tit, *Parus major* L. *Journal of Animal Ecology* **34**(3): 601–647.

Perrins, C. M. (1970). Timing of birds' breeding seasons. *Ibis* **112**(2): 242–255.

Perrins, C. M. (1979). *British Tits*. London, Collins.

Perrins, C. M. (1991). Tits and their caterpillar food supply. *Ibis* **133**(suppl.): 49–54.

Perrins, C. M. & P. J. Jones (1974). Inheritance of clutch size in great tit (*Parus major* L). *Condor* **76**(2): 225–228.

Perrins, C. M. & R. H. McCleery (1989). Laying dates and clutch size in the great tit. *Wilson Bulletin* **101**(2): 236–253.

Perrins, C. M. & R. H. McCleery (1994). Competition and egg-weight in the great tit *Parus major*. *Ibis* **136**(4): 454–456.

Perrins, C. M. & D. Moss (1975). Reproductive rates in the great tit. *Journal of Animal Ecology* **44**(3): 695–706.

Pettifor, R. A., C. M. Perrins & R. H. McCleery (1988). Individual optimization of clutch size in great tits. *Nature* **336**(6195): 160–162.

Phillips, D. L. & P. L. Koch (2002). Incorporating concentration dependence in stable isotope mixing models. *Oecologia* **130**(1): 114–125.

Pierotti, R. & C. A. Annett (1991). Diet choice in the herring gull: constraints imposed by reproductive and ecological factors. *Ecology* **72**(1): 319–328.

Podlesak, D. W., S. R. McWilliams & K. A. Hatch (2005). Stable isotopes in breath, blood, feces and feathers can indicate intra-individual changes in the diet of migratory songbirds. *Oecologia* **142**(4): 501–510.

Poesel, A. & T. Dabelsteen (2005). Territorial responses of male blue tits to simulated dynamic intrusions: effects of song overlap and intruder location. *Animal Behaviour* **70**(6): 1419–1427.

Pons, J. M. (1992). Effects of changes in the availability of human refuse on breeding parameters in a herring gull *Larus argentatus* population in Brittany, France. *Ardea* **80**(1): 143–150.

Ramos, R., F. Ramirez, C. Sanpera, L. Jover & X. Ruiz (2009). Diet of yellow-legged gull (*Larus michahellis*) chicks along the Spanish western Mediterranean coast: the relevance of refuse dumps. *Journal of Ornithology* **150**(1): 265–272.

Ramsay, S. L. & D. C. Houston (1997). Nutritional constraints on egg production in the blue tit: a supplementary feeding study. *Journal of Animal Ecology* **66**(5): 649–657.

Ramsay, S. L. & D. C. Houston (1998). The effect of dietary amino acid composition on egg production in blue tits. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**(1404): 1401–1405.

Redfern, C. P. F. & J. A. Clark (2001). *Ringers' Manual*. Thetford, BTO.

Reese, K. P. & J. A. Kadlec (1984). Supplemental feeding: possible negative effects on black-billed magpies. *Journal of Wildlife Management* **48**(2): 608–610.

Reynolds, S. J., S. J. Schoech & R. Bowman (2003a). Diet quality during pre-laying and nestling periods influences growth and survival of Florida scrub-jay (*Aphelocoma coerulescens*) chicks. *Journal of Zoology* **261**(3): 217–226.

Reynolds, S. J., S. J. Schoech & R. Bowman (2003b). Nutritional quality of prebreeding diet influences breeding performance of the Florida scrub-jay. *Oecologia* **134**(3): 308–316.

Reynolds, S. J., R. Mänd & V. Tilgar (2004). Calcium supplementation of breeding birds: directions for future research. *Ibis* **146**(4): 601–614.

Ricklefs, R. E., D. C. Hahn & W. A. Montevecchi (1978). Relationship between egg size and chick size in laughing gull and Japanese quail. *Auk* **95**(1): 135–144.

Robb, G. N., R. A. McDonald, D. E. Chamberlain & S. Bearhop (2008a). Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment* **6**(9): 476–484.

Robb, G. N., R. A. McDonald, D. E. Chamberlain, S. J. Reynolds, T. J. E. Harrison & S. Bearhop (2008b). Winter feeding of birds increases productivity in the subsequent breeding season. *Biology Letters* **4**(2): 220–223.

Robb G. N., R. A. McDonald, R. Inger, J. Newton, R. A. R. McGill, D. E. Chamberlain, S. J. Reynolds, T. J. E. Harrison & S. Bearhop (In review). Using stable isotope analysis as a technique for determining individual use of supplementary food in birds. *Journal of Field Ornithology*.

Robbins, C. T. (1981). Estimation of the relative protein cost of reproduction in birds. *Condor* **83**(2): 177–179.

Robertson, B. A. & R. L. Hutto (2006). A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* **87**(5): 1075–1085.

Robertson, B. C., G. P. Elliott, D. K. Eason, M. N. Clout & N. J. Gemmell (2006). Sex allocation theory aids species conservation. *Biology Letters* **2**(2): 229–231.

Rodewald, A. D. & D. P. Shustack (2008a). Consumer resource matching in urbanizing landscapes: are synanthropic species over-matching? *Ecology* **89**(2): 515–521.

Rodewald, A. D. & D. P. Shustack (2008b). Urban flight: understanding individual and population-level responses of Nearctic-Neotropical migratory birds to urbanization. *Journal of Animal Ecology* **77**(1): 83–91.

Rofstad, G. & J. Sandvik (1987). Morphology of hatchling hooded crows and its relation to egg volume. *Condor* **89**(3): 494–499.

Romanoff, A. L. & A. J. Romanoff (1949). *The Avian Egg*. New York, Wiley.

Royama, T. (1966). Factors governing feeding rate, food requirement and brood size of nestling great tits *Parus major*. *Ibis* **108**(3): 313–347.

Rytkönen, S. & M. Orell (2001). Great tits, *Parus major*, lay too many eggs: experimental evidence in mid-boreal habitats. *Oikos* **93**(3): 439–450.

Saino, N., M. Romano, R. Ambrosini, R. P. Ferrari & A. P. Møller (2004). Timing of reproduction and egg quality covary with temperature in the insectivorous barn swallow, *Hirundo rustica*. *Functional Ecology* **18**(1): 50–57.

Sallabanks, R. (2002). Effects of forest fragmentation on breeding bird populations: conflicting views from North America. In Chamberlain, D. E. & A. Wilson (eds) *Avian Landscape Ecology: Pure and Applied Issues in the Large-Scale Ecology of Birds*. Conference proceedings. University of East Anglia, International Association for Landscape Ecology, UK Region: 3–14.

Sanz, J. J. (1996). Effect of food availability on incubation period in the pied flycatcher (*Ficedula hypoleuca*). *Auk* **113**(1): 249–253.

SAS Institute Inc. (2008). *SAS/STAT® 9.2 User's Guide.* Cary, NC, USA, SAS Institute Inc..

Savard, J. P. L., P. Clergeau & G. Mennechez (2000). Biodiversity concepts and urban ecosystems. *Landscape and Urban Planning* **48**(3–4): 131–142.

Schifferli, L. (1973). Effect of egg weight on subsequent growth of nestling great tits *Parus major*. *Ibis* **115**(4): 549–558.

Schmidt, K. -H (1988). Site fidelity and isolation of great tits (*Parus major*) in urban habitats. Acta XIX Congress of International Ornithology, Ottawa: 1794–1801.

Schmidt, K. -H. & H. Einloft-Achenbach (1984). Können isolierte meisenpopulationen in städten ihren bestand erhalten? *Die Vogelwelt* **105**: 97–105.

Schmidt, K. -H. & J. Steinbach (1983). Low breeding-success for great tits (*Parus major*) in urban parks and cemeteries. *Journal Für Ornithologie* **124**(1): 81–83.

Schoech, S. J. & T. P. Hahn (2008). Latitude affects degree of advancement in laying by birds in response to food supplementation: a meta-analysis. *Oecologia* **157**(3): 369–376.

Schoech, S. J., R. Bowman & S. J. Reynolds (2004). Food supplementation and possible mechanisms underlying early breeding in the Florida scrub-jay (*Aphelocoma coerulescens*). *Hormones and Behavior* **46**(5): 565–573.

Schoech, S. J., R. Bowman, E. S. Bridge & R. K. Boughton (2007). Baseline and acute levels of corticosterone in Florida scrub-jays (*Aphelocoma coerulescens*): effects of food supplementation, suburban habitat, and year. *General and Comparative Endocrinology* **154**(1–3): 150–160.

Schoech, S. J., E. S. Bridge, R. K. Boughton, S. J. Reynolds, J. W. Atwell & R. Bowman (2008). Food supplementation: a tool to increase reproductive output. A case study in the threatened Florida scrub-jay. *Biological Conservation* **141**(1): 162–173.

Sears, J., S. A. Hatch & D. M. O'Brien (2009). Disentangling effects of growth and nutritional status on seabird stable isotope ratios. *Oecologia* **159**(1): 41–48.

Shaw, L. M., D. Chamberlain & M. Evans (2008). The house sparrow *Passer domesticus* in urban areas: reviewing a possible link between post-decline distribution and human socioeconomic status. *Journal of Ornithology* **149**(3): 293–299.

Slabbekoorn, H. & M. Peet (2003). Birds sing at a higher pitch in urban noise: great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* **424**(6946): 267–267.

Smith, C. C. & S. D. Fretwell (1974). Optimal balance between size and number of offspring. *American Naturalist* **108**(962): 499–506.

Smith, G. C. & N. Carlile (1993). Food and feeding ecology of breeding silver gulls (*Larus novaehollandiae*) in urban Australia. *Colonial Waterbirds* **16**(1): 9–17.

Smith, H. G., T. Ohlsson & K. J. Wettermark (1995). Adaptive significance of egg size in the European starling: experimental tests. *Ecology* **76**(1): 1–7.

Sokal, R. R. & F. J. Rohlf (1995). *Biometry*. New York, Freeman.

Soler, M. & J. J. Soler (1996). Effects of experimental food provisioning on reproduction in the jackdaw *Corvus monedula*, a semi-colonial species. *Ibis* **138**(3): 377–383.

Solonen, T. (2001). Breeding of the great tit and blue tit in urban and rural habitats in southern Finland. *Ornis Fennica* **78**(2): 49–60.

Spaans, A. L. (1971). Feeding ecology of herring gull *Larus argentatus* pont. in the northern part of the Netherlands. *Ardea* **59**(3–4): 73–188.

Staicer, C. A., D. A. Spector & A. G. Horn (1996). The dawn chorus and other diel patters in acoustic signaling. In Kroodsma, D. E. & E. H. Miller (eds) *Ecology and Evolution of Acoustic Communication in Birds*. New York, Cornell University Press: 426–453.

Styrsky, J. D., R. C. Dobbs & C. F. Thompson (2000). Food-supplementation does not override the effect of egg mass on fitness-related traits of nestling house wrens. *Journal of Animal Ecology* **69**(4): 690–702.

Svensson, E. & J. Å. Nilsson (1995). Food-supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). *Ecology* **76**(6): 1804–1812.

The Royal Society for the Protection of Birds (2006). http://www.rspb.org.uk/advice/helpingbirds/feeding/whentofeed.asp

Thompson, K. R. (1992). Quantitative-analysis of the use of discards from squid trawlers by black-browed albatrosses *Diomedea melanophris* in the vicinity of the Falkland Islands. *Ibis* **134**(1): 11–21.

Thompson, K. R. & M. D. Riddy (1995). Utilization of offal and discards from finfish trawlers around the Falkland Islands by the black-browed albatross *Diomedea melanophris*. *Ibis* **137**(2): 198–206.

Thorington, K. K. & R. Bowman (2003). Predation rate on artificial nests increases with human housing density in suburban habitats. *Ecography* **26**(2): 188–196.

Tilgar, V., R. Mänd & A. Leivits (1999). Effect of calcium availability and habitat quality on reproduction in pied flycatcher *Ficedula hypoleuca* and great tit *Parus major*. *Journal of Avian Biology* **30**(4): 383–391.

Tipping, E., S. A. Thacker, D. Wilson & J. R. Hall (2008). Long-term nitrate increases in two oligotrophic lakes, due to the leaching of atmospherically-deposited N from moorland ranker soils. *Environmental Pollution* **152**(1): 41–49.

Toms, M. & P. Sterry (2008). *Garden Birds and Wildlife*. Basingstoke, AA Publishing.

Török, J. (1985). The diet niche relationships of the great tit (*Parus major*) and blue tit (*Parus caeruleus*) nestlings in an oak forest. *Opuscular Zoologica* **19–20**: 99–113.

Török, J. (1986). Food segregation in three hole-nesting bird species during the breeding season. *Ardea* **74**(2): 129–136.

Tortosa, F. S., J. M. Caballero & J. Reyes-Lopez (2002). Effect of rubbish dumps on breeding success in the white stork in southern Spain. *Waterbirds* **25**(1): 39–43.

United Nations (2008). *World Urbanization Prospects: The 2007 Revision (Executive Summary)*. New York, United Nations Department of Economic and Social Affairs/Population Division.

van Noordwijk, A. J. (1987). Quantitative ecological genetics of great tits. In Cooke, F. & P. A. Buckley (eds) *Avian Genetics: A Population and Ecological Approach*. London, Academic Press: 363–380.

Verhulst, S. & J. M. Tinbergen (1991). Experimental-evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. *Journal of Animal Ecology* **60**(1): 269–282.

Visser, M. E. & C. Both (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences* **272**(1581): 2561–2569.

Visser, M. E., L. J. M. Holleman & S. P. Caro (2009). Temperature has a causal effect on avian timing of reproduction. *Proceedings of the Royal Society of London Series B-Biological Sciences* **276**(1665): 2323–2331.

von Brömssen, A. & C. Jansson (1980). Effects of food addition to willow tit *Parus montanus* and crested tit *Parus cristatus* at the time of breeding. *Ornis Scandinavica* **11**(3): 173–178.

Votier, S. C., R. W. Furness, S. Bearhop, J. E. Crane, R. W. G. Caldow, P. Catry, K. Ensor, K. C. Hamer, A. V. Hudson, E. Kalmbach, N. I. Klomp, S. Pfeiffer, R. A. Phillips, I. Prieto & D. R. Thompson (2004). Changes in fisheries discard rates and seabird communities. *Nature* **427**(6976): 727–730.

Walsberg, G. E. (1983). *Avian ecological energetics*. New York, Academic Press.

White, G. C. & K. P. Burnham (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**(suppl.): 120–139.

Wiebe, K. L. & K. Martin (2000). The use of incubation behavior to adjust avian reproductive costs after egg laying. *Behavioral Ecology and Sociobiology* **48**(6): 463–470.

Wilby, R. L. & G. L. W. Perry (2006). Climate change, biodiversity and the urban environment: a critical review based on London, UK. *Progress in Physical Geography* **30**(1): 73–98.

Wilkin, T. A., D. Garant, A. G. Gosler & B. C. Sheldon (2006). Density effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data with GIS techniques. *Journal of Animal Ecology* **75**(2): 604–615.

Wilkin, T. A., A. G. Gosler, D. Garant, S. J. Reynolds & B. C. Sheldon (2009). Calcium effects on life-history traits in a wild population of the great tit (*Parus major*): analysis of long-term data at several spatial scales. *Oecologia* **159**(2): 463–472.

Williams, T. D. (1994). Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* **69**(1): 35–59.

Williams, T. D. (1996). Variation in reproductive effort in female zebra finches (*Taeniopygia guttata*) in relation to nutrient-specific dietary supplements during egg laying. *Physiological Zoology* **69**(5): 1255–1275.

Wood, N. (1985). *Birds in Your Garden*. London, Peerage Books.

Ydenberg, R. C. (1984). The conflict between feeding and territorial defense in the great tit. *Behavioral Ecology and Sociobiology* **15**(2): 103–108.

Yom-Tov, Y. (1974). Effect of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone* L). *Journal of Animal Ecology* **43**(2): 479–497.

You, Y. Y., J. Feng, H. T. Wang, J. L. Wang, C. Dong, X. R. Su, H. M. Sun & W. Gao (2009). Variation in egg size and nestling growth rate in relation to clutch size and laying sequence in great tits *Parus major*. *Progress in Natural Science* **19**(4): 427–433.