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Unintended Consequences: How Human Intervention Affects the Ecology of Urban Birds

Hugh James Hanmer

School of Biological Sciences

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Abstract

Urbanisation is an ever-growing threat to global wildlife. Nevertheless, urban areas around the world hold significant wild bird populations and urban birds provide a key connection between people and wildlife. Many people provide supplementary resources, such as food and nesting sites. However, even apparently beneficial actions may have unintended negative consequences. This work explores some of these direct and indirect effects.

Grey Squirrels *Sciurus carolinensis* are a widespread, introduced species in the UK, acting both as a competitor for resources with birds and predator of their nests. When present, Grey Squirrels effectively excluded birds from supplementary feeding stations. Allowing them unrestricted access both supports their energy requirements and reduces its availability to target taxa, through both behavioural exclusion and food consumption. In addition, nest predation was higher in artificial nests adjacent to filled bird feeders which were frequented by potential nest predators and the exclusion of these predators did not significantly reduce nest predation. Providing point attractants during the breeding season may therefore depress local urban bird breeding success in addition to directly supporting predator/competitor populations. Garden supplementary feeding stations may also represent a threat to wild bird and human health through pathogen transmission. Bacterial communities were found to differ between two bird feeder types but there was little association between feeder usage by animals and bacterial load or pathogen presence in a typical UK suburban garden bird-feeding setting. Nest boxes are commonly provided for cavity nesting urban birds as an additional supplementary resource. Nest box using Blue Tits *Cyanistes caeruleus* and Great Tits *Parus major* differed in their use of anthropogenic material. Anthropogenic nest material was associated with lower arthropod diversity and ectoparasite predator abundance but higher ectoparasite loads. Higher arthropod diversity was linked to lower flea numbers, implying more complex arthropod communities depressed ectoparasite abundance though no direct link was found between these factors with breeding success. Domestic cats *Felis catus* are the most abundant predator in many urban ecosystems. Cat home ranges varied with level of urbanisation and they ranged significantly further during the night. To reduce the probability of Domestic Cats entering local protected areas a management zone of 300-400m from the nearest housing was estimated to be of management value and must be adjusted to the local landscape to ensure effectiveness.

Despite the various negative effects highlighted in this thesis, the findings suggest that many of them can be mitigated, to ensure that our best intentions do effectively benefit urban birds.

Chapter 1: Introduction

1.1. Urbanisation

Urbanisation is a global phenomenon representing an extreme form of landscape modification, resulting in the restructuring of habitats (Crosby & Blair 2001; Chamberlain et al. 2009). Today, over half of people live in urban areas (UN 2011), and in countries such as the UK and USA, over 80% of the population resides in urban environments (UNPFA 2007). With the world's population growing by around 1% every year (UN 2011), cities are expanding at an even faster rate (Seto et al. 2012), further threatening local and global biodiversity (Aronson et al. 2014). Here in the UK, urban areas cover 6.8% of the land surface (UK National Ecosystem Assessment 2011).

The replacement and fragmentation of natural habitat with urban sprawl has dramatic effects on native wildlife. There is a strong correlation between both population and household density with an increase in local species endangerment (Peterson et al. 2007), and biodiversity in general is homogenised within urban environments across geographical scales (Clergeau et al. 2006; McKinney 2006; Devictor et al. 2007; Aronson et al. 2014). Biodiversity typically displays a non-linear response to urbanisation with the highest levels often present at intermediate levels in the 'suburban' area (Marzluff 2001; Tratalos et al. 2007; McKinney 2008). Taxa richness tends to decrease within the extreme urbanisation found in city and town cores (Marzluff 2001; Chace & Walsh 2006; Clergeau et al. 2006). At more moderate levels of urbanisation (i.e. suburban areas), a mosaic of potential habitat can be found, and here responses to variation differs among taxa (Jones & Leather 2012). A majority of plant studies (65%) found increased species richness in suburban areas, but a minority of invertebrate studies (30%) and fewer studies of non-avian vertebrates (12%) showed this pattern (McKinney 2008).

Moderate levels of human disturbance may promote the coexistence of more species in these cases, with both adaptable successional natives and introduced exotics benefitting from increased habitat heterogeneity at a local level (Zerbe et al. 2003; McKinney 2008; Cox et al. 2016). Given that 64% of invertebrate studies found that species richness decreased as levels of urbanisation moved from low to mid, and by 79% from mid to high levels of urbanisation, this suggests that urbanisation may have important consequences higher up the food chain (McKinney 2008). Nevertheless, 20% of all bird species occur in cities globally, with the highest densities found in Europe, suggesting cities still have significant conservation value despite the threat to biodiversity that urbanisation represents (Aronson et al. 2014).

1.2. Urban green spaces

In the UK, gardens account for 22-27% of urban areas and are a major component of the total green space in cities (Loram et al. 2007). They are home to an estimated 28.7 million trees (just under a quarter of all non-woodland trees), more than 4.7 million bird nest boxes and almost 3.5 million ponds

(Davies et al. 2009). These human-associated habitats hold significant proportions of many native bird populations (Bland et al. 2004; Newson et al. 2005), such as the Common Blackbird *Turdus merula*, the red listed Song Thrush *Turdus philomelos*, Common Starling *Sturnus vulgaris* (Robinson et al. 2005) and House Sparrow *Passer domesticus* (Siriwardena et al. 2002). Around 12.6 million households (48%) actively feed their garden birds (Davies et al. 2009) influencing bird abundance and communities at local and regional levels (Fuller et al. 2008; Galbraith et al. 2015). The level of food provisioning nationally potentially supports a significant proportion of our garden birds and could have numerous unforeseen ecological effects (Orros & Fellowes 2015b).

The value of gardens to wildlife has long been recognised with a myriad of popular books, TV programmes, information leaflets, magazine features advising on how to garden in a ‘wildlife friendly’ way (Goddard et al. 2010). The effectiveness of many of these approaches is questionable but the public’s enthusiasm for garden wildlife is clear (Gaston et al. 2007) and tends to increase with personal knowledge (Evans et al. 2005; Clucas et al. 2015). When considered individually a typical urban/suburban garden is too small to have much ecological value and the division of habitat in this environment makes studying it’s wildlife challenging (Cox et al. 2016), but together their value may be enormous (Goddard et al. 2010).

Aside from the direct conservation value and the research opportunities they represent there are other benefits to urban green spaces and their associated wildlife. Green spaces and increased biodiversity are believed to improve mental wellbeing; increasing happiness and reducing stress (Fuller et al. 2007; Dean et al. 2011; Cox et al. 2017b) though some consider the evidence to be inconclusive (Dallimer et al. 2012; Lovell et al. 2014). Encouraging an interest in garden wildlife is also an important factor in generating interest in conservation more generally in a time of decreased connectivity from the natural world (Pyle 2003; Miller 2005; Cox & Gaston 2016; Cox et al. 2017a) and increased knowledge in turn may yield greater health and well-being benefits (Cox & Gaston 2015). Urban conservation is an area where members of the public contribute enormously to ecological research via citizen science, increasing our understanding and helping to conserve biodiversity (Evans et al. 2005; Cooper et al. 2007; Davies et al. 2009). Therefore, improving the value of gardens for wildlife, especially birds as a charismatic flagship taxa (Walpole & Leader-Williams 2002), will not only benefit those species, but could also in turn improve overall human health and wellbeing (Davies et al. 2009; Dearborn & Kark 2010; Cox & Gaston 2016; Cox et al. 2017b).

1.3. Urban birds

For birds, urban ecosystems can be a habitat to exploit, for those able to adapt (Kark et al. 2007; Evans et al. 2011). Not all species are able to adapt and overall urban avifauna tends to be relatively species-poor, dominated by generalist broad niche species, found at high densities (Evans et al. 2011) with diversity along with adult survival and condition potentially peaking in the intermediate suburban area (Partecke et al. 2006b; McKinney 2008; Evans et al. 2015). Granivores and other birds that consume plant material in their adult diets tend to be favoured (Chace & Walsh 2006; Evans et al. 2011), possibly due to their use of supplementary food (Jokimäki et al. 2002; Fuller et al. 2008). Meanwhile insectivores may be selected against (Chace & Walsh 2006; Kark et al. 2007; Máthé & Batáry 2015; but see Evans et al. 2011), possibly due to the decline in invertebrate diversity with increasing levels of urbanisation (McKinney 2008). There is little evidence for phylogenetic correlation in species success in urban areas, with closely related species such as House Sparrows and Tree Sparrows *Passer montanus* differing markedly in their adaptation to urbanisation in Britain (Evans et al. 2009; Evans et al. 2011). In addition open cup, ground and low nesting birds may be at a disadvantage (Máthé & Batáry 2015), possibly due to increased predation risks (Chamberlain et al. 2009) and/or due to a loss of suitable nesting habitat (Evans et al. 2011).

Aside from directly affecting abundance and diversity, urbanisation has a number of other less obvious effects, particularly on breeding parameters. Urban birds show consistent patterns of earlier lay dates, lower clutch size, lower nestling weight and lower productivity per nesting attempt (reviewed extensively by Chamberlain et al. 2009). The availability of supplementary food compared to rural sites is believed to be an important driver of some of these changes. Supplementary food has been consistently linked to advances in lay dates (Chamberlain et al. 2009; Amrhein 2014), which is generally considered beneficial, at least in more natural habitats (Perrins & Jones 1974; van Noordwijk et al. 1995; Charmantier et al. 2008). However, the exact nature of its effects on avian productivity is unclear (Robb et al. 2008b; Harrison et al. 2010; Plummer et al. 2013a). Environmental factors also play an important role. Increased ambient environmental temperatures associated with the urban heat island effect (Zhang et al. 2010) may be particularly important in advancing lay dates (Chamberlain et al. 2009; Amrhein 2014). One direct mechanism may be by influencing changes in the physiological changes in avian reproductive organs prior to the breeding season (Schaper et al. 2012). Other subtler actions may also affect breeding success and behaviours with factors such as nest construction and parasites rarely considered in the context of urbanisation (Reynolds et al. 2016). The ubiquity of artificial lighting and noise may also play a role in modifying breeding behaviour and timing, influencing territoriality and physiological (hormonal) changes (Kempenaers et al. 2010; Dominoni et al. 2013). Such factors act on traits which show heritable variation (Schaper et al. 2012) which may lead to selection and/or drift resulting in population level differentiation between urban and rural areas. Urban birds typically exhibit high levels of boldness and lower stress responses than rural conspecifics and such traits are believed to be heritable (Rebolo-Ifrán et al. 2015; Abolins-Abols et al. 2016). As well as the ability to potentially exploit novel resources and habitats more swiftly (Atwell et al. 2012; Charmantier et al. 2017), it also may allow urban males to maintain higher levels of territorial behaviour under acute stress compared to rural conspecifics (Abolins-Abols et al. 2016).

This potentially increases their breeding success in stressful conditions allowing birds to retain territory and mate in the face of frequent disturbance and thus the heritability of these traits in urban populations (Abolins-Abols et al. 2016). However, direct evidence for such an environmental effect on breeding success is weak (Partecke et al. 2006a) and may partially depend on other factors, such as dispersal, migration and other behavioural and environmental factors (Björklund et al. 2010; Delaney et al. 2010; Kekkonen et al. 2011; Plummer et al. 2015).

While supplementary food is typically of benefit to adult birds (Robb et al. 2008a), supplementary food is rarely appropriate for the nestlings of these species (Cowie & Hinsley 1988). With the decline of invertebrate diversity with increasing urbanisation (McKinney 2008; Jones & Leather 2012) it seems likely that the supply of such natural food will decline leading to decreases in breeding success. Indeed some authors find indications of increased starvation rates and lower chick survival rates due to lack of natural invertebrate food in urban areas (Perrins 1965; Cowie & Hinsley 1987; Solonen 2001). This may in turn be linked to advances in breeding phenology caused by supplementary food and/or the environment, leading to a phenological mismatch between reproduction and peak natural food availability (Visser et al. 2012; Reed et al. 2013a; Reed et al. 2013b).

Predation may also play a role in the decline in breeding success as well as changes in bird diversity and abundance with urbanisation. Potential nest predators such as corvids can increase in density (Antonov & Atanasova 2003; Sorace & Gustin 2009; Madden et al. 2015) and open cup nesting birds are particularly vulnerable to nest predation (Ricklefs 1969; Martin & Li 1992). While it is unclear if these increases in nest predator density directly depress prey abundance (Shochat 2004; Madden et al. 2015) open cup nesters do decline in abundance with increasing urbanisation suggesting there may be a link (Jokimäki & Huhta 2000; Máthé & Batáry 2015). The fact that many of these potential nest predators directly compete for and benefit from supplementary feeding, particularly the invasive Grey Squirrel *Sciurus carolinensis* in the UK (Bonnington et al. 2014c; Bonnington et al. 2014a) may play an additional role in the decline in urban bird breeding success. This is in addition to the threat of the urban areas most abundant predator, the Domestic Cat *Felis catus*, occurring at exceptionally high densities far beyond what could be supported naturally (Baker et al. 2008; Sims et al. 2008). Globally they are concentrated in urban areas and kill billions of prey items annually (Thomas et al. 2012; Blancher 2013; Loss et al. 2013).

Isolating these various effects in the urban area itself is difficult given the complex interwoven nature of this anthropogenic environment. However, despite the challenges birds face, urban areas hold large populations of many species (Bland et al. 2004; Cannon et al. 2005) exploiting the vast potential resources available. Although our knowledge has increased dramatically in recent years (Marzluff et al. 2001; Chace & Walsh 2006; Marzluff 2017) better understanding of the interplay between the myriad of factors influencing urban bird populations is key in our efforts to build opportunities for bird and wildlife conservation in our towns and cities (Murgui & Hedblom 2017).

1.4. Supplementary Feeding

1.4.1. Scale and extent

Garden bird feeding is the most important way for people to engage with wildlife in many parts of the world (Cox & Gaston 2016). Some 48% of households in Britain (Davies et al. 2009), 47% in New Zealand (Galbraith et al. 2014) and 53 million (~42%) households in the USA feed wild birds (US Fish and Wildlife Service 2014), providing an enormous and highly localized additional food resource. For example, in suburban Reading, UK, where the majority of the research for this thesis was carried out, over 55% of householders provide supplementary food for wild birds, enough to support a minimum of 131, 750 individual birds, based on the energy requirements of the UK's 10 commonest bird species utilising bird feeders in gardens (Orros & Fellowes 2015b). Across the UK more generally the minimum estimated provisioning rate (101 kcal/garden/day) could hypothetically support 31 million of these 'average birds' with the median (628 kcal/garden/day) supporting as many as 196 million 'average' individuals (Orros & Fellowes 2015b). Given the estimated UK total breeding population of these 10 species is 71.1 million individuals, supplementary food could be significantly supporting their national populations.

Birds from families as diverse as hummingbirds (Hill et al. 1998; Courter et al. 2013) and raptors (Orros & Fellowes 2014; Orros & Fellowes 2015a) may benefit from supplementary food provided in urban areas, but the main targeted beneficiaries of most supplementary feeding stations are typically seed-eating and omnivorous passerines (Cannon et al. 2005; Chamberlain et al. 2005; Horn et al. 2014). Some species may also benefit more than others due to the suitability of food provided (Robb et al. 2011; Horn et al. 2014) and relative competiveness and adaptability of some species (Evans et al. 2009; Evans et al. 2011). This supplementary resource is believed to be particularly important in urban areas where natural resources such as invertebrates and mature trees may be relatively scarce (Chace & Walsh 2006; McKinney 2008) and feeders will be abundant due to the concentration of the human population.

In temperate climates feeder use by wild birds is likely to peak in midwinter when energy demands simply to survive are highest (Chamberlain et al. 2005) though the specific peak point can vary between individual species (Siriwardena et al. 2008). As such feeding effort is generally concentrated at this point in the Northern Hemisphere with the intention to support bird populations (Orros & Fellowes 2015b). Providing food generally but particularly at this time of year when birds most use it provides an important connection between people and wildlife (Cox & Gaston 2015; Cox & Gaston 2016; Cox et al. 2017a).

Positive associations between supplementary feeding, breeding population size and reproductive success have been documented (Fuller et al. 2008; Robb et al. 2008b), although this is not always the case (Harrison et al. 2010; Plummer et al. 2013a). Combined with interlinking changes to productivity and survival, supplementary feeding directly and indirectly affects the structure of bird communities, particularly in the urban area (Galbraith et al. 2015).

1.4.2. Adult body condition and survival

Aside from the pleasure many people gain from feeding wild birds, the primary motivation for providing supplementary food is arguably to improve bird survival, though separating out effects on small mobile birds is challenging (Robb et al. 2008a). Generally it appears that supplementary feeding improves fledged bird body condition and so their survival (Boutin 1990). In Ohio, USA, supplementary food was found to increase body condition, as indicated by the faster regrowing of feathers in several species (Grubb & Cimprich 1990). Body condition for individual birds was found to be generally improved over a three year period of continuous feeding compared to unfed sites in central Illinois, USA, on forest sites with the difference disappearing by 10 months after the cessation of feeding (Wilcoxen et al. 2015). Higher survival probabilities among supplemented populations has been detected in species such as Willow Tits *Parus montanus* and Crested Tits *Lophophanes cristatus* (Jansson et al. 1981), Great Tits *Parus major* (Källander 1981; Orell 1989), Varied Tit *Parus varius* (Nakamura & Kubota 1998), Black-capped Chickadees *Poecile atricapillus* (Brittingham & Temple 1988; Desrochers et al. 1988; Egan & Brittingham 1994), and Carolina Chickadees *Poecile carolinensis* (Doherty & Grubb 2002). These examples come from the Paridae (Tit) family, perhaps indicating why some species are considered strong urban adaptors (Chamberlain et al. 2004; Cannon et al. 2005; Chamberlain et al. 2005; Evans et al. 2011) or that this pattern may simply reflect a sampling bias. However, evidence of higher condition/survival has been found in other groups too, although few studies have found direct links between supplementary food and adult survival (Rogers & Heath-Coss 2003).

However, other studies have found conflicting evidence or no differences in body condition and/or survival associated with bird feeding in several species. For example, evidence has been found for an increase in body condition and by proxy, survival, in Downy Woodpeckers *Picoides pubescens* (Grubb & Cimprich 1990), while later studies found no significant difference in survival (Doherty & Grubb 2002) or apparent nutritional state (Doherty et al. 2003). In the same studies no difference was found in White-breasted Nuthatches *Sitta carolinensis* or Tufted Titmice *Baelophus bicolor* survival (Doherty & Grubb 2002), although the Nuthatches did show evidence of a decline in condition (Doherty et al. 2003). There are also examples of decreases in survival, with one study in Canada finding that Song Sparrows *Melospiza melodia* had lower survival rates if feeding stations were present in their territories, despite positive effects on reproductive success (Arcese & Smith 1988). In the case of urban birds there is evidence from House Sparrows that birds born in urban areas may be of significantly lower quality then rural born individuals, indicating lower survival rates generally, even with an almost *ad libitum* food supply (Liker et al. 2008).

Even if birds in wild habitats are able to gain higher body masses from supplementary feeding (Boutin 1990) such increased condition associated with higher body fat stores may also bring disadvantages. Heavier individuals may place themselves at increased predation risk due to slower take-off speeds, necessitating a trade-off that changes with energy requirements and perhaps explaining why body condition may not change as much as expected in the presence of supplementary food (Lima 1986; Cresswell 2008; Bonter et al. 2013; Rogers 2015).

Isolating such complex interacting effects in a Western urban setting can be difficult considering the ubiquitous nature of supplementary feeding in such landscapes combined with the mobility of birds and difficulty of detecting mortalities in the general environment.

1.4.3. Density and distribution

A combination of immigration, emigration and changes in survival will determine the effects of supplementary feeding on bird density both in and outside of the breeding season (Newton 1998; Amrhein 2014). A number of studies have found supplementary feeding to be associated with higher densities of birds in urban areas, possibly resulting from higher survival rates (Chamberlain et al. 2005; Fuller et al. 2008). More broadly the evidence is mixed (Newton 1998) but any effects will likely lead to changes in the bird community structure in an area (Galbraith et al. 2015).

If birds provided with supplementary food are able to successfully breed on smaller territories, then the total number of potential territories in a given area could be increased (Enoksson & Nilsson 1983; Roth & Vetter 2008; Amrhein 2014). However, such increases in density may depress individual breeding success even with supplementation, possibly due to the lack of insects in smaller habitats, or increased rates of territorial conflicts associated with access to feeders (Jansson et al. 1981; Maher & Lott 2000).

On the broader scale supplementary food may be responsible for some large-scale changes in bird population dynamics and migration strategies (Robb et al. 2008a). The northwards expansions in North America of the breeding populations of hummingbirds (Hill et al. 1998; Courter et al. 2013), Northern Cardinals *Cardinalis cardinalis,* and American Goldfinches *Carduelis tristis* (Morneau et al. 1999; Robb et al. 2008a) are prime examples of this effect. It may also lead to overwintering populations of birds occurring further north than usual (Jokimäki et al. 1996) or concentrated in specific areas (Tryjanowski et al. 2015). It can also provide a buffer against natural resource variation on a shorter time scale, for example in winters with poor UK Sitka Spruce *Picea sitchensis* cone crops Eurasian Siskins *Carduelis spinus* and Coal Tits *Periparus ater* tend to utilise garden bird feeders more frequently (McKenzie et al. 2007). Similarly Chamberlain et al. (2007) found a larger number of species utilised UK garden feeders more in years of poor beech mast crops, possibly buffering the effects of reduced natural food supplies (van Balen 2002).

Perhaps the most dramatic change in a bird's distribution linked to supplementary feeding is that seen in the migratory and physiological adaptations of German populations of the Eurasian Blackcap *Sylvia atricapilla*, with increasing numbers wintering in Northwest Europe rather than the Mediterranean and North Africa (Rolshausen et al. 2009; Plummer et al. 2015). Such changes may represent a selective advantage, allowing birds to be closer to their breeding grounds in the spring to claim the best territories and commence breeding earlier (Tryjanowski et al. 2013) and over time drive genetic separation between populations of the same species (Plummer et al. 2015).

Such adaptation may be risky if populations influenced by this provisioning become overly dependent and expand to sizes that can no longer be supported by the local natural resources (Orell 1989), possibly representing an ecological trap if the resource were to suddenly be dramatically reduced or withdrawn (Robb et al. 2008a). Few studies have explored this, but the survival rates of Black-capped Chickadees following the cessation of long term feeding did not differ from those of Chickadees in areas where no feeders had been present (Brittingham & Temple 1992) and similar results were found with Blue Tits *Cyanistes caeruleus* and Great Tits (Cowie & Hinsley 1988), suggesting they had not become over-reliant. However, lower survival was detected in Willow Tits (Jansson et al. 1981) and Song Sparrows (Arcese & Smith 1988), while Wilcoxen et al. (2015) found health status in Black-capped Chickadee, Gray Catbird *Dumetella carolinensis*, Indigo Bunting *Passerina cyanea*, Northern Cardinal and Tufted Titmouse returned to the pre-supplementary level.

1.4.4. Productivity

Carry-over effects from consumption of non-natural food resources in the winter may alter the body condition of individuals in ways that affects their performance in the subsequent breeding season (Harrison et al. 2011). Supplementary feeding may cause earlier egg laying (Harrison et al. 2010) and increased fledging success (Arcese & Smith 1988; Svensson & Nilsson 1995; Robb et al. 2008b), improved egg quality (Blount et al. 2002; Reynolds et al. 2003), increased clutch size (Rooney et al. 2015) and survival (Brittingham & Temple 1988; Norris 1993). Across 59 studies reviewed by Robb et al. (2008a) covering a wide variety of bird families, 64% found an increase in fledging success with supplementary feeding, with all but three of the remaining studies finding no significant effect.

Much of the supplementary food provided is not directly appropriate for passerine chicks which primarily require invertebrate food. Typically it either influences adult breeding condition before the breeding season or may make satisfying their own energy requirements easier for adults in the breeding season, allowing them to spend less time foraging or more time to forage for food for nestlings (Dawson & Bortolotti 2002; Grieco 2002; Robb et al. 2008b). More specialised feeding effort such as through the provision of mealworms (*Tenebrio molitor*) has been found to directly increase nestling condition in Great Tits (Bańbura et al. 2011), recruitment into local breeding population in Pied Flycatchers (Verhulst 1994) and overall breeding success in House Sparrows (Peach et al. 2013).

However, evidence of a positive carry-over effect on subsequent life-history stages in species of birds frequenting garden feeding stations is more mixed. During the breeding season, supplementary feeding can lead to a reduction in average clutch and brood size in Great Tits and Blue Tits, and reduced hatching success in the latter following overwinter supplementation (Harrison et al. 2010). Plummer et al. (2013a) reported a reduction in reproductive success in Blue Tits supplemented over winter with fat, documenting reduced mean offspring weight, size and survival in comparison to control nests. Further investigation by the authors suggested that fat provisioning did not supply the required storable dietary micronutrients for egg production such as vitamin E, and so impaired productivity (Plummer et al. 2013b; Plummer et al. 2013a) Interestingly Crates et al. (2016) who unlike others was able to directly quantify the use of feeders by parents prior to the breeding season, found no strong influence of individual feeder use on the following breeding season productivity in Blue Tits and Great Tits.

If as suggested above, more birds survive to breed in areas with supplementary feeding (Robb et al. 2008a) then it appears likely that more poor quality individuals attempt to breed with a correspondingly lower success rate (Plummer et al. 2013a; Crates et al. 2016). This combined with the suitability of supplied nutrients (Plummer et al. 2013b) may explain drops in individual productivity with supplementary feeding even if a larger, denser breeding population can be supported.

Many of these reported effects on productivity are similar to those linked to urbanisation more generally, possibly suggesting a connection with both advances in breeding phenology and reductions in per brood breeding success (Chamberlain et al. 2009). However, isolating such an effect in the urban area is difficult and other multi-linked factors may play a role in influencing urban bird breeding success, such as the potential for nest predation discussed below.

1.4.5. Predation

It has been informally suggested that supplementary feeding stations may unintentionally attract in predators to prey directly on birds using them (Dunn & Tessaglia 1994; Rogers & Heath-Coss 2003). However, empirical evidence for this link is limited and the mobile nature of both predators and prey make investigation on any scale difficult (Dunn & Tessaglia 1994; Roth & Lima 2007b; Roth & Lima 2007a). Rogers & Heath-Coss (2003) found that predation rates on seven species of songbird by Cooper's Hawk *Accipiter cooperi* and Sharp-shinned Hawk *A. striatus* were no higher in an area supplied with supplementary food, compared with control (unfed) sites. As suggested above there may be an indirect effect on the body condition of birds using feeders where they are forced to trade off the increased risk of predation linked to higher weights with the risk of starvation, particularly in harsh conditions, (Lima 1986; Cresswell 2008; Rogers 2015). The reduced time needed to spend foraging with the provision of a reliable food source (Roth & Vetter 2008; Roth et al. 2008) and the increased collective vigilance by concentrations of birds under the many eyes hypothesis (Lima & Dill 1990; Roberts 1996) may also mitigate against the predation risk around supplementary feeding stations (Robb et al. 2008a). In addition, it is logical to suggest our perception of predation rates around supplementary feeding stations may be skewed by the fact that we are simply more likely to witness predation around as this is where many people primarily watch birds.

However, there is evidence predation may also occur indirectly around supplementary feeders. Predation is a key cause of breeding failure, particularly for open-cup nesters (Ricklefs 1969; Martin & Li 1992), which may limit their populations in urban areas while still being present (Jokimäki & Huhta 2000; Máthé & Batáry 2015). As suggested above, some nest predators may have higher densities in urban areas, such as corvids (Jokimäki & Huhta 2000; Antonov & Atanasova 2003; Jokimäki et al. 2005; Sorace & Gustin 2009), although it is unclear if this apparent increase actually depresses prey populations (Shochat 2004; Madden et al. 2015). Nest predators such as Eurasian Magpies *Pica pica* and introduced Grey Squirrels (discussed in more detail later) are common in UK urban areas including at garden feeding stations (Chamberlain et al. 2005; Väisänen 2008; Bonnington et al. 2014b) and are frequent nest predators (Eaton et al. 2013; Bonnington et al. 2014a). Increased nest predation in an urban area has been associated with increased corvid density, but not so far with Grey Squirrels (Bonnington et al. 2015).

At a domestic garden scale the provision of bird feeders reduces the local abundance of insects apparently through increased local predation by birds attracted to the bird feeders (Orros & Fellowes 2012; Orros et al. 2015), a fact that most people putting out supplementary food are unlikely to consider. Similarly the provision of supplementary food for ungulates (Cooper & Ginnett 2000; Selva et al. 2014), vultures (Cortés-Avizanda et al. 2009) and woodland predators (Borgmann et al. 2013) has been linked to increased local nest predation. In each case the supplementary food appears to attract predators, including non-target species, to a point source, which in turn foraged locally on other prey. This suggests that the presence of a reliable or high quality food resource both increases the number of potential nest predators and the time they spend foraging near the food source which was confirmed by recent research (Malpass et al. 2017). It is not known if large scale supplementary feeding increases the risk of local nest predation in urban and suburban habitats but given its near ubiquity in urban areas, it appears likely that if this effect is replicated around garden feeders with bird nests then we may be encouraging local nest predation. This is particularly important as we may also be inadvertently supporting nest predatory populations with supplementary feeding (Chamberlain et al. 2005; Väisänen 2008; Bonnington et al. 2014b). In response, if access to supplementary feeders is restricted to only target species we may be able to both reduce the support of non-target species populations and their negative effects.

1.4.6. Pathogen transmission

There are other risks associated with supplementary feeding as supplementary food sources may potentially represent an important source of pathogen transmission to both wildlife and from them to humans (Benskin et al. 2009; Lawson et al. 2014). Pathogen transmission is generally believed to be density dependent (Anderson & May 1992) so a higher concentration of infected and susceptible individuals increases the risk of spread through direct and indirect contact (Benskin et al. 2009; Murray et al. 2016). Such density increases are most likely to occur in winter (Chamberlain et al. 2005; Chamberlain et al. 2007), when immunity is likely to be compromised (Nelson & Demas 1996). Such effects may be magnified by reduced natural resource availability in urban areas, which acts to further increase effective densities (Jones & Reynolds 2008). Therefore supplementary feeding may increase the risk of pathogen transmission if present in local bird populations (Kirkwood 1998; Pennycott 1998; Pennycott et al. 2002).

Much of the recent UK research at a national level has taken place under the wide ranging Garden Wildlife Project (Garden Wildlife Health 2014) and its predecessor the BTO Garden Bird Health initiative, although further research is required particularly at a local level. Different species are affected by different diseases. For example Trichomonosis (*Trichomonas gallinae*) has severely affected some finch populations (Robinson et al. 2010; Lawson et al. 2012b), and Avian Pox is prevalent in Great Tits, reducing survival rates and often leading to death (Lawson et al. 2012a). Diseases such as Salmonella (*Salmonella enterica*) which is widely recorded in wild birds are of particular interest both as a cause of garden bird mortality and source of human infection (Tizard 2004; Lawson et al. 2014). Gregarious granivorous passerines are particularly prone to infection by the subspecies *enterica* serovar Typhimurium phage types 40, 56(v) and 160 (Lawson et al. 2014) though the pathogen is highly host adaptable with the ability to infect various animal types including humans and our companion animals (Tauni & Österlund 2000; Rabsch et al. 2002). Most recorded UK passerine outbreaks have occurred at and around feeding stations. Spatial and temporal outbreak patterns, as well as pathogen isolates, match human outbreaks, suggesting that garden feeding places are likely to be sites of public exposure to infected/dead birds and their faeces (Lawson et al. 2014). Infection has also been recorded in pet cats in an outbreak area, presumably due to the cats hunting birds (Tauni & Österlund 2000). The overall importance of garden birds as a reservoir for *S. e. typhimurium* infection is small (Rouffaer et al. 2016) with the strain only accounting for 0.2% of all salmonella and 1.6% of *S. e. typhimurium* human cases in the UK (Lawson et al. 2014). Virulent forms of *E. coli* can also be readily carried by garden birds and while there are currently no known direct links between outbreaks in garden birds and humans, a plausible threat does exist (Foster et al. 2006; Hughes et al. 2009).

Zoonotic pathogens are of particular interest with wild birds potentially acting as reservoirs for diseases such as avian influenza (Kilpatrick et al. 2006), West Nile Virus (Rappole et al. 2000), *Campylobacter* (Abulreesh et al. 2006; Weis et al. 2016), *Salmonella typhimurium* (Lawson et al. 2014) and pathogenic *Escherichia coli* (Foster et al. 2006). *Salmonella typhimurium* as discussed represents a prime example of the potential for risks to human health with the same strain being detected in wild bird and human outbreaks in the same geographical area (Lawson et al. 2014), though the relative importance of such a threat (at least in this case) may be small (Rouffaer et al. 2016).

Although interest has increased in recent years with the spread of bird population-threatening pathogens (Dhondt et al. 1998; Lawson et al. 2012b) and zoonotic pathogens passing from wildlife to humans (Benskin et al. 2009; Murray et al. 2016), we still know relatively little about the direct spread of pathogens and other bird associated microorganisms at garden bird feeding stations.

1.5. Nest boxes

1.5.1. Nest boxes as a resource

Aside from the widespread provision of supplementary food, other resource and habitat provisioning may also help support some urban bird populations, with anthropogenic bird nest boxes potentially being a key resource. The UK has an estimated 4.7 million bird nest boxes in gardens alone, equating to at least one nest box for every six breeding pairs of cavity nesting birds (Davies et al. 2009). The availability of suitable nesting sites limits the breeding density of birds (Newton 1998) and the availability of natural cavities in particular is likely to be reduced in urban areas due to the removal of mature and dead trees (Wiebe 2011). Cavities in buildings may partially compensate for this but modern and refurbished houses tend to have fewer potential nesting cavities (Mason 2006; Shaw et al. 2008). As a result this widespread provision of artificial nest sites in urban areas may be a particularly valuable resource (Chace & Walsh 2006; Wiebe 2011) and also opens up the opportunity to investigate factors affecting urban bird breeding biology.

1.5.2. Nest construction and parasitism

As discussed above, urbanisation profoundly affects bird productivity. Such changes may be influenced by the birds' nests themselves, with the potential alteration of nest construction and parasite loads associated with urbanisation occurring through a number of mechanisms (Reynolds et al. 2016). Changes in ambient air temperature linked with the urban heat island (UHI) effect may cause nests from more highly urbanised areas to need less insulation and so require less energy investment to build (Deviche & Davies 2014). Material availability may also change, with some key natural nesting materials becoming rarer (McKinney 2008), while the availability of potentially suitable anthropogenic materials increases. Depending on behavioural preferences and their chosen nest site, this may force some birds to expend more energy finding suitable natural nesting material or they may utilise whatever is readily available (Britt & Deeming 2011) and so with higher urbanised levels incorporate more anthropogenic material (Reynolds et al. 2016). Given the high insulation value of some anthropogenic materials, they may even be preferred (Surgey et al. 2012).

Any changes in nest construction in turn may influence invertebrates living in nests. Although the influence of nest construction on ectoparasite load has been explored in a number of studies (Moreno et al. 2009; Suárez-Rodríguez et al. 2013) so far only one has occurred in the urban environment (Reynolds et al. 2016). Generalist nest-dwelling ectoparasites are common in passerine nests (Moreno et al. 2009; Cantarero et al. 2013) and may influence reproductive success in a number of ways. They most obviously impact nestling growth and survival (Merino & Potti 1995), though they may also affect adult health (Tomás et al. 2007). Nest composition can influence ectoparasite larval mortality and growth through effects on nest humidity (Heeb et al. 2000) or through the attraction/repellence properties of the nest materials themselves (Remeš & Krist 2005; Mennerat et al. 2009a; Tomás et al. 2012). In addition to ectoparasites, bird nests are home to an array of other arthropods, some of which will prey on these ectoparasites (Tryjanowski et al. 2001). Few published studies have considered the influence of nest construction on this diversity and in turn its effect on ectoparasite load. The influence of urbanisation on this diversity and any associated interactions with productivity is unknown.

1.6. Competition and predation

1.6.1. Invasive birds

Invasive non-native species are of concern around the world (Sakai et al. 2001) and in urban areas many utilise supplementary feeders intended for native birds. The Rose-ringed Parakeet *Psittacula krameri*, is an invasive species of importance to UK and European urban areas (Strubbe & Matthysen 2009; Pârâu et al. 2016). Although spreading slowly they are most commonly associated with urban areas and supplementary feeding may sustain their populations in temperate Europe (Strubbe & Matthysen 2009; Clergeau & Vergnes 2011). Elsewhere in Europe and locally in the UK the Monk Parakeet *Myiopsitta monachus* has also been introduced (Strubbe & Matthysen 2009; Tayleur 2010). Quite how damaging these species are is still unclear (Newson et al. 2011) but they have the potential to competitively exclude native species from both food and nest sites (Strubbe et al. 2010; Czajka et al. 2011; Peck et al. 2014). Although data is still lacking, they have probably spread beyond realistic possibilities of control, even with drastic management action, particularly if they take advantage of warming conditions associated with climate change (Strubbe & Matthysen 2009; Tayleur 2010; Pârâu et al. 2016).

1.6.2. Grey Squirrels

In the UK, the most visible invasive species at supplementary feeding stations is the Eastern Grey Squirrel (hereafter the Grey Squirrel). Grey Squirrels were deliberately introduced into different parts of Europe on several occasions (Bertolino et al. 2008). In Britain the Grey Squirrel is common in urban areas (Baker & Harris 2007; Bonnington et al. 2014a), and is spreading rapidly in other parts of Europe (Bertolino et al. 2008). They are a significant conservation threat, particularly to the native Red Squirrel *Sciurus vulgaris* (Bertolino et al. 2014); Grey Squirrels carry disease (squirrel pox, Bruemmer et al. 2010; *Borrelia burgdorferi*, the cause of Lyme disease, Millins et al. 2015, Millins et al. 2016), and cause economic losses in forestry (Mayle & Broome 2013).

The population size and density of urban Grey Squirrels is strongly associated with the provision of supplementary food in gardens (Bowers & Breland 1996; Parker & Nilon 2008) and there is some evidence that they can competitively exclude birds at supplementary feeders (Hewson et al. 2004; Bonnington et al. 2014b). However, we have little quantitative data on how the presence of Grey Squirrels affects feeder usage by garden birds, nor how much of the food provided is taken by the squirrels though it has the potential to support a considerable proportion of the UK population (Orros & Fellowes 2015b). Even if they take only 10% of available supplementary food at UK garden feeding stations that has the potential to support ~1 million individual Grey Squirrels even at the lowest estimated supplied energy levels (Orros & Fellowes 2015b) and the last British population estimate was only ~2.5 million individuals (Harris et al. 1995; Battersby 2005) though they are likely to have increased considerably since (Aebischer et al. 2011). This is particularly relevant in urban bird conservation, as the Grey Squirrel is both a direct competitor for supplementary resources and a nest predator, and so may locally directly and indirectly affect the populations and breeding success of some native bird species (Newson et al. 2010; Bonnington et al. 2014c).

1.6.3. Domestic Cats

Domestic Cats are a common predatory component of urban ecosystems across the globe. They represent one of the greatest single threats to global biodiversity (Nogales et al. 2004; Loss et al. 2013), and are implicated as the leading risk to over 8% of threatened reptiles, birds and mammals (Medina et al. 2011; Doherty et al. 2016). As companion animals they reach high densities in urban areas, far beyond what could be naturally supported (Baker et al. 2008; Sims et al. 2008; Thomas et al. 2012).

In the UK there are more than 10 million individual pet cats (Murray et al. 2010) and more than 800,000 feral cats, outnumbering all other mammalian predators combined several times over (Harris et al. 1995; Battersby 2005). Predation studies suggest Domestic Cats take over 180 million prey individuals annually (55 million birds, 119 million mammals) in the UK (Thomas et al. 2012) with even greater numbers running into the billions being taken annually in the far larger USA and Canada

(Blancher 2013; Loss et al. 2013). This makes cats one of the most important anthropogenic causes of bird mortality in North America and likely elsewhere (Loss et al. 2015). Even without direct predation, their mere presence may depress wild bird populations and how they interact with the supplementary resources we supply is unknown (Beckerman et al. 2007; Bonnington et al. 2013).

Whether this large scale predation has population level consequences for prey remains controversial (Baker et al. 2005; Baker et al. 2008; McDonald et al. 2015). However, given the enormity of these estimates and the spread of global urbanisation bringing more cats into biodiverse areas (Morgan et al. 2009; McDonald et al. 2015) the precautionary principle suggests that we should act to mitigate cat predation (Lilith et al. 2006; Calver et al. 2011). One proposed management response to reduce potential cat predation is to introduce buffer zones around areas of greater conservation value, with housing development prevented or at least cat ownership restricted within a set distance of the protected area (Lilith et al. 2006; Lilith et al. 2008; Metsers et al. 2010; Thomas et al. 2014).

Such buffer zones have been proposed to keep cats away from protected areas (Metsers et al. 2010) with cat-free buffer zones of 300-400 m between housing developments and areas of higher biodiversity value suggested for Australia (Lilith et al. 2008) and the UK (Thomas et al. 2014). Australia has led the way in the use of buffer zones, combined with other management techniques such as the removal of feral cats (Lilith et al. 2008; Denny & Dickman 2010; Dickman & Newsome 2015). Similarly in the UK 400 m buffer zones to prevent construction have been introduced around the Thames Basin Heaths Special Protected Areas (SPAs) to protect fragile habit and its wildlife populations (Thames Basin Heaths Joint Strategic Partnership Board 2009). Such cat exclusion zones could be incorporated into development planning near protected areas elsewhere but must be scaled appropriately to the landscape for effective management, as what is appropriate in one geographical area or habitat may not be appropriate in another (Metsers et al. 2010; Hall et al. 2016b). Social attitudes play an important role in the acceptability and practicality of such management actions (Thomas et al. 2012; Toukhsati et al. 2012; Hall et al. 2016a) and there are still questions over the effectiveness of some actions short of simply keeping all cats indoors (Denny & Dickman 2010). In particular urbanisation may play an important role in modifying cat ranging though few direct comparisons have been made with cats on the edge of the urban areas perhaps presenting the biggest threat to biodiversity (Metsers et al. 2010; van Heezik et al. 2010; Thomas et al. 2014; Hall et al. 2016b).

1.7. Thesis rational, aims and objectives

The success (or otherwise) of urban birds is tightly linked to decisions made by people. We provide direct help to some species as we choose what to feed and who to feed, and offer nesting opportunities directly through specialised nest boxes and indirectly through planting. At the same time, we do things that may have negative effects, either inadvertently, or through active decisions by supporting species such as the Domestic Cat. In this thesis, I address gaps in our knowledge of urban birds, emphasising the unexpected consequences of how we choose to interact with wildlife. My hope is that the answers to these questions will help improve how we interact with urban wild birds, to their benefit and ours.

The general intention of this thesis is to investigate the role of supplementary resources in influencing urban bird populations. Supplementary feeding as already discussed is perhaps the key way we intentionally influence urban birds and hence was the primary focus of this research. However, despite its ubiquity and the general assumption that it is beneficial, we still lack knowledge and confirmation of some of its possible unintentional side effects. It clearly has the potential to attract and support high densities of competitive and potentially predatory species but little has been done to quantify this and test if and how it effects the target bird species we want to support. Chapter 2 sought to quantify the effect of larger non-target species using supplementary feeders on small target bird species, with a focus on the Grey Squirrel as a common introduced competitor in UK urban ecosystems. While Chapter 3 built on this to examine possible links between supplementary feeding and local nest predation as many of the larger competitive species are also known nest predators. Chapter 4 investigated the importance of an additional unintended effect of supplementary feeding, that of the possibly increased probably of pathogen transmission due to the unnatural concentrations of animals at feeding stations using a novel technique. Meanwhile Chapter 5 focuses on artificial nest boxes, an additional supplementary resource we supply to urban birds. It investigates the nests and productivity of the birds that use them in the context of urbanisation in the hopes of shedding new light on the causes of changes in bird productivity across the urbanisation gradient. Chapter 6 was initially conceived to investigate if cats frequented gardens and other areas containing supplementary feeders and thus potentially affected their usage. Any associations could indicate another unintentional link between supplementary feeding and predation as well as factors effecting cat roaming behaviour. However, this component was unsuccessful and instead this Chapter 6 was devoted to examining the effects of urbanisation on cat roaming and the potential management implications of this major ‘unnatural’ predatory species.

Study location

The purpose of this study is to address some of our gaps in knowledge identified above, by investigating the effect of human activity on birds using the area in and around the large town of Reading, South East England (51^{o}27’N, 0^{o}58’W). Including its contiguous suburbs the Greater Reading area covers approximately 72 km^{2} with a population of ~290 000 people in c. 96 000 households (Office for National Statistics 2013; following Orros & Fellowes 2015b). Some additional data collection was carried out on rural sites immediately outside this area for Chapters 5 and 6.

In the following research chapters I ask:

1. If the use of supplementary feeding stations by Grey Squirrels affects resource availability for wild birds?
2. If the provision of supplementary food during the breeding season increases the likelihood of nest predation in the vicinity of bird feeders?
3. If there is an association between the bacterial pathogens found on bird feeders and the assemblage of species visiting them, as determined by food type and feeder design?
4. How urbanisation affects nest construction of two urban passerines (Blue Tit, Great Tit), if this affects the invertebrate assemblage found within, and if these factors influence breeding success?
5. If degree of urbanisation affects the ranging behaviour of predatory Domestic Cats and what the possible management implications are for urban and peri-urban bird conservation?

Chapter 2: Been caught stealing: Introduced Grey Squirrels subvert supplementary feeding of suburban wild birds

Submitted to Landscape and Urban Planning

2.1. Abstract

Globally, feeding wild birds is perhaps the most widespread intentional interaction between people and wildlife. In the UK, around half of households provide supplementary food for wild birds, frequently in the form of peanuts and mixed seed supplied in hanging feeders. Such food is taken by non-target species including the introduced and highly invasive Grey Squirrel. Grey Squirrels are thought to exclude birds from feeders, reducing the potential benefits of supplementary food to wild birds, while gaining access to large volumes of high quality resources. Nevertheless, direct empirical evidence of the consequences of Grey Squirrel presence at feeding stations is limited. We used camera traps to record the numbers of animals visiting feeding stations in suburban gardens. We asked if exclusionary guards (to prevent access by Grey Squirrels but not small birds) and food type (peanut, mixed seed) affected feeder use. We recorded 24825 bird and 8577 Grey Squirrel visits. The presence of Grey Squirrels on a feeding station almost completely prevented birds from feeding at the same time (>99.99%) and reduced the amount of food available to birds through both behavioural exclusion and consumption by >40%. Squirrel usage, food type and guard status all influenced bird activity and timing of feeder use, although responses varied among species. We suggest that the provision of food for wild birds may inadvertently be benefitting Grey Squirrels, with negative consequences for other species, and that the use of guarded feeders will reduce this effect.

2.2. Introduction

We now live in an urban world. Globally, over half of people live in urban areas (UN 2011), and in the developed world such as the UK and USA, this rises to over 80% of national populations (UNPFA 2007). Urban areas are extremely altered, novel ecosystems, where native species face challenges and opportunities unlike any other. For birds, our most visible animal neighbours, urban ecosystems can be a place to exploit for urban adapters (Kark et al. 2007; Evans et al. 2011), in part due to the very high volumes of supplementary food (Davies et al. 2009; Orros & Fellowes 2015b) and numbers of artificial nest sites (Gaston et al. 2005; Davies et al. 2009) provided by human residents. Conversely, urban ecosystems can be highly challenging, as urban areas have exceptionally high densities of predators, such as the Domestic Cat (Thomas et al. 2012), and introduced competitor/predator species such as the Grey Squirrel (Bonnington et al. 2014a; Bonnington et al. 2014c). Understanding the interplay between such factors and bird abundance and diversity must be a key link in our efforts to build opportunities for bird conservation in our towns and cities.

Urban areas hold large populations of many bird species (Bland et al. 2004; Cannon et al. 2005), and for some species suburbia provides a refuge for declining populations (e.g. the UK Red listed Song Thrush*;* Gregory & Baillie 1998). While there is evidence of an increasing disconnection between people and nature (Miller 2005), garden bird feeding is perhaps the most important way for people to engage with wildlife in many parts of the world (Cox & Gaston 2016). Some 48% of households in Britain (Davies et al. 2009) and 53 million households in the USA feed wild birds (US Fish and Wildlife Service 2014), providing an enormous and highly localized additional food resource. In suburban Reading, UK, over 55% of householders provide supplementary food for wild birds, enough to support a minimum of 131750 individual birds, based on the average energy requirements of the UK's 10 commonest bird species utilising bird feeders in gardens (Orros & Fellowes 2015b).

While species such as hummingbirds (Hill et al. 1998; Courter et al. 2013) and Red Kites *Milvus milvus* (Orros & Fellowes 2014; Orros & Fellowes 2015a) may have specialist food provided for them, suburban feeding stations typically provide supplementary food for seed-eating and omnivorous passerines (Cannon et al. 2005; Chamberlain et al. 2005). In the UK, the most common supplementary food types provided (i.e. non-table scraps) are peanuts and mixed seed, each typically provided in specialist feeders (Orros & Fellowes 2015b). This supplementary resource is believed to be particularly important in urban areas where natural resources may be relatively scarce (Chace & Walsh 2006; McKinney 2008). Positive associations between supplementary feeding, breeding population size and reproductive success have been documented (Fuller et al. 2008; Robb et al. 2008b), although this is not always so (Harrison et al. 2010; Plummer et al. 2013a). Indeed, recent work suggests that supplementary feeding during the breeding season may increase local nest predation (Hanmer et al. 2017; Malpass et al. 2017). Some species may also benefit more than others due to the suitability of food provided and relative competitive ability and adaptability of some species (Evans et al. 2009; Evans et al. 2011), and the provision of supplementary food is argued to be the instrumental selection pressure leading to changes in the migratory and physiological adaptations of German populations of the Eurasian Blackcap (Rolshausen et al. 2009; Plummer et al. 2015). Therefore, supplementary feeding may be directly and indirectly affecting the structure of urban bird communities (Galbraith et al. 2015).

Despite the enormous influence of supplementary food on the ecology of urban birds, we have little understanding of how this may be utilised by non-target species, and the consequential effects on the species the resource is intended to support. In the UK, the most visible mammal at supplementary feeding stations is the Grey Squirrel. Grey Squirrels were deliberately introduced into Great Britain on several occasions between 1876 and 1929, into Ireland in 1913, and into Italy between 1948 and 1994 (Bertolino et al. 2008). In Britain the Grey Squirrel is common in urban areas (Baker & Harris 2007; Bonnington et al. 2014a), and is spreading rapidly from introductions in other parts of Europe (Bertolino et al. 2008). Grey Squirrels are considered a significant conservation threat, particularly to the native Red Squirrel. Red Squirrels have been replaced by Grey Squirrels where the latter have been introduced (Bertolino et al. 2014); Grey Squirrels carry disease (squirrel pox, Bruemmer et al. 2010; *Borrelia burgdorferi*, the agent of Lyme disease, Millins et al. 2015, Millins et al. 2016), and cause economic losses in forestry (Mayle & Broome 2013). In the context of this work, evidence suggests that urban Grey Squirrel population size and density is associated with the provision of supplementary food in gardens (Bowers & Breland 1996; Parker & Nilon 2008) and there is some evidence that they can competitively exclude birds at supplementary feeders (Hewson et al. 2004; Bonnington et al. 2014b). Bonnington et al. (2014b) used taxidermied Grey Squirrels on feeders, and showed that resource use by birds was reduced by 98% in the presence of a mounted animal. However, we have no quantitative data on how the presence of Grey Squirrels affects feeder usage by garden birds, nor how much of the food provided is taken by the squirrels. This is crucial, as the Grey Squirrel is both a competitor for supplementary resources and a nest predator, and so may locally directly and indirectly affect the breeding success of some native bird populations (Newson et al. 2010; Bonnington et al. 2014c; Hanmer et al. 2017).

Furthermore, a highly conservative estimate suggests that enough supplementary food is provided in the UK (Orros & Fellowes 2015b) to support a Grey Squirrel population around four times the estimated 2.5 million individuals found in the UK (Battersby 2005). What is not understood is how much supplementary food is actually taken by Grey Squirrels. It is known that Grey Squirrels typically spend considerable periods of time using supplementary feeders (Pratt 1987), but no published study to our knowledge has attempted to quantify this experimentally using live wild animals over a prolonged period or considered how this affects feeder use by different urban bird species.

While data are lacking, both consumers and manufacturers of feeding stations have recognised that Grey Squirrels may be consuming food intended for birds, as specialised feeders and feeder guards are produced to counter this indirect competition. Typically, standard feeders are surrounded by guards to prevent access by squirrels and other large species such as corvids and invasive parakeets (Antonov & Atanasova 2003; Sorace & Gustin 2009). Such guards should decrease the food taken by Grey Squirrels and thus reduce their negative impact on supplementary feeder usage by target birds (Bonnington et al. 2014b; Hanmer et al. 2017). Furthermore, if the presence of Grey Squirrels reduces resource intake rates by birds (Bonnington et al. 2014b), we may expect to see a behavioural response to their presence. We speculate that excluded species may respond to high levels of Grey Squirrel presence by altering the timing of their visits to established supplementary feeding stations, thus extending foraging opportunities or utilising alternative food sources.

The provision of supplementary food for wild birds is in many countries the most widespread form of active engagement with wildlife, and it is becoming clear that the provision of food may have unintended consequences for other species (e.g. Orros & Fellowes 2012; Orros et al. 2015; Hanmer et al. 2017). However, we have little understanding of how providing food may be unintentionally affecting the very species people wish to support due to the use of feeding stations by non-target species, such the invasive Grey Squirrel. Here, we report the results of a manipulative field experiment in suburban gardens to ask for the first time a) how Grey Squirrel presence affected the rate and timing of feeder use by garden birds, and whether this interaction was b) affected by the type of food resource provided (peanuts or mixed seed) or c) the presence of a feeder guard. Furthermore, we examine how these overall patterns of feeder utilisation were influenced by local (urban) habitat or weather conditions.

2.3. Materials and Methods

2.3.1. Study Area

This study was conducted in the suburbs of the large urban district centred on Reading, South East England. Greater Reading covers approximately 72 km^2 and has a population of ~290 000 people (Office for National Statistics 2013; following Orros & Fellowes, 2015b). The eastern suburbs of Lower Earley and Woodley where fieldwork was carried out have human populations of 32,000 and 35,470 individuals respectively.

2.3.2. Individual Site Selection

Twenty study areas of predominately detached/semi-detached houses at least 500m apart and >100m away from any patches of natural or public urban green space (such as parks and playing fields) were selected to represent typical suburban residential areas in the southern UK. One volunteer participant who already fed birds regularly using bird feeders was recruited in each of the 20 areas. Areas selected were broadly similar in terms of local habitat availability, with housing densities of ~10 households/ha and 30-50 % constructed surfaces, with garden sizes of 100-200 m^2.

2.3.3. Study Design

Experimental work was carried out between 4 September and 30 November 2014. A paired peanut and two port seed feeder (CJ Wildlife small defender feeders, Shrewsbury, UK) on the same feeder stand was placed in each of the 20 volunteer back gardens. Food supplied was the Hi-Energy No Mess Seed Mix (c.550 calories per 100g) and Premium Whole Peanuts (c.560 calories per 100g) from CJ Wildlife (Shrewsbury UK). Feeding stations were placed ca. 2m clear from garden boundaries and vegetation cover, and the feeders were within 0.5m of each other at least 10 days before the start of data recording to allow animals to discover them. Ten gardens received a guarded pair of feeders to exclude Grey Squirrels and other large animals (locally these are primarily Eurasian Magpies, Western Jackdaws *Corvus monedula* and Great Spotted Woodpeckers *Dendrocopus major*) and ten received a pair of identical but unguarded feeders. No other feeders or artificial food sources were present in the study gardens during this period. Feeders may have been present in adjacent gardens, but all were at least 20m distant. Feeder visitors were recorded using an infra-red motion triggered camera trap (Ltl Acorn 5310; Ltl Acorn Inc, Wisconsin, USA) which could record visits to both feeders at the same time. The camera was set to record 10 second video clips with a one minute gap between each recording to maximise memory and battery life. The lag time between triggering movement and the camera recording was 0.6 s. Feeders were refilled up to twice a week depending on need, to ensure that feeders were never empty.

2.3.4. Video processing

The presence of all individuals was recorded to species for every video featuring an animal on a feeder. Feeding visits were recorded to feeders rather than to individuals as individual identification was not possible. The time spent on the feeders by every individual videoed animal was recorded to the nearest full second. Visits to each food type (peanut or seed) were recorded separately. Days where part of the data was missing such as through the temporary loss of a feeder, view obstruction or with gaps where food had clearly been consumed but the camera not triggered were not included in the analyses.

2.3.5. Meteorological and habitat data

Meteorological data for each study day was sourced from the metrological station on the University of Reading's Whiteknights campus (51°270N, 0°580W) on the edge of Lower Earley, positioned within 4.4 km of all the study gardens. The proportion of the day spent raining, mean wind speed (m/s) at 2m above the ground and mean temperature (°C) was recorded for the 24 hour period beginning 0900 GMT but for simplicity was attributed to the calendar date. The proportion of a 200m buffer around each study garden covered by garden habitat for was calculated in ArcGIS 10 (ESRI 2011) using land use data from the Ordnance Survey Mastermap collection (EDINA 2015, University of Edinburgh) to provide a measure of the local habitat of primary interest to garden birds and supplementary feeding and the distance (km) to the closest woodland fragment (defined as a wooded area of over 400 m^2 in area) measured.

2.3.6. Analysis

All analyses were carried out within the program R version 3.3 (R Core Team 2016). The species identity, length of time (in seconds) and time of visit was noted for every single animal recorded utilising a feeder. Daily total numbers and recorded time on feeders were calculated for each individual feeder and garden for every full recording day. Individual records were pooled to create a summary for the feeder usage for each day, for every individual bird feeder, as well as an overall summary daily for each feeding station.

To examine effectors on daily visits to different types of bird feeders by birds and squirrels, Poisson distribution general linear mixed effect models (GLMMs) were fitted in R package lme4 (version 1.1-12; Bates et al. 2015) with an observation-level random effect added to account for high levels of over-dispersion (Harrison 2014). Feeding station (i.e. study garden) and observation day were included as random effects to account for repeated measures. Because food/feeder type, weather and local habitat may potentially influence bird feeder usage the factors considered in the GLMMs for individual feeder usage were; whether the feeders were guarded, food type, total proportion of recorded animal visit time made up by Grey Squirrels that day for that feeding station, the proportion of garden habitat, constructed surfaces and woodland habitat within 200m, the distance in kilometres to the closest patch of woodland, mean wind speed (m/s), mean temperature (°C) and the proportion of the 24 hour period spent raining. Because precipitation and temperature were highly correlated alternative models were fitted to consider only one of these factors at a time. Proportional Grey Squirrel time on feeders was used as a proxy for Grey Squirrel feeder usage in preference to raw Grey Squirrel numbers or time on feeders as it better allowed for the overall variation in feeder usage between site and days within sites as well as providing better model stability. To account for the various potential influences of feeder guards and food type on Grey Squirrel and bird feeder usage a three-way interaction between guard presence, food type and proportion time taken by squirrels was included. Separate models were fitted for all birds and individual species of birds as well as Grey Squirrel visit data. For GLMMs considering factors affecting squirrel feeder visits this variable with the proportion of squirrel time on feeder was not included, making a two interaction between food type and guard status instead. To ensure statistical robustness only models for individual species of bird with more than 500 records across at least 10 study gardens were fitted.

To explore the effect of guarding feeding stations on the timing of the first feeding first in a day Mann-Whitney U tests were carried out within species and for birds overall. To account for changes in day length, time of first visit was converted to hours from sunrise. Spearman’s rank correlation was then used to test for any significant correlations between Grey Squirrel feeder visit numbers and bird visit timing for both the raw time and mean time of first visit for each species recorded on at least 50 recording days. To account for multiple comparisons made between species, p was automatically adjusted to account for the false discovery rate (Benjamini & Hochberg 1995).

2.4. Results

2.4.1. Feeder visitation

A total of 24825 individual bird (of 16 species) and 8577 individual Grey Squirrel visits were recorded (Table 2.1), totalling 128473 and 77178 recorded seconds respectively across 881 recording days. Accounting for camera errors and other data loses, 19 gardens and 38 bird feeders were each monitored for a mean of 48 days (median = 45, range = 17 – 80). Blue Tits, Great Tits, Grey Squirrels and Robins *Erithacus rubecula* combined accounted for the majority of feeder usage across all feeder types and occurred in the majority of study gardens (Figure 2.1, Table 2.1).

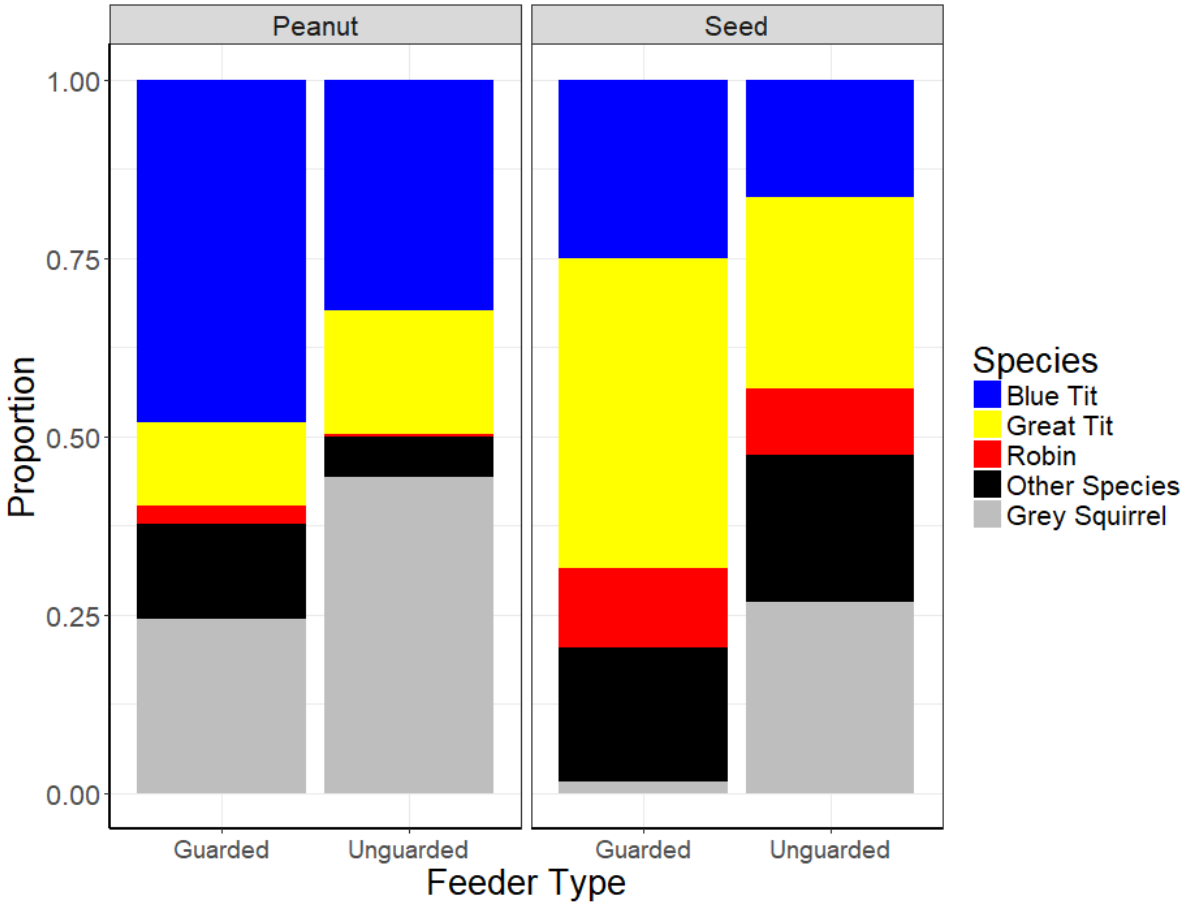

Figure 2.1. The overall proportion of animal visit records for the different types of animal over the course of the study across all bird feeder types. N = 426 and 454 total observation days for guarded and unguarded supplementary feeding stations respectively.

Grey Squirrels were the only mammals recorded and occurred at the majority of study garden feeding stations (Table 2.1). The only bird species with adult weights heavier than 40g (Robinson 2005) recorded were Jays (2 records in 2 gardens), Magpies (77 records in 5 gardens), Blackbirds (8 records in 1 garden) and Great Spotted Woodpeckers (98 records in 5 gardens) (Table 2.1).

Of the small passerines with more than a handful of records the majority of records for several species came from a limited number of study gardens with 51% of Coal Tit, 65% of Dunnock *Prunella modularis*, 90% of European Goldfinch *Carduelis carduelis*, 84% of Greenfinch *Chloris chloris* and 62% of House Sparrow records coming from single study gardens (Figure 2.2). In the case of Goldfinches, Greenfinches and House Sparrows this was the same study garden (Figure 2.2).

Table 2.1. Summary of the median visits per study garden (with IQR), total visits per feeder type and total visits overall for all recorded animal species, overall bird visits and overall animal visits to feeders. Recorded gardens indicates the number of study gardens the species was recorded in.

Species	Median Visits per Garden (IQR)	Total Guarded Peanut Visits	Total Unguarded Peanut Visits	Total Guarded Seed Visits	Total Unguarded Seed Visits	Total Visits	Recorded gardens
Blackbird	0 (0 - 0)	0	0	0	8	8	1
Blue Tit	383 (49 - 640)	1520	2629	1728	2503	8380	18
Chaffinch	0 (0 - 0)	0	0	0	2	2	1
Coal Tit	0 (0 - 10)	37	31	208	183	459	9
Dunnock	0 (0 - 8)	60	3	432	81	576	7
Goldfinch	0 (0 - 2)	2	7	7	453	469	6
Greenfinch	1 (0 - 26)	34	58	24	1201	1317	10
Great Tit	154 (80 - 647)	371	1416	2989	4091	8867	18
Great Spotted Woodpecker	0 (0 - 2)	49	49	0	0	98	5
House Sparrow	0 (0 - 48)	21	111	296	974	1402	7
Jay	0 (0 - 0)	0	2	0	0	2	2
Long-tailed Tit	2 (0 - 23)	162	103	16	3	284	12
Magpie	0 (0 - 1)	0	37	0	40	77	5
Nuthatch	0 (0 - 4)	47	56	308	194	605	6
Robin	58 (14 - 171)	79	29	764	1406	2278	19
Wren	0 (0 - 0)	0	0	0	1	1	1
Total Birds	**1087** **(203 - 2034)**	**2390**	**4531**	**6772**	**11132**	**24825**	**19**
Grey Squirrel	76 (3 - 787)	774	3603	116	4084	8577	16
Total Animals	**1262** **(494 - 2874)**	**3164**	**8134**	**6888**	**15216**	**33402**	**19**

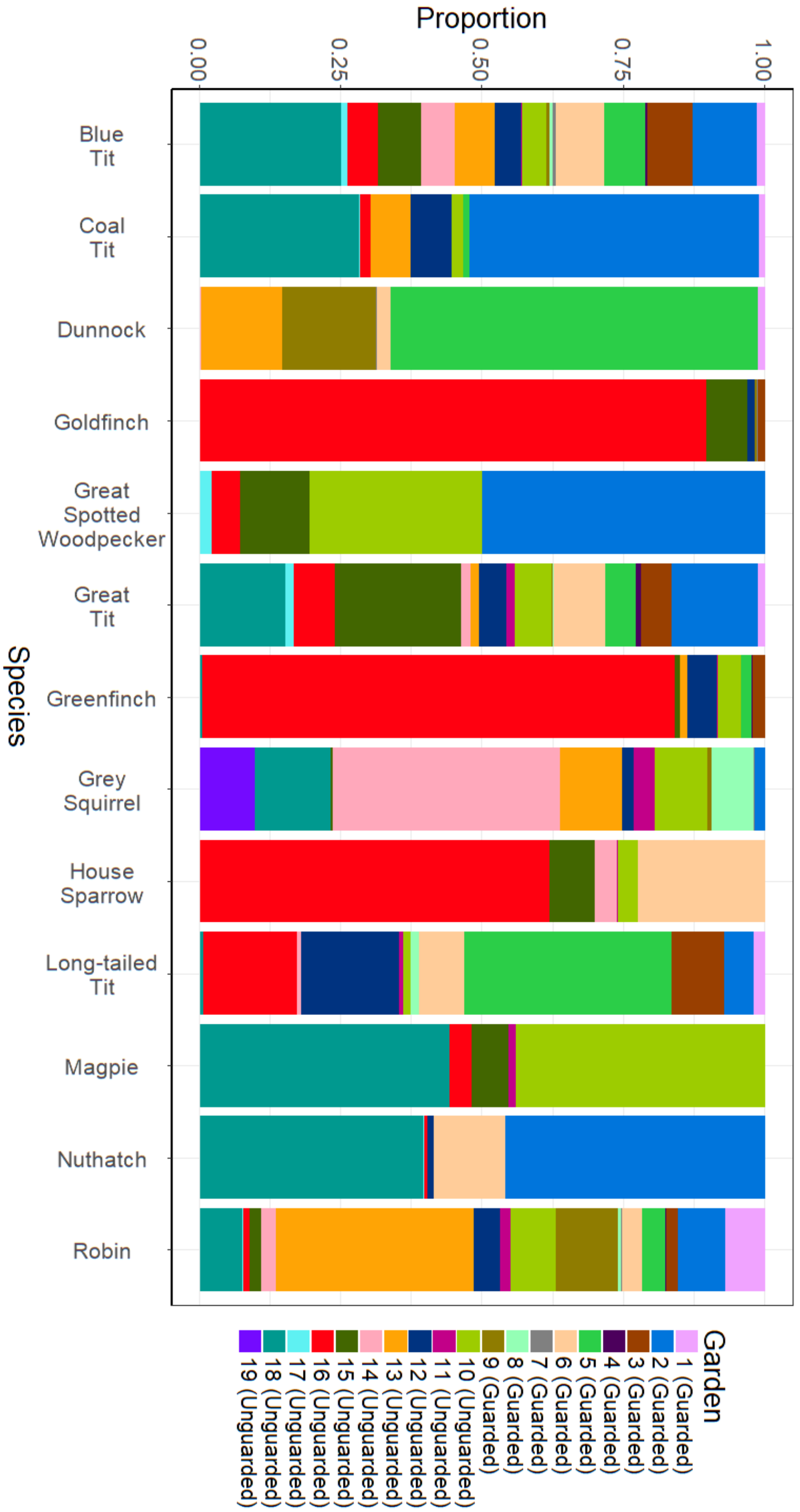

Figure 2.2. The proportional distribution of visit records for all species with more than 8 records across all study garden feeding stations.

The presence of a Grey Squirrel effectively excluded all birds from a feeding station while present. Only 10 cases were recorded (<99.99% of records) of a bird (all either Blue Tit or Great Tit) taking food while a squirrel was present at a feeding station and never when two squirrels were present. They took up 25.7% of all recorded visits and 37.5% of all recorded time across feeding stations. They were most common on unguarded feeding stations, present on average for 44.3% of the recorded total feeding time on across these feeding stations. Because video clips were limited to 10 seconds per minute, and in contrast to Grey Squirrels, most bird species appeared to spend much less than this time per visit (Figure 2.3) this is likely to be an underestimate.

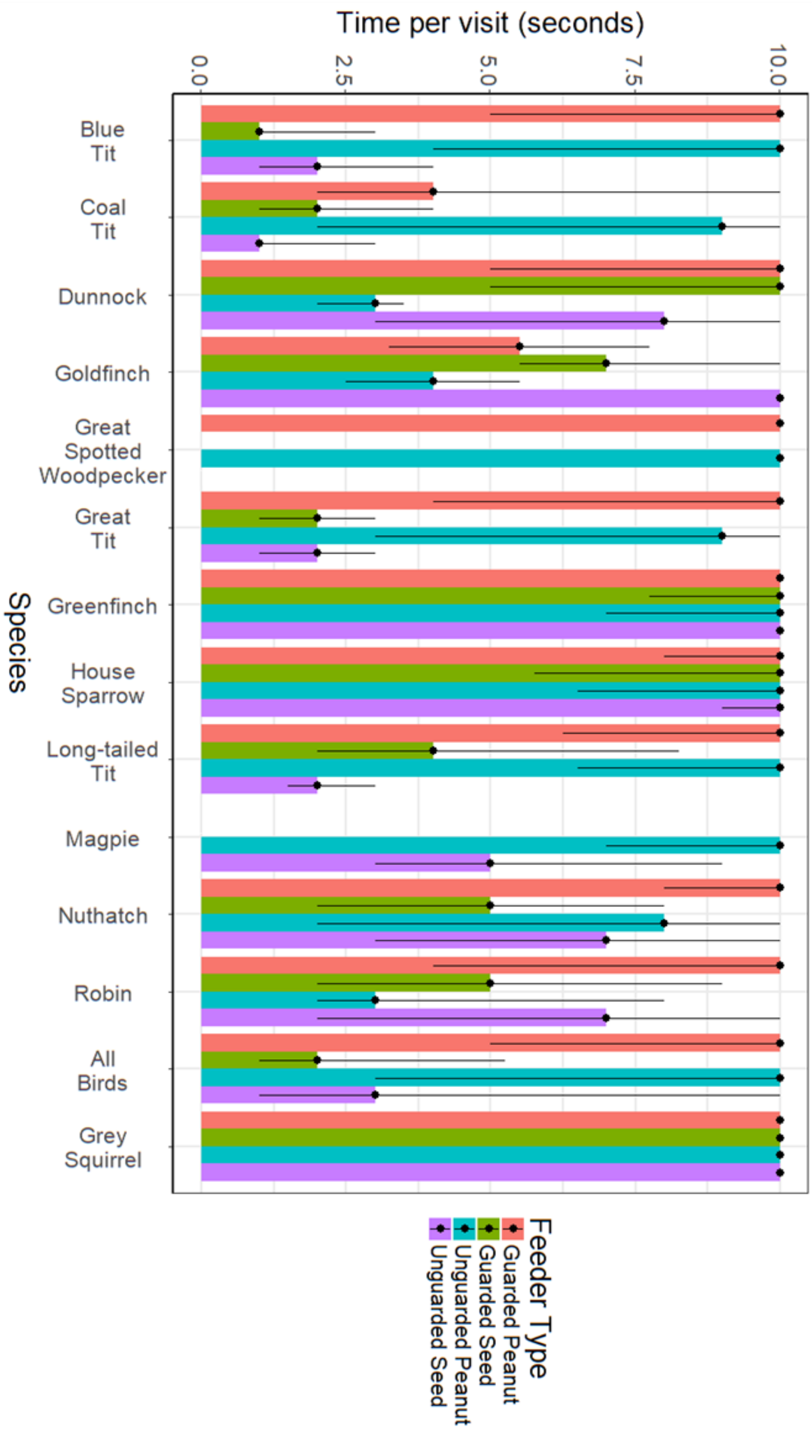

Figure 2.3. Median recorded individual visit time (up to the maximum video length of 10 seconds) spent on all different types of bird feeders in the study by species plotted with interquartile ranges.

2.4.2. Overall bird and Grey Squirrel feeder use

Seed feeders received significantly more daily bird visits than peanut feeders ($p < 0.001$ across all fitted models; Table 2.2). In models using proportion of garden habitat within 200 m as a habitat measure increased Grey Squirrel usage was borderline weakly negatively associated with reduced use of feeders by birds ($p = 0.066$; Table 2.2; Figure 2.4). In this model the area of garden within 200 m ($p = 0.059$) and rainfall ($p = 0.059$) were both borderline associated with reduced feeder use (Table 2.2). In an alternative model considering mean temperature instead of rainfall, temperature was found to be non-significant across all versions while seed feeders, Grey Squirrel usage and garden habitat retained similar relationships and associated levels of significance ($p < 0.001$, $p = 0.064$ and $p = 0.056$; Table 2.2). Guard status, wind speed, distance to nearest woodland patch and all interaction terms were found to be non-significant across all fitted models.

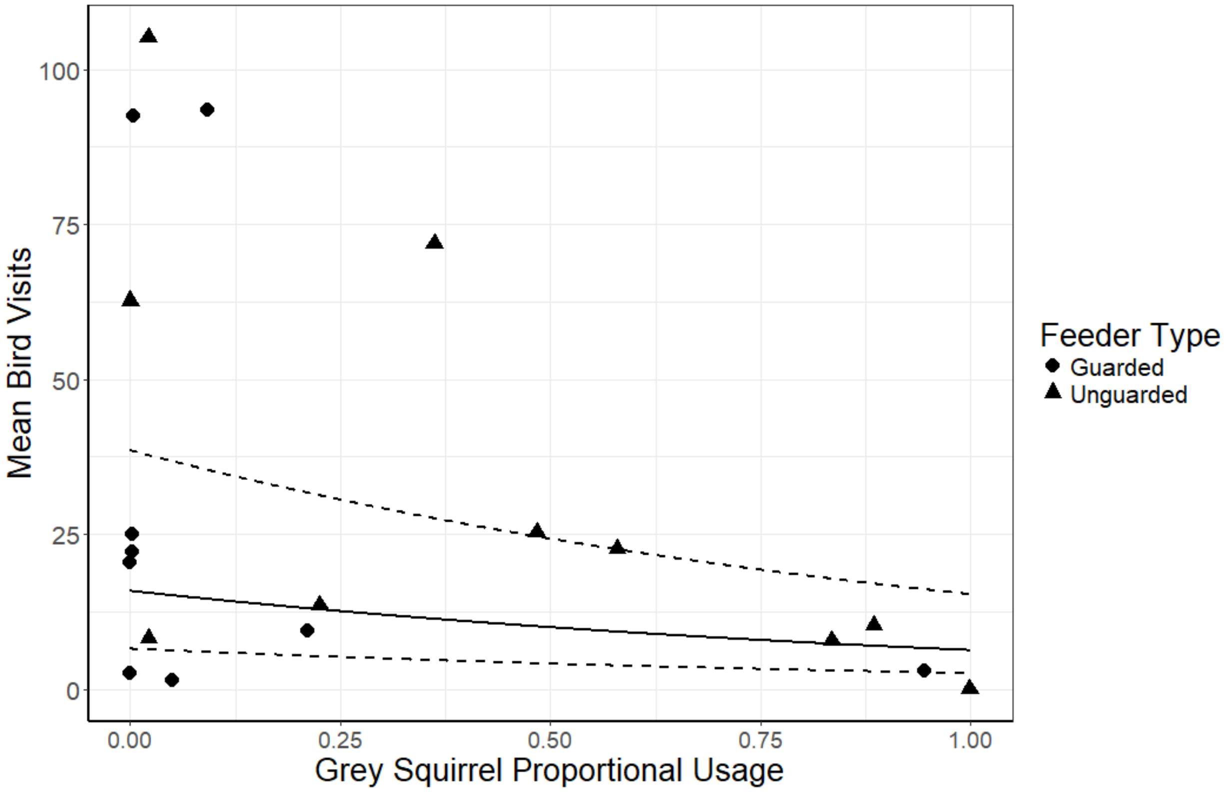

Figure 2.4. Effect of Grey Squirrel feeder usage on mean bird visits for each feeding station (both feeders together). Each point represents the mean for a study garden and the point type indicates its guard status. The plotted line of best fit (with 95% confidence intervals) is based on predictions extracted from the first global mixed effect model for bird visits in Table 2.2 using the raw data. Study garden and day were random factors in the model.

Grey Squirrel visit records were significantly higher on unguarded feeders ($p = 0.038$) and significantly higher on peanut feeders ($p < 0.001$). Increased distance from woodland ($p < 0.001$) and rainfall ($p = 0.046$) resulted in lower feeder visits by Grey Squirrels. While increased mean wind speed was associated with increased Grey Squirrel visits ($p = 0.003$). The interaction between seed feeders and unguarded feeders was also significant ($p < 0.001$), suggesting that Grey Squirrels were associated with unguarded rather than guarded seed feeders. In the alternative model including mean temperature instead of rainfall, mean temperature was found to be positively associated with increased Grey Squirrel visits ($p = 0.026$) while guard status, food type, distance to woodland, wind speed and the interaction between food type and guard status retained similar relationships and associated levels of significance ($p = 0.039$, $p < 0.001$, $p < 0.001$, $p = 0.008$ and $p < 0.001$; Table 2.2). Garden habitat was not a significant predictor in either model.

Table 2.2. Poisson mixed effect global models of effectors on daily visit records of total birds and Grey Squirrels on bird feeders (residual d.f = 1745 and 1749 respectively). Where the identity of the individual feeding station and study day were random effects. Food = food type (peanut set to intercept), Guard = guard status (guarded set to the intercept), Distance = distance to closest woodland patch, Garden% = proportion of habitat made up by gardens within 200m, Rain% = proportion of the day spent raining, Wind = average windspeed, Temperature = mean temperature and ‘**:**’ indicates an interaction term. For P value significance: ● p = 0.1 - 0.05, * p < 0.01, ** p < 0.001, *** p < 0.0001.

Dependent variable	Tested model	Variables	Estimate	SE	P
Bird visits	Global model including rainfall	Intercept	6.4992	3.5003	0.0633 ●
		Distance	2.4233	3.8211	0.5260
		Food	1.0571	0.0825	<0.0001 ***
		Food:Guard	-0.0789	0.1256	0.5301
		Food:Guard:Squirrel%	0.4761	0.5435	0.3810
		Food:Squirrel%	-0.6577	0.5015	0.1897
		Garden%	-10.8746	5.7668	0.0593 ●
		Guard	-0.0104	0.3283	0.9747
		Guard:Squirrel%	-0.5308	0.2812	0.0591 ●
		Rain%	-0.5235	0.2846	0.0658 ●
		Squirrel%	-0.5454	1.0081	0.5885
		Wind	0.0157	0.0348	0.6514
	Global model including mean temperature	Intercept	6.4498	3.4059	0.0583 ●
		Distance	2.3908	3.7832	0.5274
		Food	1.0552	0.0825	<0.0001 ***
		Food:Guard	-0.0821	0.1258	0.5139
		Food:Guard:Squirrel%	0.4815	0.5449	0.3769
		Food:Squirrel%	-0.6383	0.5023	0.2038
		Garden%	-10.6639	5.5804	0.0560 ●
		Guard	-0.5390	0.9988	0.5894
		Guard:Squirrel%	0.0039	0.3291	0.9906
		Squirrel%	-0.5297	0.2855	0.0635 ●
		Temperature	-0.0083	0.0095	0.3801
		Wind	0.0208	0.0356	0.5584
Grey Squirrel visits	Global model including rainfall	Intercept	-0.8906	3.8917	0.8190
		Distance	-15.1948	4.4116	0.0006 ***
		Food	-1.8899	0.2845	<0.0001 ***
		Food:Guard	2.0241	0.3258	<0.0001 ***
		Garden%	1.7613	6.3612	0.7819
		Guard	2.4091	1.1625	0.0382 *
		Rain%	-1.3318	0.6688	0.0464 *
		Wind	0.1575	0.0527	0.0028 **

	Global model including mean temperature	Intercept	-1.6747	4.0402	0.6785
		Distance	-15.1600	4.5350	0.0008 ***
		Food	-1.8767	0.2847	<0.0001 ***
		Food:Guard	2.0069	0.3262	<0.0001 ***
		Garden%	1.7977	6.5895	0.7850
		Guard	2.4361	1.1805	0.0391 *
		Temperature	0.0496	0.0222	0.0256 *
		Wind	0.1413	0.0535	0.0082 **

2.4.3. Effect of food type and guard status on individual bird species

Blue Tits, Great Tits, Greenfinches and Robins all had sufficient records to be considered for visit record models (Tables 2.1 and 2.3). Of these, models for Greenfinches failed to converge, likely due to most of their records (83.5%) coming from a single study garden (Figure 2.2). Robins were more likely to visit guarded feeders ($p = 0.041$) while Blue and Great Tits showed no overall preference (Table 2.3). Great Tits and Robins were significantly more likely to visit seed feeders (both $p < 0.001$), while Blue Tits showed no food preference. There were significant interactions between food and guard type for Great Tits and Robins. Great Tits responded negatively, which may indicate a preference for unguarded feeders regardless of food type preference, while Robins showed a positive association, suggesting a preference for guarded seed feeders (both $p < 0.001$; Table 2.3).

Increased proportional time spent on feeders by Grey Squirrels was associated with a decrease in Blue Tit visits ($p = 0.004$; Table 2.3) but not in either of the other species. No interaction terms that included Grey Squirrel usage were significant for any species.

Rain was a significant negative predictor in for Blue Tit and Great Tit (borderline) visits ($p = 0.023$ and $p = 0.052$ respectively). Proportion of gardens within 200m was borderline negatively associated with Blue Tit (borderline) and Great Tit visits ($p = 0.072$ and $p = 0.044$; Table 2.3).

Utilising temperature instead of rainfall found Grey Squirrel usage and garden habitat (borderline) to show similar significant negative relationships in Blue Tits ($p = 0.003$ and $p = 0.079$) but no other significant predictors were found. While Great Tits still showed a similar preference for seed feeder, negative association with garden habitat and negative interaction between food type and guard status ($p < 0.001$, $p = 0.048$ and $p < 0.001$ respectively). Robins retained similar significant positive relationships with seed feeders, negative relationships with unguarded feeders and positive interaction term between the two factors ($p < 0.001$, $p = 0.045$ and $p < 0.001$ respectively). They also showed a negative relationship with increased temperature ($p = 0.020$; Table 2.3), indicating reduced feeding with increased temperatures.

Wind speed and distance to woodland were non-significant in all fitted models (Table 2.3).

Table 2.3. Poisson mixed effect global models of effectors on daily visit records of Blue Tits, Great Tits and Robins on bird feeders (residual d.f = 1745 across all models). Where the identity of the individual feeding station and study day were random effects and Food = food type (peanut set to intercept), Guard = guard status (guarded set to the intercept), Distance = distance to closest woodland patch, Garden% = proportion of habitat made up by gardens within 200m, Rain% = proportion of the day spent raining, Wind = average windspeed, Temperature = mean temperature and. '**:**' indicates an interaction term. For P value significance: ● p = 0.1 - 0.05, * p < 0.01, ** p < 0.001, *** p < 0.0001.

Species	Tested model	Variables	Estimate	SE	P
Blue Tit	Global model including rainfall	Intercept	5.7790	3.3088	0.0807 ●
		Distance	1.1289	3.6617	0.7579
		Food	0.0587	0.0957	0.5393
		Food:Guard	-0.0471	0.1454	0.7461
		Food:Guard:Squirrel%	1.3377	0.9381	0.1539
		Food:Squirrel%	-0.8262	0.9061	0.3619
		Garden%	-9.7820	5.4437	0.0724 ●
		Guard	-0.5971	0.9686	0.5376
		Guard:Squirrel%	0.0621	0.4352	0.8866
		Rain%	-0.7497	0.3293	0.0228 *
		Squirrel%	-1.1262	0.3900	0.0039 **
		Wind	0.0028	0.0383	0.9421
	Global model including mean temperature	Intercept	5.6810	3.2839	0.0836 ●
		Distance	1.0726	3.6954	0.7716
		Food	0.0558	0.0958	0.5603
		Food:Guard	-0.0491	0.1458	0.7361
		Food:Guard:Squirrel%	1.3181	0.9384	0.1601
		Food:Squirrel%	-0.7817	0.9059	0.3882
		Garden%	-9.5068	5.4053	0.0786 ●
		Guard	-0.5893	0.9697	0.5434
		Guard:Squirrel%	0.0872	0.4378	0.8422
		Squirrel%	-1.1412	0.3928	0.0037 **
		Temperature	-0.0083	0.0111	0.4579
		Wind	0.0087	0.0392	0.8233
Great Tit	Global model including rainfall	Intercept	4.0695	3.6363	0.2631
		Distance	5.1631	4.0395	0.2012
		Food	2.3719	0.1406	<0.0001 ***
		Food:Guard	-1.0311	0.1913	<0.0001 ***
		Food:Guard:Squirrel%	1.0239	1.0277	0.3191
		Food:Squirrel%	-1.1296	0.9819	0.2500
		Garden%	-12.0713	6.0010	0.0443 *
		Guard	0.3968	1.0736	0.7117
		Guard:Squirrel%	-0.4523	0.7274	0.534

		Rain%	-0.7791	0.4005	0.0518	●
		Squirrel%	0.0057	0.6870	0.9934	
		Wind	-0.0326	0.0333	0.3267	
	Global model including mean temperature	Intercept	4.0381	3.6027	0.2620	
		Distance	5.1260	4.0704	0.2080	
		Food	2.3721	0.1407	<0.0001	***
		Food:Guard	-1.0397	0.1916	<0.0001	***
		Food:Guard:Squirrel%	1.0783	1.0331	0.2970	
		Food:Squirrel%	-1.1329	0.9863	0.2510	
		Garden%	-11.7616	5.9473	0.0480	*
		Guard	0.4037	1.0731	0.7070	
		Guard:Squirrel%	-0.4568	0.7309	0.5320	
		Squirrel%	0.0130	0.6904	0.9850	
		Temperature	-0.0151	0.0138	0.2720	
		Wind	-0.0252	0.0346	0.4660	
Robin	Global model including rainfall	Intercept	1.1696	3.2541	0.7193	
		Distance	-4.1551	3.6221	0.2513	
		Food	2.4145	0.1671	<0.0001	***
		Food:Guard	1.7904	0.3502	<0.0001	***
		Food:Guard:Squirrel%	1.9184	1.2793	0.1337	
		Food:Squirrel%	-1.0329	0.8717	0.2361	
		Garden%	-4.9074	5.3648	0.3603	
		Guard	-2.0312	0.9944	0.0411	*
		Guard:Squirrel%	-1.2147	1.0565	0.2502	
		Rain%	0.3432	0.4370	0.4322	
		Squirrel%	0.0078	0.539	0.9885	
		Wind	0.0069	0.0411	0.8667	
	Global model including mean temperature	Intercept	1.5514	3.2750	0.6357	
		Distance	-4.1328	3.6547	0.2581	
		Food	2.4236	0.1670	0	***
		Food:Guard	1.756	0.3492	<0.0001	***
		Food:Guard:Squirrel%	2.0241	1.2750	0.1124	
		Food:Squirrel%	-1.0936	0.8722	0.2099	
		Garden%	-4.7556	5.3944	0.378	
		Guard	-2.0117	1.0026	0.0448	*
		Guard:Squirrel%	-1.2287	1.0499	0.2419	
		Squirrel%	0.0380	0.5382	0.9437	
		Temperature	-0.0350	0.0150	0.02	*
		Wind	0.0164	0.0411	0.6893	

2.4.4. Squirrel presence and timing of first visit to feeders

In the raw data Blue Tits and Robins arrived first to feeders earlier in the day with increasing Grey Squirrels visits during a study day (r_s = -0.09, p = 0.036 and r_s = -0.10, p = 0.044 respectively; Figure 2.5), suggesting increasing feeder use by Grey Squirrels causes these species to arrive early to feed. While Great Tits, Greenfinches and House Sparrows arrived later (r_s = 0.14, p = 0.002; r_s = 0.27, p = 0.018; r_s = 0.32, p = 0.004; respectively; Figure 2.5). No other bird species showed a significant relationship. This suggests that increased Grey Squirrels feeder usage may alter the behaviour of some bird species also utilising the same supplementary feeders. However, we note that the correlations are weak and when mean data for each individual study garden across the study was utilised instead of the raw data no significant correlations were found (all p > 0.1).

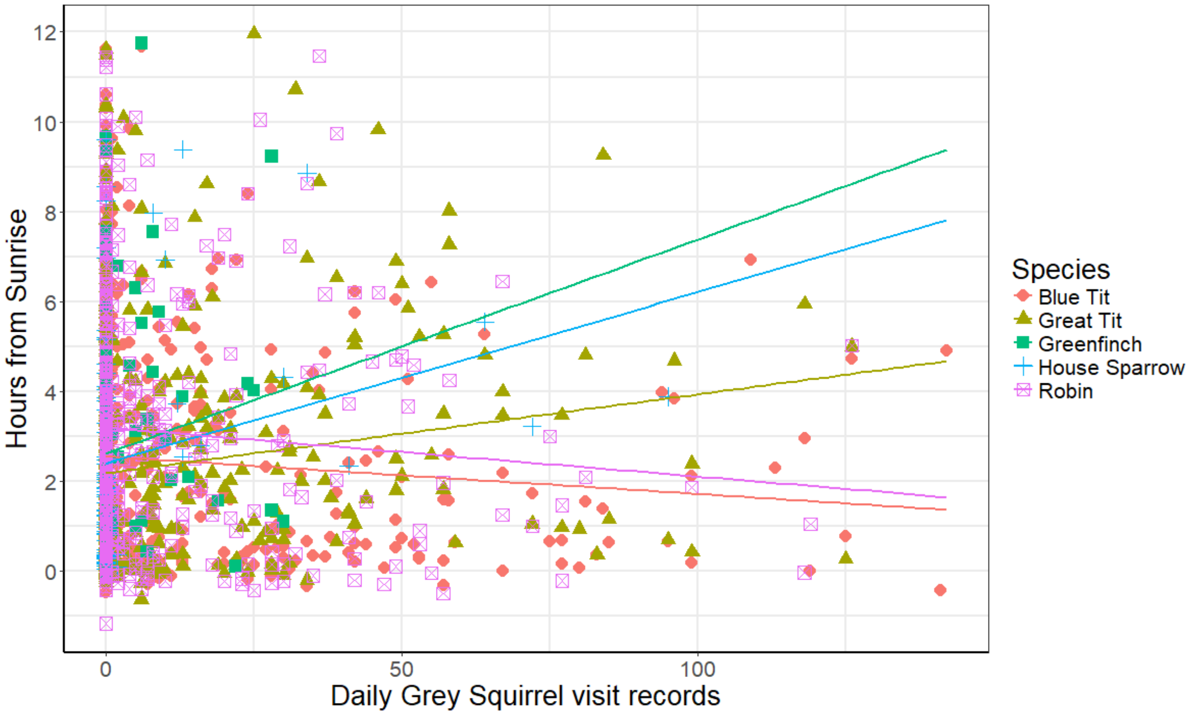

Figure 2.5. The relationship between the number of daily Grey Squirrel visit records to supplementary feeders with the timing (hours from sunrise) of the first visit in a day by different species of birds across all gardens and observation days. Linear lines of best fit are shown for each species. To aid interpretation only species showing a significant correlation are displayed.

Birds overall, Grey Squirrel and Blue Tit were found to make their first visit in a day significantly earlier to unguarded feeding stations than guarded whereas Coal Tits, Greenfinches (borderline), House Sparrows and Long-tailed Tits *Aegithalos caudatus* showed the opposite pattern (Figure 2.6). Only 147 visits (0.044% of all visits) by all animal types were recorded before sunrise.

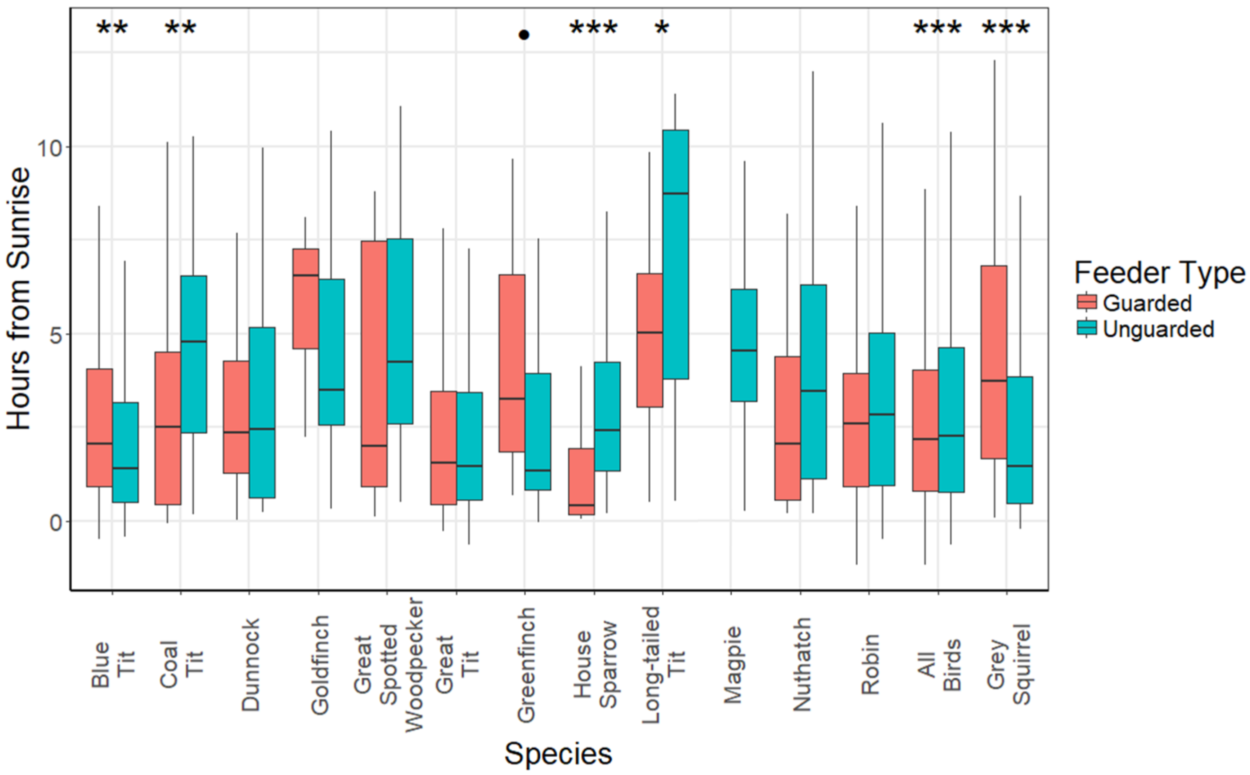

Figure 2.6. Summary of the median first visit after sunrise for Grey Squirrels, all birds and all common bird species for guarded and unguarded feeding stations. Mann-Whitney test statistics are between the first visit by that species/grouping in a day to a guarded and unguarded feeding station. For P value significance: • p = 0.1 - 0.05, * p < 0.01, ** p < 0.001, *** p < 0.0001 (adjusted using the false discovery rate).

2.5. Discussion

The presence of Grey Squirrels on bird feeders in our study system appeared to reduce the numbers of birds accessing supplementary food, confirming anecdotal and past indirect experimental evidence though it is clear species are differentially affected (Bonnington et al. 2014b) and the evidence was weak. The presence of a Grey Squirrel effectively excluded all birds from a feeding station, and at our study sites they were present on average for 44.3% of the recorded total feeding time on unguarded feeding stations during a day. Grey Squirrels and most bird species were more often associated with unguarded feeders; more birds were recorded using seed feeders, but Grey Squirrels showed no preference other than avoiding guarded seed feeders. While the evidence for environmental factors affecting bird feeder use was equivocal, Grey Squirrels were less likely to use feeders on days with increased rainfall, and less likely to use feeders that were further away from woodland patches. Intriguingly, increased feeder use by Grey Squirrels was associated with changes in the start of feeding for several bird species, suggesting that they were altering their foraging behaviour in response to this species. Together, we show that Grey Squirrels are dominant at bird feeders, reduce food availability to target bird species, and that visiting birds may alter their patterns of feeder use to compensate for reduced feeding opportunities.

Grey Squirrels effectively prevent small birds from accessing feeders while present, and overall most species studied showed a reduction in numbers using feeders associated with an increase in feeder use by Grey Squirrels. Only 10 cases were recorded (<99.99% of records) of a bird (all either Blue Tit or Great Tit) taking food while a squirrel was present at a feeding station and never when two squirrels were present. Furthermore, the overall reduction in bird activity with increasing Grey Squirrel usage suggests that the effect lasts longer than individual squirrel visits to feeders. It is worth speculating on what this means in terms of Grey Squirrel energy consumption at feeding stations. Taking the estimated energy supplied per garden per day for UK from Orros & Fellowes (2015b) which was a median of 628 kcal/day and a minimum provisioning of 101 kcal/day (assuming all food was consumed and ignoring food type differences), and making the highly conservative assumption that all species feed at the same rate, then a median of 278 kcal/day (45 kcal/day minimum) of food intended for wild birds is being taken by Grey Squirrels at unguarded feeders in this experimental system. While by necessity this is simply an estimate, this suggests that such feeder use alone could support the average daily energy requirements (137 kcal/day) of two adult Grey Squirrels (Harris & Yalden 2008; Orros & Fellowes 2015b). This is compared to the far lower average daily requirements of 14, 25 and 15 kcal/day for a Blue Tit, Great Tit and Robin respectively (Orros & Fellowes 2015b). At guarded feeding stations Grey Squirrels were largely but not entirely excluded, as they were sometimes able to access food though the top of the guarded bird feeders, particularly peanut feeders. This shows that feeder guards are an effective means of reducing the volume of food taken by unintended beneficiaries (Orros & Fellowes 2015b).

Nevertheless, while the use of guards did reduce competition with small birds by Grey Squirrels; some bird species still appear to prefer unguarded feeders, suggesting that guards may discourage them. Of the common species, Great Tits and Robin appeared to avoid guard feeders while Blue Tits showed no preference. This suggests that while garden owners can reduce the volume of food taken by species such as Grey Squirrels, it may come at a cost in terms of reduced use of guarded feeders by small birds. We speculate that this may be a result of the feeder guards presenting a barrier to escape or delaying predator detection (Devereux et al. 2006; Cresswell et al. 2009), increasing the risks associated with using the feeders.

The use of baffles designed to stop Grey Squirrels from being able to access feeders may offer an alternative means of reducing access of squirrels to food, while not restricting or discouraging bird access. However, such feeding equipment will still allow other potential competitors and nest predators such as corvids (Hanmer et al. 2017) to access food. Feeders which are capable of excluding animal access to food based on weight avoid this problem, but the increased costs involved in purchasing such exclusionary feeders may greatly discourage members of the public from purchasing them, although the greater cost may be offset by the reduced volumes of food taken by larger feeder users with higher energy requirements (Orros & Fellowes 2015b).

We have some weak evidence that birds may alter their daily first visiting times in response to local rates of feeder use by Grey Squirrels; similar patterns have been seen with increased activity of hawks (Roth & Lima 2007b). Blue Tits and Robins arrived at feeders earlier and Great Tits, Greenfinches and House Sparrows arrived later with increasing use of feeders by Grey Squirrels. The two species arriving earlier may be showing a behavioural response where they attempt to feed before the arrival of Grey Squirrels to feeders and so avoid exclusion from the resource by extending their potential feeding time. Whereas the three species arriving later may be unable to adapt in this way or are utilising other resources first instead to account for this exclusion. Guarding feeding stations also significantly altered the first visit timing with Grey Squirrels, Blue Tits, Greenfinches as well as birds overall arriving significantly earlier to feed on unguarded feeders, while Coal Tits, House Sparrows and Long-tailed Tits responded the opposite way. When feeders are guarded there may be less need to adjust feeding behaviour to avoid exclusion by larger competitors such as the Grey Squirrel.

Sites were purposefully selected to be broadly similar in local habitat and garden size. However, local habitat did indeed influence both bird and Grey Squirrel supplementary feeder usage. For birds overall and specifically for Blue Tits and Great Tits, an increasing proportion of garden habitat within 200m of a feeding station was borderline negatively associated with feeder usage, suggesting that where alternative food sources were available, these were increasingly used. Grey Squirrel feeder usage declined with increasing distance from nearest woodland patch. These patches are likely to provide resting sites and enemy free space given Domestic Cat roaming behaviour (Thomas et al. 2014; Chapter 6). This suggests that feeding stations in urban areas further away from woodland patches may be more available to small birds due to fewer Grey Squirrels being present, although bird numbers may still be depressed at supplementary feeding stations in more highly urbanised areas even in the absence of this competition (Chace & Walsh 2006; Tratalos et al. 2007; Bonnington et al. 2014c).

The autumn of 2014 was relatively mild with no frosts, snow or extreme weather events recorded during the monitoring period so it was unsurprising that no influence of temperature or wind speed was found on overall bird visits. However, increased rain duration depressed both bird (specifically Blue Tits and Great Tits) and Grey Squirrel feeding activity. Increased temperatures were associated reduced Robin visits, perhaps implying their energy requirements were reduced with increased environmental temperatures (Ockendon et al. 2009a). While increased windspeed was associated with increased Grey Squirrel usage, possibly due to the increased difficulty of finding natural food in winder conditions and/or a wind chill effect increasing energy requirements (Cowie & Simons 1991). For the birds these results conflict with Cowie & Simons (1991) who found wind but not rain to be related to feeding activity and Zuckerberg et al. (2011) who found precipitation (including snowfall) to be associated with increased winter feeder usage in some North American passerines.

Interestingly several bird species only frequented a minority of feeding stations, in particular Greenfinches, Goldfinches and House Sparrows records were concentrated at a single unguarded feeding station and rarely detected elsewhere, suggesting perhaps they were highly localised in the general study area. One species that was commoner than might be expected were Dunnocks which are generally considered ground feeders (Davies & Lundberg 1984; Davies 1992), though again the majority of records came from a single study garden, suggesting a limited number of individuals accounted for the majority of records. While other species that might have been expected at supplementary feeding stations and known to be present in the local environment were absent, such as Wood Pigeons and Collared Doves (pers. obs.). This may be because the feeders were unsuitable for use by these large species even without exclusionary guards.

It is perhaps worth thinking of the relationship between the garden owners who provide supplementary food and the garden birds who feed on that food as a mutualism, where in exchange for food resources, birds provide pleasure and perhaps even health benefits to the many millions of people who feed them (Cox & Gaston 2015; Cox & Gaston 2016; Cox et al. 2017b). In this context, Grey Squirrels act as a cheat, directly subverting food from the intended beneficiaries, with the longer-term consequence of supporting Grey Squirrel population size. This leads to both increased competition for food and potentially increasing rates of nest predation in the breeding season (Hanmer et al. 2017) in gardens, and may contribute to the success of Grey Squirrels as their range expands and further comes into conflict with forestry and Red Squirrel conservation efforts. People can use guarded feeders as a counter-measure, but at the cost of reduced feeder use by most garden birds. Despite this, we suggest that given the potential direct and indirect consequences of unintentionally providing very large volumes supplementary food to Grey Squirrels, it would be wise to provide supplementary food in a manner which limits access to this introduced species. The Grey Squirrel is considered to be one of the world’s 100 most important invasive species (Lowe et al. 2004); it would be unfortunate if people’s wish to support urban biodiversity contributed to their success.

Chapter 3: Provision of supplementary food for wild birds may increase the risk of local nest predation

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3.1. Abstract

In countries such as the UK, USA and Australia, approximately half of households provide supplementary food for wild birds, making this the public's most common form of active engagement with nature. Year round supplementary feeding is currently encouraged by major conservation charities in the UK as it is thought to be of benefit to bird conservation. However, little is understood of how the provision of supplementary food affects the behaviour and ecology of target and non-target species. Given the scale of supplementary feeding, any negative effects may have important implications for conservation. Potential nest predators are abundant in urban areas and some species frequently visit supplementary feeding stations. We asked if providing supplementary food affected the likelihood of nest predation in the vicinity of the feeder, by acting as a point attractant for potential nest predators. We provided feeding stations (empty, peanut feeder, peanut feeder with guard to exclude potential nest predators) in an area of suburban parkland in the UK and monitored the predation rate experienced by eggs placed in artificial nests located at distances which replicate the size of typical suburban gardens. Nest predators (Magpies, Grey Squirrels) were frequent visitors to filled feeders, and predation caused by Magpies, European Jays and Grey Squirrels was significantly higher when nests were adjacent to filled feeders. The presence of a feeder guard did not significantly reduce nest predation. As supplementary feeding is becoming increasingly common during the breeding season in suburban habitats, we suggest that providing point attractants to nest predators at this time may have previously unconsidered consequences for the breeding success of urban birds.

3.2. Introduction

Garden bird feeding engages more people with wildlife than any other activity. Some 48% of households in Britain (Davies et al. 2009) and 53 million households in the USA feed wild birds (US Fish and Wildlife Service 2014), providing an enormous and highly localised additional food resource. For example, in suburban Reading, UK, over 55% of householders provide supplementary food for wild birds, two-thirds of whom feed year round (Orros & Fellowes 2015b). The majority of individuals provide peanuts, a range of seed types (e.g. sunflower, nyger, wheat) and fat to birds visiting their gardens. A conservative estimate suggests that enough food is annually provided in the UK to support over 30 million garden birds (Orros & Fellowes 2015b). This is reflected by the size of the bird feeding industry, which ten years ago was estimated to be worth £200 million *per annum* (BTO. 2006). This figure is likely to be considerably higher today.

Supplementary feeding in urban areas affects the abundance and distribution of species as diverse as the Red Kite (Orros & Fellowes 2014; Orros & Fellowes 2015a), hummingbirds (Hill et al. 1998; Courter et al. 2013) and the Eurasian Blackcap (Chamberlain et al. 2005; Rolshausen et al. 2009; Plummer et al. 2015). While feeding has been shown to increase adult overwinter survival (Jansson et al. 1981; Brittingham & Temple 1988), effects on bird productivity are variable, and overwinter supplementary feeding has been found to both increase (Robb et al. 2008b) and decrease (Plummer et al. 2013b; Plummer et al. 2013a) breeding success in subsequent seasons. Similarly, supplementary feeding experiments during the breeding period have found mixed results, with evidence for both decreases (Harrison et al. 2010) and increases (Peach et al. 2013; Smith & Smith 2013) in productivity. Furthermore, feeding stations may facilitate the transmission of disease (Bradley & Altizer 2007), which can lead to rapid population declines (e.g. Trichomonosis in Greenfinches; Robinson et al. 2010).

Urban birds tend to lay eggs earlier, have smaller clutch sizes, lower nestling weight, and lower productivity per nesting attempt (Chamberlain et al. 2009). Open-cup nesters decline with increasing urbanisation but remain part of the avifauna (Máthé & Batáry 2015) and UK gardens hold significant populations of several such species (Bland et al. 2004). While food availability and habitat suitability are important limiting factors for urban bird populations (Shochat 2004; Máthé & Batáry 2015), nest predation is a key cause of nest failure for open-cup nesters (Ricklefs 1969; Martin & Li 1992), possibly also limiting their populations (Jokimäki & Huhta 2000). Predator densities in urban areas may be higher than in rural areas for some nest predators, such as corvids (Jokimäki & Huhta 2000; Antonov & Atanasova 2003; Jokimäki et al. 2005; Sorace & Gustin 2009), although it is unclear if this apparent increase in potential predator density depresses prey populations (Shochat 2004; Madden et al. 2015). Eurasian Magpies and introduced Grey Squirrels are common in UK urban areas and are frequent nest predators (Eaton et al. 2013; Bonnington et al. 2014a). Increased nest predation in an urban area is associated with increased corvid density, although no association was found with Grey Squirrel population size (Bonnington et al. 2015).

Nest predators, such as Eurasian Magpies and Grey Squirrels, can be attracted by garden feeding stations (Chamberlain et al. 2005; Väisänen 2008; Bonnington et al. 2014b). As a result, those providing supplementary food can also purchase caged feeders, which aim to exclude larger species, including squirrels and corvids. At a domestic garden scale the provision of bird feeders reduces the local abundance of insects (Orros & Fellowes 2012; Orros et al. 2015), and the provision of supplementary food for ungulates (Cooper & Ginnett 2000; Selva et al. 2014) and woodland predators (Borgmann et al. 2013) increased local nest predation. In each case the supplementary food appears to attract predators to a point source, which in turn foraged locally on other prey. The most parsimonious explanation is that the presence of a reliable or high quality food resource both increases the numbers of potential nest predators and the time they spend foraging near the food source.

It is not known if supplementary feeding of the type practised by tens of millions of garden owners increases the risk of local nest predation in urban and suburban habitats. These habitats support significant populations of native bird species in the UK including a number of open-cup nesting species that have undergone national declines in recent decades, such as the Blackbird, the Dunnock, and the UK red-listed Song Thrush (Gregory & Baillie 1998; Bland et al. 2004). Given the near ubiquity of supplementary feeding in urban areas, and the recommendation from bird conservation NGOs (e.g. RSPB 2009) to feed birds throughout the year, it is possible that individuals providing supplementary food in their gardens are inadvertently increasing nest predation rates suffered by their garden birds. To investigate this further it is first necessary to establish if nest predation is elevated near bird feeding stations. By using both guarded (food inaccessible to nest predators) and unguarded feeders (food accessible), we can test if it is the presence of food (both accessible and inaccessible) or the availability (food accessible in unguarded feeders) of food which affects predation rates.

Studying nest predation using real nests would result in considerable practical and ethical challenges. As a result, artificial nests provide an important tool for studying bird nest predation (Major & Kendal 1996; Miller & Hobbs 2000). Typically nests are baited with quail and/or model eggs and monitored over a set period. Artificial nests are undefended by adults and lack the activity of real nests; nevertheless, they provide experimental nest predation data at scales which would be difficult to achieve in natural studies, while avoiding the ethical issues of experimenting with natural nests (Major & Kendal 1996; Moore & Robinson 2004). Using camera monitored artificial nests we investigated nest survival around caged (guarded), uncaged (unguarded) and empty bird feeders. Our objectives were to determine if a) potential nest predators were attracted to bird feeding stations providing supplementary food, b) if so, if this was associated with differences in rates of nest predation, c) if increased nest predation was associated with access to food (unguarded feeders) or the presence of food (guarded and unguarded feeders) and d) if nest predation rates were affected by distance from the supplementary food source.

3.3. Materials and Methods

3.3.1. Study area

The study was conducted at the University of Reading's Whiteknights Campus (UK; 51°27'N, 0°58'W), in an area of open parkland and woodland comprising approximately 68% natural surfaces overall, embedded in a typical UK suburban landscape broadly conforming to Marzluff et al. (2001). The town of Reading covers approximately 40 km^2 with a population of 230 000 people (Office for National Statistics 2013).

3.3.2. Experimental design

Experimental work was carried out between the 5th of May and the 17th of June 2014, which is during the peak bird breeding season for the UK (Robinson 2005). Fifty-four locations were selected on the edge of grassy clearings and open spaces with adjacent areas of shrubs and bushes, 50-100m apart, replicating typical suburban feeder distribution (Fuller et al. 2008). The exact distance between feeder locations varied slightly due to the availability of suitable sites. The experiment consisted of six two-week sample cycles. During each cycle, nine peanut feeders (CJ Wildlife small defender feeder, Shrewsbury, UK) were positioned (three each of empty, filled and unguarded, filled and fitted with a cage guard). Feeders were randomly placed in each of the study locations, one week before the nests, to allow habituation. Sites were not reused and all were at least 20 m away from the closest building and 50m from the edge of the campus. Experimental cycles were staggered at one week intervals to reduce the sampling time required for the whole experiment. This meant at any one time a maximum of 18 bird feeders where present in the whole study area.

Two artificial nests were placed diametrically opposed ca. 5m ('near') and 10m ('far') from each feeder (±1 m), replicating typical distances between feeders and suburban garden boundaries (Gaston et al. 2007). In total 108 nests were placed (one 'near', one 'far', at each of the 54 feeder locations). Nests were constructed of 15x15cm squares of small-gauge wire mesh lined with dried grass and attached to branches to imitate a Blackbird nest (Kurucz et al. 2010; Kurucz et al. 2012). Nest height was at 1.5 ± 0.5m and were placed to mimic natural Blackbird nest-sites and attempted to provide similar visual accessibility to potential predators following Swanson et al. (2012). Two fresh Quail *Coturnix japonica* eggs were placed in each nest (Buler & Hamilton 2000). Blackbirds are a common breeding species in UK gardens along with the less common but similarly sized Song Thrush (Bland et al. 2004), making them an appropriate species to simulate. Nests were monitored for seven days (168 hours) as 90% of predation events occur within 6 days of placement (Burke et al. 2004).

Each nest was continually monitored by a concealed motion-triggered camera trap (Ltl Acorn 5310; Ltl Acorn Inc, USA), set to the highest sensitivity setting, taking three photographs with a three second interval when triggered.

Feeders were checked every 3.5 days and refilled where necessary. Feeder usage was sampled using camera traps, but each was monitored for 3.5 days either at the beginning or end of the week to ensure coverage with limited traps. At any one time one of each feeder type was monitored and two thirds of all feeders were sampled for usage.

Nest fate was recorded and for predated nests, predation time and predator identity determined. Any damage to or removal of eggs was considered a predation event. Visitation rates per species were recorded at the feeders; as visitors could not be individually identified, a visitor was considered an individual when either separated by a photograph without the animal or when four or more minutes had elapsed without a feeding event.

3.3.3. Data Analysis

All analyses were carried out within the program R (R Core Team 2016), with nest survival tested using Cox’s proportional hazard model in base R survival package (version 2.39-4, Therneau 2015). This approach was used over a logistic exposure or regression approach (Shaffer 2004) because exact survival time and fate was known for each nest and exposure period did not vary. Covariates were feeder type (empty, guarded, unguarded), distance from feeder (near, far) and study week block (as a random effect) with time until predation (hours) and predation status as response variables. No interaction terms were used. We evaluated the relative fit of each candidate model using Akaike’s Information Criterion with a small-sample bias adjustment, comparing models using Akaike weights and delta AIC_c (Burnham & Anderson 2002).

Mean daily feeder visitation (as a proxy for usage) was first compared using Kruskal-Wallis tests between treatment, by individual species, all potential ‘predator’ species, all small birds and all animals. Binomial logistic mixed model regression was then used to test for specific relationships between animal feeder usage and predation overall. Two separate global models were constructed both with study week block as a random effect factor and whether a nest was predated as the binomial response variable in the R lme4 package (version 1.1-12, Bates et al. 2015). First, a model that considered overall predator visits and small bird visits to feeders as variables effecting nest predation. Second, a model considering feeder visits by Squirrels, Magpies and small birds as variables effecting nest predation. Because Magpie and squirrel visits are subsets of overall predator visits it is not possible to utilise species and overall visits in the same model. Jays were not included in the individual models due to their infrequent visits. Relative model fit was then separately evaluated using delta AIC$_c$ and Akaike weights for both global models as above against a null model containing only the intercept and study week as a random factor. There was insufficient data to effectively compare effectors on predation for individual predator species or at specific feeder types.

3.4. Results

3.4.1. Feeder visitation

Thirty-three of the 54 feeders were monitored (10 empty, 11 guarded, 12 unguarded). Eleven species were recorded making 5251 individual feeder visits (empty feeders: 17; guarded: 3522; unguarded: 1712 visits).

Grey Squirrels contributed 43.9% of visits to unguarded and 9.3% of visits to guarded feeders while smaller birds were more likely to visit guarded feeders (Table 3.1). Magpies were a regular visitor to unguarded feeders but rare at empty and guarded feeders. One exception was an individual guarded feeder, which did receive frequent visits (Figure 3.1). Despite predating 27.5% of all recorded nests, Jays only visited feeders eight times. All species visiting more than two individual feeders (excluding unknowns) show a significant difference between their feeder usages (Table 3.1; Figure 3.1).

Table 3.1. Median daily species visits and Kruskal-Wallis tests by feeder type (all d.f = 2). Only common species that visited at least two individual bird feeders are included.

Species	Empty median	Guarded median	Unguarded median	Kruskal-Wallis chi-squared	P	Number of feeders where species was recorded
Grey Squirrel	0.0[1]	6.9	17.86	23.02	<0.001	26
Magpie	0.0[2]	0.0	0.9	6.88	0.032	13
Great Tit	0.0[3]	47.7	4.1	25.59	<0.001	27
Blue Tit	0.0[4]	24.6	1.6	18.18	<0.001	21
Nuthatch	0.0[5]	4.9	0.0	13.76	0.001	14
Robin	0.0[6]	0.3	0.0	8.12	0.017	14

Footnote: The 17 individual animals visited empty feeders were [1] 8 Grey Squirrels, [2] 1 Magpie, [3] 1 Great Spotted Woodpecker, [4] 5 Great Tits, [5] 1 Blue Tit and [6] 1 Robin.

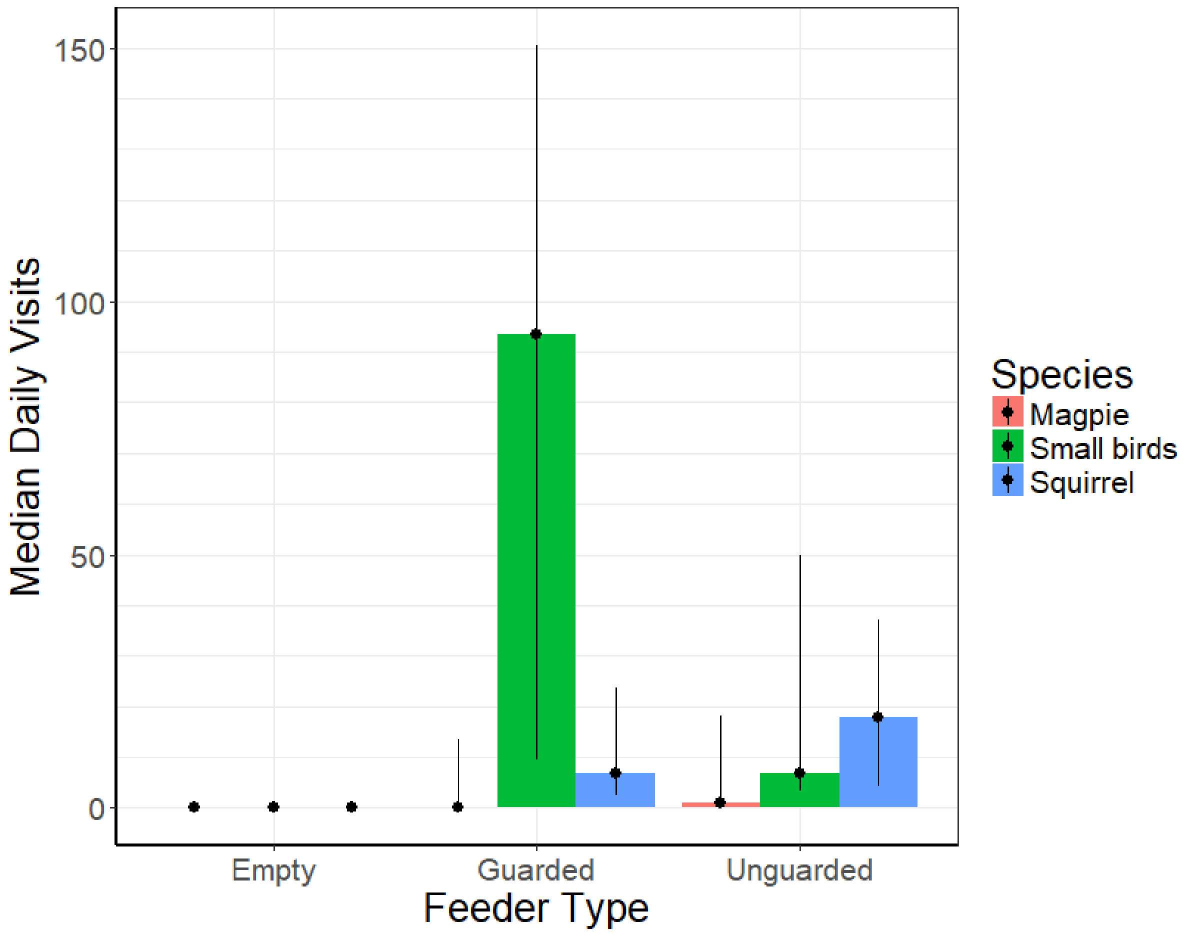

Figure 3.1. Median (+/- interquartile range) daily animal visits to each feeder treatment by species/grouping. Only species that visited at least two individual bird feeders are included. Small bird species are Blue Tit, Great Tit, Nuthatch and Robin.

3.4.2. Nest survival

Of the 108 experimental nests, 102 were successfully monitored, with 74 recorded predation events (Magpie: 37; Jay: 28; Grey Squirrel: 8; one unknown). Six nest predation events were missed due to camera errors or human interference and so were omitted from the analysis (3 empty, 2 guarded and 1 unguarded). From the different feeder types 51.5% of empty feeder nests, 76.5% of guarded feeder nests and 88.6% of unguarded feeder nests were predated during the course of the experiment. No predation events were recorded between 20:10 and 05.32.

When AIC$_c$ selection was carried out on the global hazard model, the AIC$_c$ selected model with distance from feeder removed had a delta AIC$_c$ of less than 2 from the global model so for completeness we present both the global (Wald = 23.05, d.f = 6.42, $p < 0.001$, AIC$_c$ = 600.4, model weight = 0.210; Table 3.2) and AIC$_c$ selected model (Wald = 22.93, d.f = 5.43, $p < 0.001$, AIC$_c$ = 598.5, model weight = 0.672; Table 3.2). Separate post hoc ANOVAs of both models (following

Therneau 2015) found feeder type and week were significant effectors of nest survival overall (χ^2 = 11.8, d.f = 2, p = 0.003 and χ^2 = 17.6, d.f = 3.4, p < 0.001 for feeder type and study week respectively in both models). In both models nests near filled feeders were significantly more likely to be predated than those near empty feeders and week was a significant covariate with identical hazard ratios after rounding (Table 3.2; Figure 3.2). Nest distance from feeder did not significantly affect predation rates in the global model (p = 0.67) and was eliminated in the AIC$_c$ selected model (Table 3.2). No significant difference in survival was found between nests adjacent to guarded and unguarded feeders (post-hoc Tukey test p = 0.82; Figure 3.2).

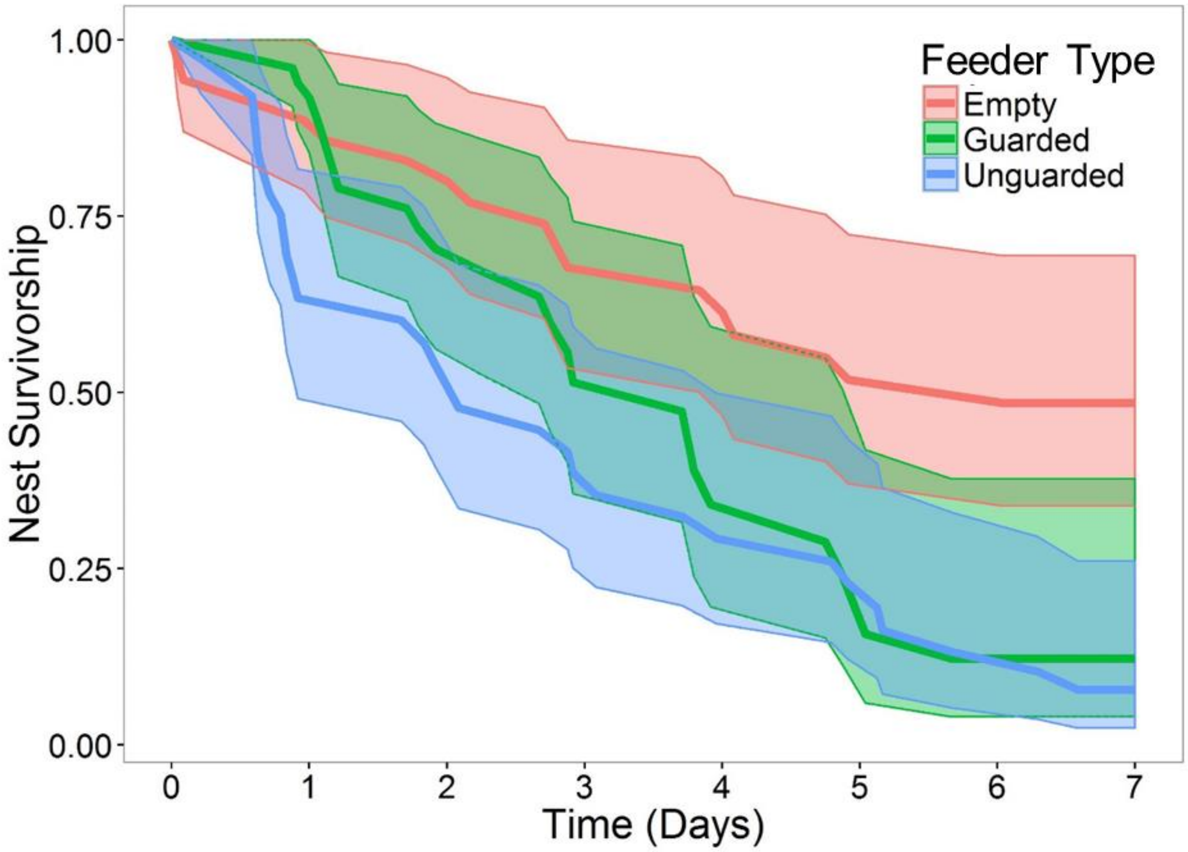

Figure 3.2. Predicted Cox's proportional hazard survival distribution by feeder nest type over the course of a mean experimental week (bold lines) with individual 95% confidence intervals (shaded). Final predicted survival rates were 0.49, 0.12 and 0.08 for empty, guarded and unguarded feeder nests respectively.

Table 3.2. Hazard ratios (relative predation risk; +/- confidence interval (CI)) and P values for covariates in the global model where h = 1 is the control (empty) feeder hazard ratio (d.f = 6.42, AIC_c = 600.4, model weight = 0.210). After the removal of distance from the AICc selected model (d.f = 5.43, AIC_c = 598.5, model weight = 0.672) the hazard ratios, CI and P values were identical after rounding.

Covariate	Hazard ratio (h)	Lower 95% CI	Upper 95% CI	P
Guarded	2.14	1.14	3.99	0.017
Unguarded	3.09	1.67	5.73	<0.001
Week (random effect)	1.00	0.58	1.73	0.010
Distance (removed in AICc selected model)	*1.08*	*0.68*	*1.71*	*0.740*

3.4.3. Nest predation and feeder usage

Overall feeder activity by predators (Grey Squirrels, Jays and Magpies) was significantly associated with increased nest predation (Wald Z = 2.518, p = 0.019) in the AIC_c selected mixed effect model (Table 3.3). In the model considering individual predator usage, Grey Squirrel usage was significantly associated with increased overall nest predation (Wald Z = 2.305, p = 0.021) in the AIC_c selected model (Table 3.3). However, support for this model is weak with little separation between all possible model AIC_cs and similar Akaike weights in several models (Table 3.3). Usage by small birds was not a significant factor in any model (Table 3.3).

Table 3.3. Binomial generalised linear mixed effect models of predation against daily visitors with model AIC$_c$ values and weights. The grouped predator models consider all predator visits together while the individual predator models consider them separately. The null model includes only the intercept and study week random effect. *indicates significance at the 95% level.

Predator variables	Model	Visit Coefficients	Estimate (95% CIs)	SE	P	Model AIC$_c$	Model weight	d.f
Grouped predators	Null	Intercept only	0.751 (-0.263 – 2.061)	0.4533	0.0976	84.1	0.024	62
	Global	All Predators	0.079 (0.022 – 0.155)	0.033	0.016*	79.4	0.255	60
		All small birds	0.004 (-0.012 – 0.021)	0.008	0.620			
	AIC$_c$ selected	**All Predators**	**0.068 (0.025 – 0.157)**	**0.029**	**0.019***	**77.3**	**0.705**	**61**
Individual predators	Null	Intercept only	0.751 (-0.263 – 2.061)	0.4533	0.098	84.1	0.024	62
	Global	Squirrel	0.068 (-0.004 – 0.141)	0.037	0.066	81.5	0.095	59
		Magpie	0.131 (-0.081 – 0.342)	0.108	0.225			
		All small birds	0.004 (-0.012 – 0.020)	0.008	0.645			
	Model 2	Magpie	0.178 (0.0197 – 0.414)	0.097	0.068	81.2	0.108	61
	Model 3	Squirrel	0.084 (0.017 – 0.174)	0.039	0.029*	80.9	0.124	60
		All small birds	0.005 (-0.010 – 0.219)	0.008	0.519			
	Model 4	Squirrel	0.070 (0.003 – 0.158)	0.038	0.063	79.3	0.277	60
		Magpie	0.061 (-0.045 – 0.391)	0.084	0.469			
	AIC$_c$ selected	**Squirrel**	**0.090 (0.022 – 0.179)**	**0.039**	**0.021***	**79.1**	**0.314**	**61**

3.5. Discussion

Our results suggest that the provision of supplementary food during the breeding season for wild birds in a form that is common in urban and suburban habitats may increase the likelihood of local nest predation. The survivorship of nests adjacent to unguarded feeders was less than 20% of that seen when artificial nests were placed near empty feeders. There was no difference in nest survival near guarded feeders when compared with those placed adjacent to unguarded feeders. Increased predation was associated with Magpies, Jays and Grey Squirrels. Magpies and Grey Squirrels were significantly more likely to visit unguarded feeders, while Jays were largely absent. Overall, nest predation was associated with increased predator visits, particularly by Grey Squirrels, to feeders. There was no effect on nest predation rates of distance to feeder at the scales we considered. Species assemblages differed between treatments; empty feeders received few visits or no visits, guarded feeders were mostly visited by small passerines and unguarded feeders attracted a higher proportion of corvids and Squirrels. Despite being unable to feed at guarded feeders, predators still made up 9.4% of total visits to them. No mammalian nest predators other than Grey Squirrels were recorded despite being present at the study site and in UK urban areas generally (e.g. Brown Rat *Rattus norvegicus*, mice *Apodemus* spp., Red Fox *Vulpes vulpes*, Domestic Cats: Baker & Harris 2007, Thomas et al. 2012). Two nests recorded mouse visits but no predation attempts were observed.

Nests adjacent to filled feeders suffered greatly increased predation rates, with the majority of nest predation events caused by corvids (Magpies and Jays) and Grey Squirrels. Nest predation by corvids is a frequent occurrence in urban habitats (Jokimäki & Huhta 2000; Thorington & Bowman 2003; Jokimäki et al. 2005; Bonnington et al. 2015), where densities are high due to their omnivorous diet and adaptability, as well as reduced numbers of larger predators and/or competitors (Soh et al. 2002; Marzluff et al. 2007).

Despite our record of animal usage and clear evidence for an effect of the presence of supplementary food, the exact nature of the link between feeder usage and local nest predation remains unclear. There is a significant positive relationship overall between feeder usage by predators, in particular Grey Squirrels, and increased nest predation. Predation by Grey Squirrels themselves was lower than the two corvid species, suggesting there was not a direct link between Squirrel feeder usage and nest predation by Squirrels. We lack sufficient samples and model support to investigate this further, but we speculate that their presence at bird feeders may influence predation rates by Jays and Magpies. We propose two non-mutually exclusive mechanisms that may lead to this.

First, Jays and Magpies may be responding to the increased density of other omnivores which have been attracted by the presence of supplementary food. They in turn may be more likely to enter the feeder area, associating it with increased feeding potential, even if they themselves are not primary users of the bird feeders. In particular the frequency of Jay predation was unexpected due to their infrequent attendance at feeders, while Magpies did utilise feeders, but in low numbers. Second, the presence of Squirrels on feeders may exclude other omnivorous predators as well as small birds, resulting in increased foraging in the vicinity of the feeders, hence increasing local nest predation. Taken together, these results suggest that feeder usage by nest predators is associated with increased predation on our experimental nests, but this effect is not simply a result of nest predators being attracted to a point source, but instead perhaps also by being attracted by other feeder users to the vicinity of the food source.

Corvids (Magpies and Jays) were also recorded in Chapter 2 and Chapter 4 at supplementary feeding stations, as well in other studies (Cannon et al. 2005; Chamberlain et al. 2005) but only in relatively low numbers, particularly in the case of Jays. This suggests that while they can and do utilise supplementary food as typically provided in an urban setting, they do not frequent them as much as small birds and Grey Squirrels. As adaptable intelligent omnivores (Emery & Clayton 2004; Bird & Emery 2009), they can utilise a wide variety of natural and human derived food sources in the urban environment such as invertebrates, plant matter, small vertebrates, carrion and human food waste in addition to supplementary food (Tatner 1982; Tatner 1983). Thus, they may not need to regularly frequent supplementary feeding stations to satisfy their energy requirements due to the ready availability of alternate high energy food sources in the environment, such as bird nests in the case of this study. The provision of other supplementary food they prefer more or low availability of other food resources may increase their frequency at feeders and possibly lead to reduced local nest predator (Borgmann et al. 2013) but we suggest they are not typically reliant on them.

We tested to see if nest predation changed with distance from the feeder, but there was no effect. The distances chosen for the study (5 and 10 metres) were relatively small and are consistent with the layout of a typical UK suburban garden (Smith et al. 2006; Loram et al. 2007). However, we suggest that there could still be a distance effect. While not explicitly recorded, we observed no evidence of increased predation suffered by nests placed close to an empty feeder when the closest replicate was a filled feeder. Therefore, we suggest that while the increased risk of nest predation is present when nests are within 10 metres of a feeder, this effect may be lost at a distance up to 40 metres away (the minimum distance between a feeder and the next closest nest associated with another feeder under our experimental design). Further testing over a larger range of distances with independent nests would be required to effectively test this theory.

The use of artificial nests does present some interpretive challenges (Buler & Hamilton 2000; Burke et al. 2004; Moore & Robinson 2004). They lack the odours, activity and defending adults of natural nests (Swanson et al. 2012). Concerns have also been raised over the use of Quail eggs in artificial nests, with suggestions that they may be too large for some small predators (Burke et al. 2004). This also means that artificial nests may not be representative of smaller common UK open cup nesting birds, such as Robins and Dunnocks, in terms of egg and nest size as well as concealment. Some studies have substituted model eggs made from modelling clay, both to give a smaller prey item and so that when nests are not monitored by cameras it allows predator identification through marks left on the eggs (Major & Kendal 1996; Burke et al. 2004). These studies have found that rodents (not including Squirrels) cause a significant proportion of artificial nest predation events. As only two nests were visited by mice and none by rats (and no feeder visits by rats were recorded) either the system in this experiment is different or previous results have been skewed by the attraction of these rodents to the smell and/or taste of the model eggs (Rangen et al. 2000). While for practical and ethical reasons the use of artificial nests remains the standard approach for understanding the causes and consequences of nest predation, such caveats suggest that interpreting the results of artificial nest studies should be taken as indicative rather than definitive, particularly when applied to bird species of different sizes or with different nesting habits such as ground or cavity nesting birds.

The urban landscape presents a challenging environment for wild birds to live and breed (Chace & Walsh 2006; Chamberlain et al. 2009). Together with potentially limited natural food (McKinney 2008) and high numbers of generalist predators (Sorace & Gustin 2009), urban areas also hold the majority of the UK’s estimated 10.3 million Cats (Murray et al. 2010) which predate millions of birds annually (Thomas et al. 2012; Thomas et al. 2014). Nevertheless, significant populations of birds are supported within urban environments (Bland et al. 2004) and species richness can be greater than in adjacent rural areas (Chace & Walsh 2006), in part because of the combined efforts of millions of people providing supplementary food (Fuller et al. 2008).

However, while some species are effectively human commensals, others including open-cup nesters such as thrushes, are increasingly under challenge in urban habitats (Máthé & Batáry 2015) and do not necessarily use the supplementary food people supply. In consequence, supplementary feeding may strongly benefit one avian guild to the detriment of others through increased local nest predation. Any effect we have on their demographic processes through supplementary feeding may have important conservation consequences and warrants further investigation. However, while we have shown that nests close to filled feeders suffer considerably higher predation rates, it is not clear if such predation would affect the population dynamics of urban birds. As with other anthropogenic pressures (e.g. the presence of Cats), testing this would not be straight-forward, in particular given the ubiquity of supplementary feeding in urban ecosystems. Nevertheless, while difficult, this work suggests that the question is worthy of further exploration.

Furthermore, we find that feeder type affects the assemblage of species feeding upon it. When feeders are unguarded, corvids and Grey Squirrels exclude small passerines (Bonnington et al. 2014a; Orros & Fellowes 2015b; this study). We suggest that this not only reduces the volume of food available to target species through competition, it may also support increased population sizes of predatory species through a demographic response (Davies et al. 2009). We suggest that people who choose to provide supplementary food for birds consider using guarded feeders to minimise opportunities to support predatory species, and consider in the context of the ecology of their own gardens if feeding during the breeding season is appropriate.

Providing supplementary food during the breeding season is widespread (Orros & Fellowes 2015b) and can increase local bird population size (Peach et al. 2013; Smith & Smith 2013). Urban areas may be important for the conservation of some bird species and species richness in suburban areas can be greater than that found in adjacent urban and rural areas largely as a result of the decisions made by millions of homeowners (Marzluff 2001; Chace & Walsh 2006; Väisänen 2008). Our results suggest a possible negative indirect effect of supplementary garden bird feeding on local nesting success by attracting nest predators to point sources of food. It would be unfortunate if our most common act of engagement with wildlife was counter-productive during the breeding season.

Chapter 4: Structure of bacterial communities on bird feeders determined by feeder design rather than animal visitors

4.1. Abstract

Wild birds represent an important potential vector of zoonotic pathogens. It has long been assumed that supplementary feeding of the type commonly practised by private individuals in the UK and other developed countries represents a major risk for pathogen transmission both between birds and to humans. Understanding the role of bird feeders in the spread of bacterial pathogens may serve as a useful model of the spread of other disease organisms in a similar setting. To explore the potential occurrence and spread of bacterial communities we set up feeding stations consisting of peanut, seed and empty control feeders (peanut and seed), in suburban gardens in the town of Reading, UK. Bird feeder usage was monitored using camera traps to record animal utilisation and bacteria were sampled using next generation DNA sequencing (NGS). We found significant differences in the bacterial communities between the seed and peanut feeders, but little association between feeder usage by animals and bacterial load or pathogen presence in this typical UK suburban garden setting. Our results suggest that differences in bacterial communities exist depending on the supplementary food provided, and that prevalence of pathogenic bacteria is likely to be low in a typical UK supplementary feeding setting.

4.2. Introduction

Providing supplementary food for wild birds in gardens is one of the most common forms of deliberate human-wildlife interaction on a global scale (Cox & Gaston 2016); more than 45% of households in Britain feed birds (Davies et al. 2009; Davies et al. 2012; Orros & Fellowes 2015b). Bird feeder designs vary considerably to allow for the use of different bird foods such as sunflower seeds, millet, nyjer seed, peanuts or suet, often in pre-prepared mixes, each designed to attract a range of species (Orros & Fellowes 2015b). Supplementary feeding can supply an important source of nutrition for birds, particularly during harsh conditions or in habitats where natural food may be scarce, such as urban/suburban gardens (Jones & Reynolds 2008). However, as an artificial point source of food they encourage high densities of birds and increase interactions among and between species that may not normally otherwise occur (Chamberlain et al. 2005; Galbraith et al. 2015). Such interactions can include the transmission of pathogens. Given their ubiquity, feeders are the most important point of indirect contact between wild birds and members of the public in many parts of the world (Cox & Gaston 2016) and hence may therefore also present an infrequently considered mode of pathogen transmission between wild birds and humans (Lawson et al. 2014).

Our awareness of the importance of birds as vectors and reservoirs of infectious diseases that pose a significant threat to animal and human populations has grown rapidly (Benskin et al. 2009; Murray et al. 2016). For example, wild birds may act as reservoirs for diseases such as avian influenza (Kilpatrick et al. 2006), West Nile Virus (Rappole et al. 2000), *Campylobacter* (Abulreesh et al. 2006; Weis et al. 2016), *Salmonella typhimurium* (Lawson et al. 2014) and pathogenic *Escherichia coli* (Foster et al. 2006). Despite differences in transmission between pathogen types (Swinton et al. 2002), monitoring the spread of bacterial pathogens can act as a useful model for studying the spread of zoonotic pathogens (Benskin et al. 2009; Lambertini et al. 2016). Understanding how pathogens may be transmitted within and between species is therefore of considerable interest, yet we have little understanding of how the widespread provision of supplementary food for wild birds may influence opportunities for such transmission to occur.

Pathogen transmission is generally believed to be density dependent (Anderson & May 1992) so a higher concentration of infected and susceptible individuals increases the risk of spread (Benskin et al. 2009; Murray et al. 2016). Therefore the provisioning of food for wild birds in bird feeders, could increase the risk of exposure and spread if pathogens are present in the bird populations (Kirkwood 1998; Pennycott 1998; Pennycott et al. 2002). Studies have most frequently considered patterns of mortality resulting from outbreaks of diseases of garden birds, as well as sampling directly from dead individuals (Brittingham & Temple 1988; Pennycott et al. 2006; Lawson et al. 2012b), but mortality is likely to be under-recorded as dead birds are difficult to locate. For example, Lawson et al. (2014)

found the same strain of *S. typhimurium* to be present in wild bird and human outbreaks in the same geographical area.

At a national level, schemes such as the Garden Wildlife Health (GWH) project in the UK, monitor the spread of wildlife diseases through wild bird populations (www.gardenwildlifehealth.org). Such outbreaks may be concentrated in urban and suburban areas, explained in part by the presence of high rates of supplementary feeding (Bradley & Altizer 2007). However, few studies have directly investigated the potential for disease spread or indeed the general diversity and prevalence of bacteria in suburban gardens by directly sampling bird supplementary feeders, the primary location where urban birds forage together at high densities (Foster et al. 2006). The provision of supplementary food may therefore present an important potential source of pathogen transmission to both wildlife and to humans (Benskin et al. 2009; Lawson et al. 2014). Pathogens may build up at feeding stations and other animals such as rodents may be attracted that act as disease vectors contaminating feeders and the surrounding area (Henzler & Opitz 1992; Hilton et al. 2002).

Different food sources and feeder designs potentially attract and support different bird species due to food preferences and animal behaviours (Horn et al. 2014; Chapter 2; Chapter 3). As some taxa which may be more strongly associated with different bacteria such as the association of Salmonella with graminivores passerines like House Sparrows (Benskin et al. 2009; Lawson et al. 2014; Rouffaer et al. 2016), the design and food type of supplementary feeders may affect the bacterial communities present on them.

Next generation sequencing (NGS) presents new opportunities to monitor bird feeder microbial communities, particularly in the absence of an overt disease outbreak. This technique allows the user to determine the diversity and abundance of bacteria, and more specifically to understand the accumulation of potentially pathogenic bacteria. Combined with a record of animals using bird feeders (Benskin et al. 2009; Rouffaer et al. 2016) it is possible to explore whether different feeding practices lead to differences in microbial populations, something that has not to our knowledge been previously explored observationally or experimentally. We therefore hypothesised that bacterial richness and diversity would a) be associated with the abundance and diversity of animals (birds, Grey Squirrel) visiting supplementary feeding stations and b) be influenced by nature of the food provided (peanut vs seed) as this would influence animal use.

4.3. Materials and Methods

4.3.1. Volunteer recruitment and study area

Ten volunteer garden owners were recruited across the Greater Reading suburban area in South East England. Greater Reading itself covers approximately 72 km^2 and has a population of ~290 000 people (Office for National Statistics 2013; following Orros & Fellowes 2015b). Volunteer gardens were at least 750m apart and more than 250m away from urban greenspaces or the edge of the urban area. These distances were chosen to represent typical UK suburban habitat and to limit the likelihood of individual birds frequenting more than one feeder. Gardens ranged in size from 100 to 200m^2, representing average UK suburban garden sizes (Gaston et al. 2007). All selected gardens usually provided food year-round in hanging bird feeders, including continuous provision in the three months preceding the experiment. The fieldwork took place in July 2015 over the course of three weeks.

4.3.2. Feeders

The bird feeders used represented typical small feeder types used commonly in the UK (Figure 4.1). Peanut feeders in the UK typically consist of a wire mesh tube with a solid lid and bottom (peanuts and small challenger peanut feeders with 3.6 mm mesh, CJ Wildlife, Shrewsbury, UK). Animals can grip onto the mesh and feed through it so they are not concentrated on any one part of the feeder. In contrast, seed feeders typically consist of a smooth clear plastic tube with a solid lid and bottom with dedicated side ports with perches where the animals feed (small ring pull seed feeders from Jacobi Jayne & Company, Kent, UK; typical UK seed mix provided by Birds & Bees, Cambridgeshire, UK).

All feeders were sterilised prior to deployment; they were immersed in a bleach solution (~0.5% chlorine) in sterile water for 10 minutes, then rinsed in sterile water and allowed to air dry. Feeders were then sealed in sterile bags for transportation.

Each garden received a set of four bird feeders; one full seed feeder, one full peanut feeder (hereafter referred to as experimental feeders) and one empty seed feeder and one empty peanut feeder (hereafter referred to as control feeders). Owners were provided with enough food for the duration of the study, along with a supply of sterile gloves and scoops to minimise contamination from refilling feeders. All feeders were placed on individual poles. Feeders were grouped together in the open where possible (a minimum of two metres apart) to ensure exposure to similar environmental conditions and to mimic typical garden bird feeder placement. They were also placed at least 1m away from garden boundaries and vegetation taller than 0.5m to prevent vegetation touching the feeders.

Figure 4.1. The two designs of bird feeders used in this study that represent typical designs used in the UK. On the left a peanut feeder, on the right a seed feeder.

4.3.3. Monitoring of feeder use

Feeders were placed for two weeks to allow discovery by the birds prior to camera placement. Feeder visitors were continually monitored using individual infra-red motion triggered camera traps (Ltl Acorn 5310; Ltl Acorn Inc, Wisconsin, USA) for the third week starting 23/07/2015. Camera traps were set to take a single photograph at a minimum of one minute intervals between triggering with a 0.6s lag between the detection of a triggering movement and the camera taking a photograph. As birds are not individually identifiable, only total visits were recorded to feeders. Visits by individuals of the same species were considered separate when either separated by a photograph without the animal or when two or more minutes of time has elapsed without a feeding event. At the end of the third week, feeders were swabbed for bacteria using sterile swabs dipped in and stored in 2ml sterile phosphate buffer solution (PBS). Due to the very different feeder designs, swab samples from the seed feeders were taken from the feeder port area (surface area approximately 3000mm^2 for both ports) while samples from the peanut feeders were taken across the wire mesh surface of the feeder (38000mm^2) as these are the areas animals were expected to be in contact with when feeding. Separate swabs were used for each side of the feeder with 100µl of PBS from one swab per feeder been taken for other purposes prior to freezing to store samples in readiness for DNA extraction.

4.3.4. DNA extraction

Genomic DNA was extracted using a MO BIO PowerSoil DNA Isolation kit (MO BIO Laboratories Inc, California, USA). In the initial processing steps, the cotton tips of frozen swabs from the feeders were broken off and transferred directly into individual a 10ml nutrient broth for each feeder and allowed to grow for 24-36 hours at 27°C. Both swab samples from each individual feeder were pooled for DNA extraction. The bacterial cells were then harvested from the culture following centrifugation at > 8000 rpm (6800 x g) for 3 minutes at room temperature (15–25°C). These pre-treated cell pellets were mixed with 60µl of Solution C1 and transferred to microcentrifuge tubes. The tubes were incubated at 65°C for 10 min and then shaken horizontally at 5.5m/sec for 45sec in a FastPrep-24 homogenizer. The remaining steps were performed following the manufacturer's instructions and the final DNA sample was eluted into 100µl of elution buffer. A sample was electrophoresed in a 0.8% agarose TBE gel to confirm DNA integrity and the concentration was measured using a NanoDrop® ND-1000 UV-Vis Spectrophotometer (NanoDrop Products, Thermo Fisher Scientific Inc, Delaware, USA). The DNA concentration was then adjusted to 50 ng/µl in a ~30µl sample sent for next generation sequencing.

4.3.5. Sequencing and phylogenetic analyses.

The sequences of genetic content from the entire bacterial communities in samples were determined by generating complements to single stranded DNA using Roche 454 Genome Sequencer FLX+ (service provided by Animal Health and Veterinary Laboratories Agency, Weybridge, UK). The sequence output from Roche 454 Genome Sequencer was processed and analysed in CLC Genomics Workbench (version 8.5) software (QIAGEN Bioinformatics, California, USA) following the procedure described in Hamady et al. (2008)**.** Only those sequences >200 bp in length with an average quality score >25 and no ambiguous characters were included in the analyses (Huse et al. 2007). Sequences were assigned to samples by examining the 12-bp barcode. Similar sequences were clustered into operational taxonomic units (OTUs) using cd-hit (17) with a minimum coverage of 97% and a minimum identity of 97%. A representative sequence was chosen from each phylotype by selecting the most highly connected sequence, i.e. the sequence that had the most hits more significant than the BLAST threshold to other sequences in the dataset (Hamady et al. 2008). Representative sequences were aligned using NAST and the Greengenes database with a minimum alignment length of 150 and a minimum identity of 75% (DeSantis et al. 2006a; Sheneman et al. 2006). The PH Lane mask (http://greengenes.lbl.gov/) was used to screen out hypervariable regions after alignment. A phylogenetic tree was inferred using Clearcut (20) with Kimura's two-parameter model. Taxonomic identity of the phylotypes was assigned with BLAST against the Greengenes database by using an E value cutoff of 1e-10 and the Hugenholtz taxonomy (DeSantis et al. 2006b).

4.3.6. Statistical Analysis

Feeder usage was compared between experimental feeder types and between experimental feeders and their paired controls using pairwise tests within gardens for the most common bird species and across all animal visits.

All further analyses where carried out in R version 3.3 (R Core Team 2016). Community analysis was undertaken primarily in the R package vegan (version 2.4-1, Oksanen et al. 2016). To allow comparisons of bacterial community between feeders Shannon diversity indices as common measures of biological community diversity were calculated for each bird feeders OTUs (Magurran 2004; Colwell 2009; Morris et al. 2014). Individual based rarefaction was carried out to produce an OTU rarefaction accumulation curve for each feeder type as a function of the overall number of individuals in the sample. This allows the direct comparison of OTU richness between feeder types while adjusting for potential differences in overall OTU abundance on different feeders that would otherwise skew comparisons (Gotelli & Colwell 2001). In addition, it indicates how representative the samples are likely to be of the whole OTU community. The steeper the slope in the curve the more OTUs there remains to discover, while approaching a plateau in the curve indicates that more intensive sampling is likely to find few additional OTUs and so indicating the sample is representative of the community in question (Hughes et al. 2001). Pairwise tests were used to compare bacterial richness and diversity across feeder experimental feeder types and with their controls (t-tests or Wilcoxon as appropriate to sample normality). R code for community plots and correlations was adapted from Ijaz (2015).

To identify taxonomic groupings significantly associated with specific feeder types we used the R package indicspecies (version 1.7-6, De Cáceres and Legendre 2009). The indicspecies function tests the associations of species patterns with sample groups, allowing the potential identification of indicator taxa through the reporting IndVal and associated p values. Bray-Curtis dissimilarity was used to cluster communities based on shared OTUs as an alternative way of exploring shared communities between feeder types.

We tested to see if there were any correlations (Kendall tau) between the overall reads and richness of bacteria with the commonest bird species or overall. We also tested to see if there were any correlations between bird visits to feeders and the occurrence of the commonest taxa from OTU up to order using Kendall correlation and correcting for the false discovery rate (Benjamini & Hochberg 1995).

4.4. Results

4.4.1. Bird feeder usage

Of the 40 original bird feeders, ten were excluded from further analysis due to camera failure resulting in visit numbers not being recorded, DNA samples being heavily contaminated by volunteers or where DNA extraction failed. This left 15 pairs of experimental feeders and their paired controls (eight peanut and seven seed) from nine gardens. Both pairs of feeder types (all four feeder types) were successfully sampled in six gardens. Across those 30 bird feeders, 15 species of bird and one mammal (Grey Squirrel) were recorded totalling 6717 individual visits across the sample week. The majority (93.4%) of those visits were made up of four species; Blue Tit (26.2%), Great Tit (19.9%), House Sparrow (40.8%) and European Robin (6.5%). Both types of control feeders were essentially ignored by animals, with only 20 visits to control peanut feeders (14 by Blue Tits, eight to one feeder) and seven to control seed feeders (four species, all to one feeder) and so had significantly fewer visitors than experimental feeders ($p < 0.05$ overall and for the commonest four species). This indicates that bacteria present on control feeders should principally be from the environment. One garden recorded only three visits to experimental peanuts and 25 to experimental seed, suggesting it acted similarly to a control apart from containing food. The maximum number of bird visits recorded on experimental feeders was 1012 for peanuts (55.8% House Sparrows) and 936 for seed (98.0% House Sparrows). Blue Tits were the commonest species on experimental peanut feeders (41.1%) and House Sparrows the commonest on seed feeders (67.5%). In pairwise tests within gardens there was no significant difference between experimental feeder usage either overall or by the commonest four bird species, although Blue Tits showed a borderline preference for peanuts and Robins and House Sparrows showed borderline preference for seed feeders (Table 4.1).

Table 4.1. Comparison of median weekly visits (with IQR) by birds to experimental bird feeders for the commonest four recorded species and overall. With paired Wilcoxon tests within study gardens.

Species	Experimental Peanut (IQR)	Experimental Seed (IQR)	W	P
Blue Tit	67 (29 – 313)	10 (3 – 21)	20	0.0625
Great Tit	93 (17 – 182)	5 (1 – 38)	14	0.1056
House Sparrow	5 (0 – 68)	226 (20 – 469)	15	0.0591
Robin	2 (1 – 3)	50 (6 – 102)	20	0.0739
Total Birds	**257** **(247 – 519)**	**510** **(245 – 572)**	**13**	**0.7000**
Grey Squirrel	4 (0 – 12)	0 (0 – 0)	6	0.1814

4.4.2. Samples

In total 1284 unique operational taxonomic units (OTUs) were recorded across all feeder types, generating 70778 reads (Table 4.2). The mean number of OTUs per individual bird feeder was 92.5 (s.e = 8.84, range = 29-222) and number of reads 2359 (s.e = 170.8, range = 779 – 4312). The 28 commonest OTUs (each >1% of the total OTUs) accounted for 68.2% of all OTU reads.

Neither experimental feeder type differed significantly from their paired controls though there was some evidence for a difference in the peanut feeders in raw numbers of OTU reads ($t_7 = 2.01$, $p = 0.084$), but not in number of identified OTUs or Shannon diversity ($p > 0.1$ in both cases; Table 4.2). However, there was no evidence for differences in the seed feeders ($p > 0.1$ in all comparisons; Table 4.2). Experimental peanut feeders held significantly higher numbers of raw OTU reads than paired experimental seed feeders in the same garden ($t_5 = 2.88$, $p = 0.035$), but a significantly lower number of identified OTUs and Shannon diversity ($W = 21$, $p = 0.031$ and $t_5 = 3.78$, $p = 0.013$ respectively; Table 4.2).

Table 4.2. Overall and mean OTU richness and diversity by feeder type with minimum and maximum values.

Feeder type (N feeeders)	Total OTUs Mean ± s.e *(Min – max)*	Total OTU reads Mean ± s.e *(Min – max)*	Total Shannon index H' Mean ± s.e *(Min – max)*
Control Peanut (8)	312 67.0 ± 8.4 *(37 – 95)*	26116 3264 ± 205 *(2579 – 4312)*	2.84 1.71 ± 0.14 *(1.20 – 2.32)*
Experimental Peanut (8)	381 58.4 ± 9.6 *(29 – 108)*	19778 2472 ± 304 *(1542 – 4212)*	3.66 1.89 ± 0.25 *(0.97 – 2.96)*
Control Seed (7)	570 150.3 ± 15.5 *(91 – 222)*	13577 1939 ± 284 *(1158 – 3303)*	3.98 2.93 ± 0.11 *(2.53 – 3.38)*
Experimental Seed (7)	488 103.0 ± 15.6 *(52 – 156)*	11307 1615 ± 254 *(779 – 2316)*	3.99 2.75 ± 0.08 *(2.48 – 3.10)*
Overall (30)	**1284** 92.5 ± 8.8 *(29 – 222)*	**70778** 2359 ± 171 *(779 – 4312)*	**4.32** 2.29 ± 0.12 *(0.97 – 3.38)*

Rarefacted OTU accumulation curves showed that control seed feeders had the steepest rarefaction curve with the highest OTU richness while control peanut feeders had the lowest further indicating the greater OTU richness and diversity on seed feeders (Figure 4.2). Of the rarefaction curves only the two peanut type feeders are approaching plateau, indicating there may be more OTUs in the bacterial communities on seed feeders not detected in this sampling and underlining their greater overall species richness. There was no overlap between samples but paired experimental and control feeders were more similar to each other than to the other feeder type. Only seven OTUs occurred in all four feeder types and two OTUs across three feeder types. More OTUs were shared between the seed feeder types (304) than peanut feeder types (135). However, the majority of OTUs were unique to just one feeder type (832, 64.8%, Figure 4.3).

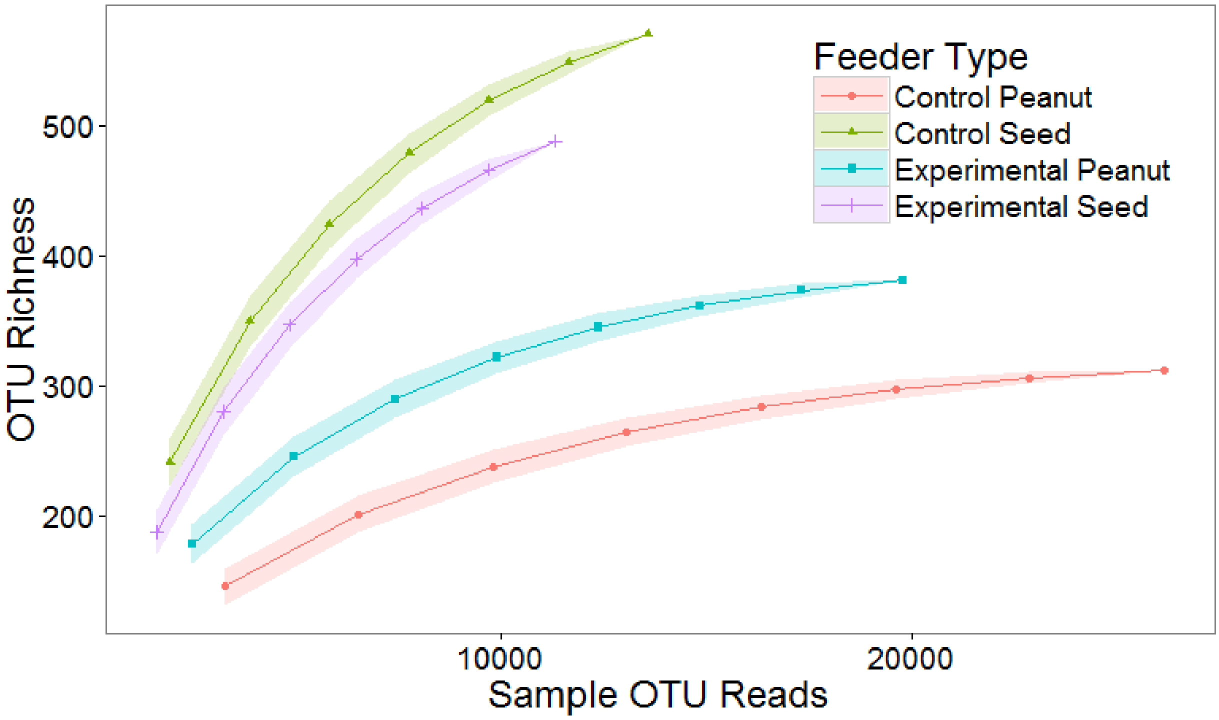

Figure 4.2. OTU rarefaction curves for each feeder type. Each point represents sampling from a garden. Plotted with 95% confidence intervals.

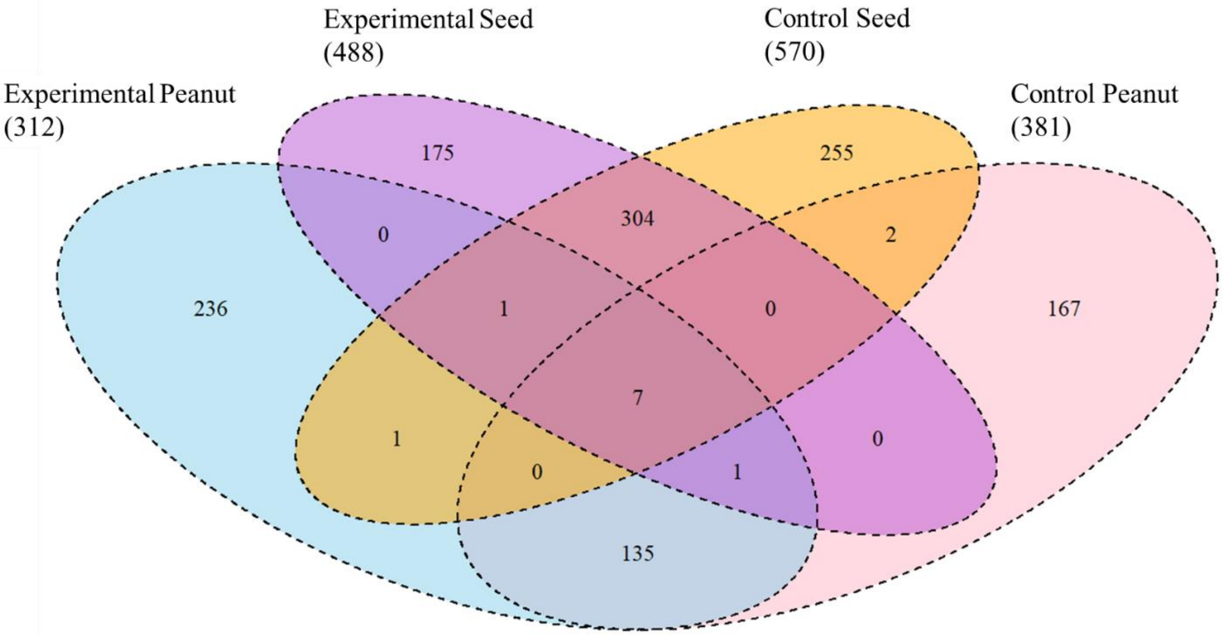

Figure 4.3. Venn diagram of the total, unique and shared OTUs between bacterial communities on the different bird feeder types.

4.4.3. Taxonomic distribution and taxa of note

Bacillales order bacteria were the commonest on the bird feeders (80.1% and 64.2 % of all peanut and seed feeder OTU reads, respectively) and formed more than 75% of bacterial sample OTUs at 20 feeders and only formed less than 50% of samples at nine feeders (Figure 4.4). Across peanut type feeders they formed more than 95% of bacterial OTUs at seven control and four experimental feeders, while they were effectively absent from three feeders (one empty, two experimental). In contrast, they did not form more than 90% of OTUs at any seed feeder, which showed considerably more variation (Figure 4.4). The families *Bacillaceae*, *Paenibacillaceae* and *Planococcaceae* (Rosenberg et al. 2014c) were represented across the feeder types, all of which are common soil bacteria, with the genus *Bacillus* the most frequently detected (Figures 4.4 and 4.5). However, a total of 4646 OTU reads within the *Bacillales* order were attributed to the *Staphylococcus* genus including two potential human pathogen species: *S. aureus* (count of only four reads, two each from an experimental peanut and control seed feeder in separate gardens) which has been associated with skin infections; and *S. sciuri* (1521 reads, 91.1% from a single control peanut feeder), which has been associated with human endocarditis, peritonitis, septic shock, urinary tract infection, pelvic inflammatory disease and wound infections (Chen et al. 2007). The other taxon principally consisting of soil bacteria was the *Microbacteriaceae* family from the order *Actinomycetales* (Rosenberg et al. 2014d) with 2342 reads, 48% from a single experimental peanut feeder and the majority of the rest divided approximately equally between two separate experimental seed feeders (Figures 4.4 and 4.5).

A number of taxonomic groups commonly associated with the gut and/or faeces were found, some of whom can be opportunistic human/animal pathogens (Leclerc et al. 2001; Rosenberg et al. 2014e). These included a number of *Clostridiales* order bacteria (count of 1563 reads, seed feeders only), with small numbers of *Clostridium* genus OTUs found (21 reads across five control seed feeders) (Leclerc et al. 2001; Cabral 2010; Rosenberg et al. 2014c). Other known gut bacteria detected included: members of the *Bacteroides* genus (only six reads total including *B. uniformis* an opportunistic pathogen, experimental seed feeders only); *Bacillus flexus*, associated with soil and bird faeces (6109 reads, 95.8% from three feeders, experimental peanut and control seed feeders within one garden and an experimental seed feeder in another) (Rosenberg et al. 2014a); members of the *Erysipelotrichaceae* family (179 reads, primarily from control seed feeders); *Morganella* and *Plesiomonas* genus bacteria (43 reads, both experimental and control seed feeders) (Rosenberg et al. 2014c).

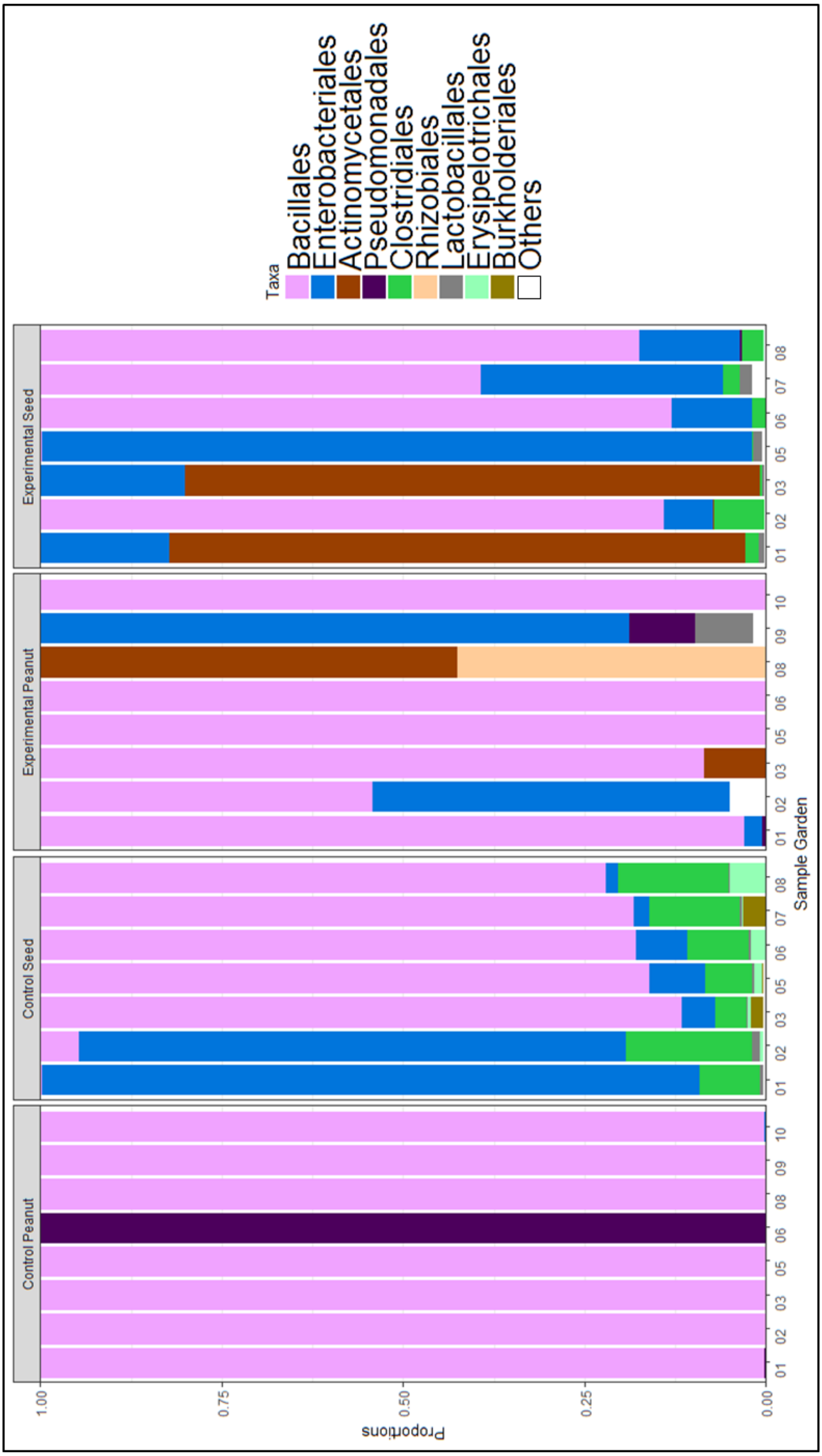

Figure 4.4. Relative abundance of the nine dominant bacterial orders across all sampled bird feeders by feeder type and sample garden.

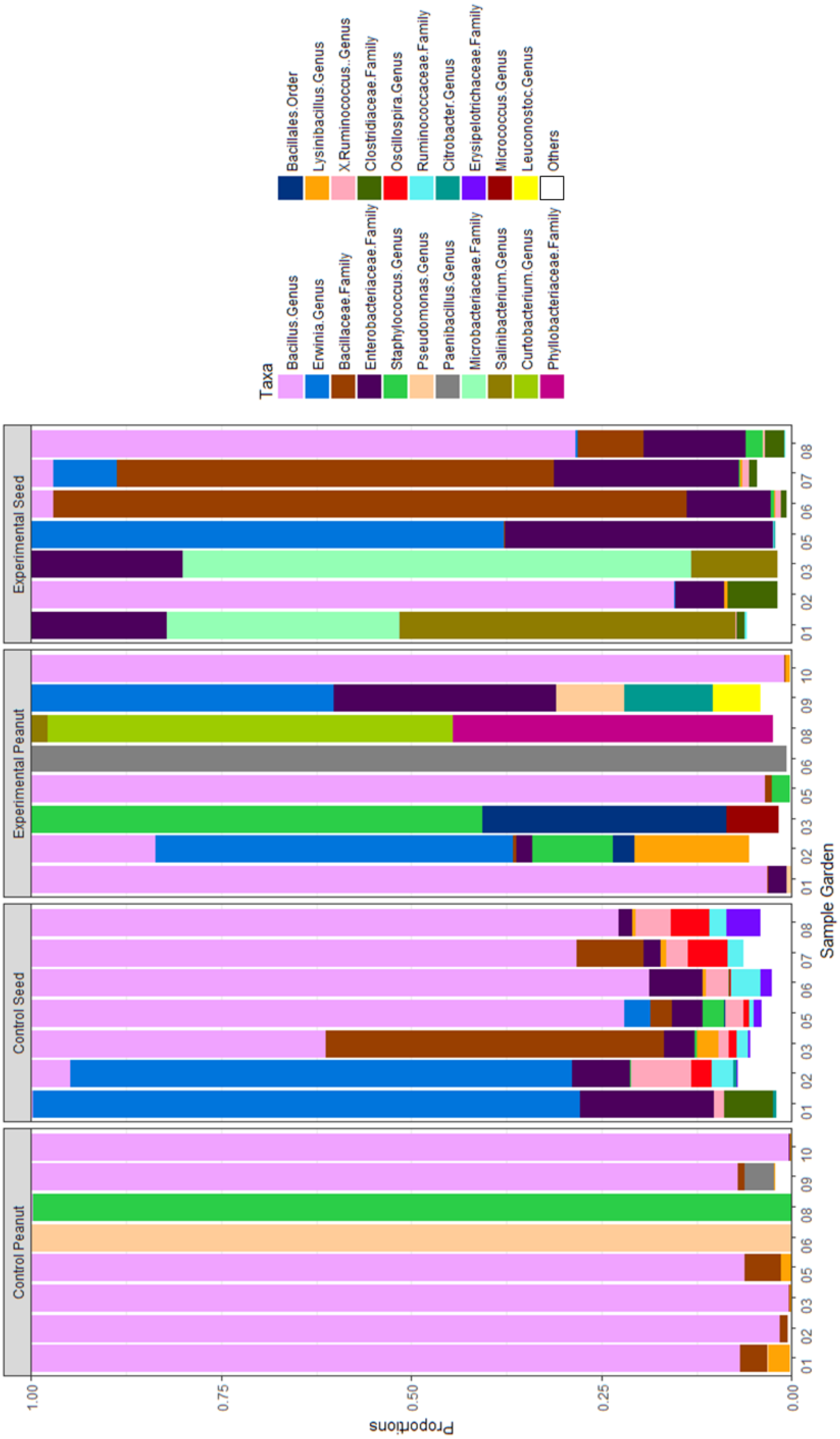

Figure 4.5. Relative abundance down to genus level of the 21 dominant taxa groupings across all individual bird feeders by feeder type and study garden. In the legend the first word indicates the taxa name and the second the taxonomic level.

Detections of other known pathogens were low, with only two reads for *Salmonella enterica* found on an experimental peanut feeder and 15 reads for *Serratia marcescens* found primarily on control feeders. Other potentially pathogenic members of the *Enterobacteriaceae* family (Cabral 2010; Rosenberg et al. 2014b) were also found in larger numbers (total 9319 reads, 8.1% and 22.5% of all peanut and seed feeder reads respectively) including a number of potential plant pathogens (57.3% from the genus *Erwinia*, experimental peanut and both seed feeder types) (Leclerc et al. 2001). OTUs from the *Pseudomonas* genus, which contains both soil bacteria and potential plant and animal pathogens (Cabral 2010), were also detected (2896 total, 91.2% from a single control peanut feeder).

Overall only 0.6% of all seed and 3.3% of all peanut (90.7% *S. sciuri* from a single control peanut feeder) OTU reads came from previously identified pathogenic bacteria. Taking into account known (and suspected) opportunistic pathogens and OTUs not identified to species but in genera containing known pathogens (including opportunists), the total possible pathogens rise to 1.8% of all seed and 17.1% of all peanut feeder OTU reads. In addition, 11.5% of all reads on seed and 6.2% from peanut feeders came from genera containing a number of potential plant pathogens (primarily *Erwinia* from the *Enterobacteriaceae* family) (Rosenberg et al. 2014b).

4.4.4. Indicator taxa and communities

Cluster analysis of OTUs indicated there were no significantly distinct bacterial communities on any feeder type, with little clear separation between feeder types based on Bray-Curtis dissimilarity (Figure 4.6). Of the common bacterial orders detected (> 1% of OTU reads each), no order was significantly associated with a single feeder type. *Clostridiales* were significantly associated with both types of seed feeder ($p = 0.001$) and *Enterobacteriales* were significantly associated with experimental peanut and both types of seed feeders ($p = 0.011$).

Across all 1284 OTUs, 109 OTUs were significantly associated ($p < 0.05$) with individual feeder types (one with experimental peanut, 18 with control peanut, 21 with experimental seed and 69 control seed) and 36 with more than one feeder type (14 with peanut feeders, 22 with seed feeders). However, when only the most common OTUs were considered (>1% of total OTUs), only two OTUs where significantly associated with experimental seed feeders (both *Bacillaceae* family), two OTUs where significantly associated with both peanut feeder types (both *Bacillus* genus) and eight OTUs were significantly associated with both seed feeders types (two *Enterobacteriaceae* family, two *Erwinia* genus, three *Bacillus* genus and one *Bacillus flexus*).

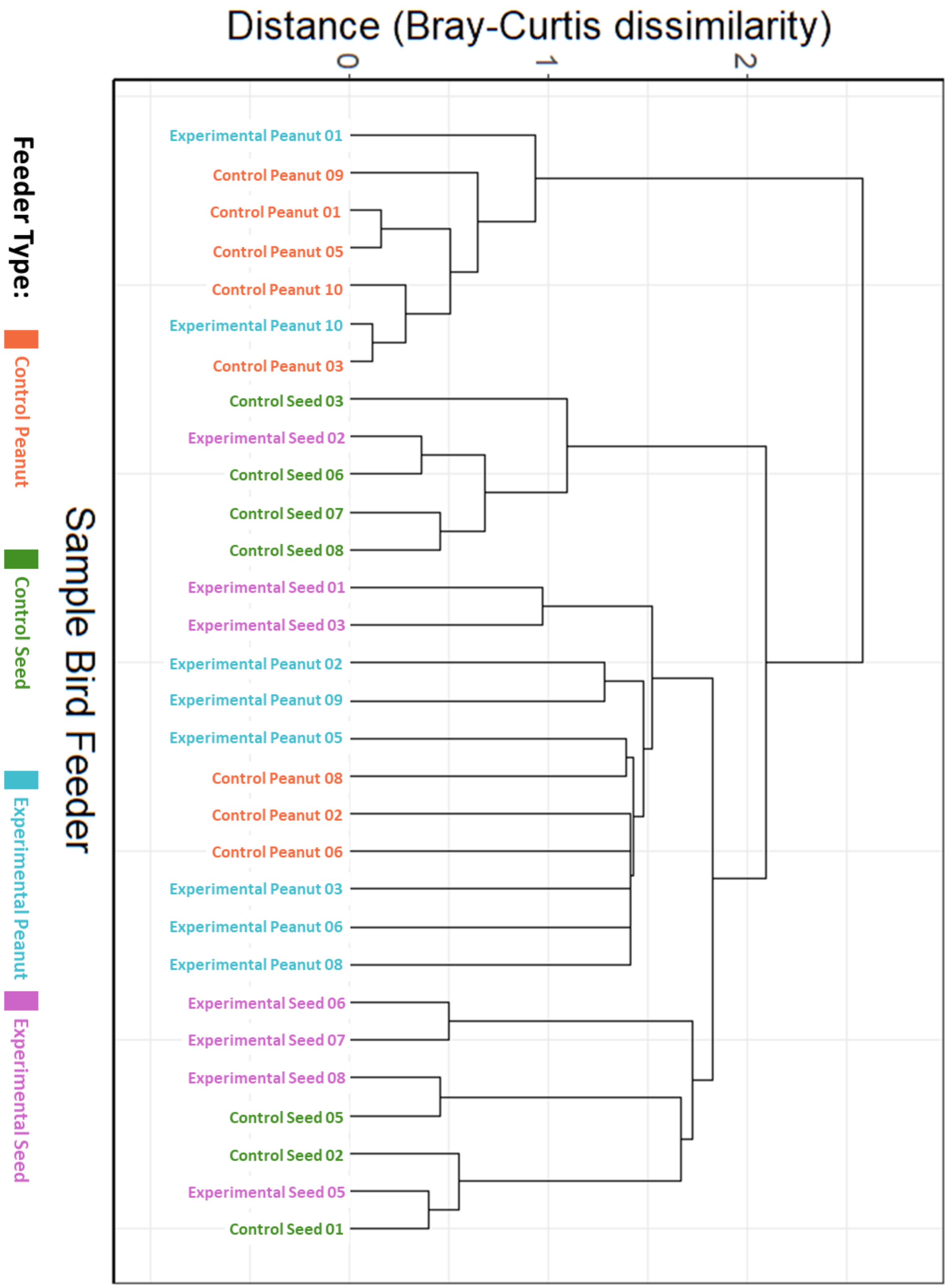

Figure 4.6. Clustering of bird feeder bacterial OTU sample communities using Bray-Curtis dissimilarity.

4.4.5. Birds and Bacteria

There was no significant correlation between overall feeder usage or individual animal species usage and bacterial load (reads or diversity) after adjusting for the false discovery rate (p > 0.1). There were non-significant positive relationships between the abundance of Blue and Great Tits at feeders with the number of reads and negatively with bacterial diversity (OTUs and Shannon diversity). Whereas House Sparrows and Robins showed the opposite relationships. However, plotting suggested that these apparent non-significant relationships were driven primarily by outliers. No significant correlation was found between the abundance of the four commonest bird species, the total number of birds, or Grey Squirrels with the reads of the commonest bacterial taxa (more than 1% of total) at any taxonomic level after adjusting for the false discovery rate (all p > 0.1). There was no significant correlation between feeder usage and the reads of known pathogens or gut flora at the species or genus level (all p > 0.1). There was no general pattern in the relationships with an approximately 50% split in positive and negative relationships between feeder usage and bacterial reads of the bacteria commonest as well as with known pathogens and gut bacteria at the species and genus level.

4.5. Discussion

This study presents the first detailed experimental investigation of bacterial communities on bird feeders using NGS, allowing us to compare two different common bird feeder types (seed, peanut) and their empty controls. This allows the systematic identification and comparison of the bacterial communities in full rather than selective culturing of a small fraction of the community such as that carried out by Foster et al. (2006). The use of automated camera traps allowed us to record the diversity and intensity of use by wild birds and Grey Squirrels. Peanut feeders had significantly higher reads of bacteria but lower OTU diversity than seed feeders. Neither type of experimental feeder differed significantly from their respective controls in terms of overall bacterial numbers, richness or diversity. Although sample sizes were small there is no clear evidence that bacterial load was driven by feeder usage by animals. We suggest that the main driver in bacterial community richness and diversity on bird supplementary feeders is food type and feeder design rather than animal usage with the vast majority of bacteria present coming from the general environment. Many of these bacteria were soil bacteria though potential pathogens were found on both feeder types, including the empty control feeders

Due to differing designs the area sampled on the peanut feeders was significantly larger than on the seed feeders and the sampling swab will have come in direct contact with the peanuts due to the peanut feeder mesh design, unlike the port design on seed feeders. This may account for the significantly higher numbers of bacteria detected on the peanut feeders though does not explain the significantly lower diversity or proportionally higher number of OTUs on seed type feeders. The majority of identified bacterial OTUs came from soil bacteria and other environmental bacteria, particularly in the *Bacillales* order and within that the *Bacillus* genus (Janssen 2006) though seed feeders showed considerably more variation than peanut feeders. The individual rarefaction curves for each feeder type do not plateau, suggesting that the full bacterial community has not been sampled (Hughes et al. 2001; Colwell 2009), particularly for the seed feeder bacteria. However, these rarefaction curves provide further evidence that the community diversity was comparatively higher on seed feeders than peanut feeders and while all the curves were distinct from each other they were most similar between paired experimental and controls feeders. This was reflected in the numbers of OTUs shared within but not between feeder types. This further indicates the bacterial community structure may be driven primarily by the effects of the feeder design on the accumulation of environmental bacteria rather than the animals utilising them.

Despite the similarities found between feeder communities, the majority of individual OTUs detected were unique to a single feeder type. A number of OTUs (109, 8.5%) were significantly associated with a single feeder type with 69 of those associated with control seed feeders. A further 36 (2.8%) were associated with either both peanut or both seed type feeders. The majority of these potential indicator OTUs were rare in the samples with only 12 indicator OTUs individually making up more than 1% of the sampled OTUs all from the *Bacillaceae* or *Enterobacteriaceae* families. This makes establishing clear indicator OTUs for both feeder types and in turn linking them to feeder usage difficult, particularly with so many of these significantly associated with control feeders in this study.

Although there was considerable variation between individual feeders and sample sizes were small, there was little difference in overall usage between the experimental feeders containing the two food types, so bird use appears to be unlikely to explain the differences in bacterial communities between feeder types in this study. This is underlined by the lack of differences in bacterial numbers and diversity between experimental feeders and their respective, effectively unvisited, controls. In addition, we find no evidence for significant associations between the reads of the most common bacterial taxa and the most common bird species or overall feeder usage. An alternative choice of experimental food types may have resulted in significantly different bird communities on the different feeders even in the same garden (Horn et al. 2014; Chapter 2). This in turn could result in different bacterial communities, but the choice of food types in this study was representative of food provided in a typical UK garden (Orros & Fellowes 2015b).

Our results suggest that at least over a relatively short period of time and in respect to bacteria only, bird feeders may not represent as significant an infection risk to birds as previously feared. However, we have not explored the risks of other pathogens in this study and many bacterial OTUs could not be identified to species, genus or even family level (Caron et al. 2009), possibly resulting in some bacterial pathogens been overlooked. Of the bacterial pathogens regularly linked with bird feeder using passerines, only *Salmonella enterica* was detected in a very small (two) single feeder count (Benskin et al. 2009; Lawson et al. 2014; Krawiec et al. 2015; Galbraith et al. 2017).

We did document a number of other known/potential animal pathogens, including some associated with risk to human health, across the feeders with proportionally more recorded on peanut than seed feeders. Nevertheless, they were still a minority on all feeder types and many are opportunistic in nature (Rosenberg et al. 2014e). Due to the very low relative abundance of such pathogens it is difficult to specifically associate pathogens with bird usage, particularly as many were found on the control feeders. This would suggest either that the rare visitors to these feeders carried pathogens, or alternatively that the detected pathogens/potential pathogens were present in the environment already with little connection to bird feeding habits. Although not of direct interest to human or bird health it is interesting to note the number of potential plant pathogens primarily associated with seed feeders, particularly from the *Erwinia* genus which may be of interest to research on the spread of plant pathogens.

The small sample size used in this study coupled with the random effects that must be accounted for in the analysis from using different gardens limited our statistical power to explore the relationships between feeder types, bird communities and bacterial communities further. This was largely due to feeder sample losses and the costs of Next Generation Sequencing limiting the number of samples that could be processed. This lack of statistical power could be remedied in several different complementary ways. Most simply greater hygiene precautions could be taken to reduce the possibility of contamination and the whole experimental set up checked at least daily to ensure the cameras functioned correctly. If cost were no longer an issue, more study gardens could be used to provide more samples and to increase the number of replicates per study garden, the bird feeders could be replaced with freshly disinfected feeders at the end of each sampling period and the process repeated further. This would not only increase the number of replicates, it would also extend the study timeframe and allow us to consider if and how communities change over time. If replicates were spread throughout the year then seasonal variation of bird and associated bacterial communities could be explored together. Comparing bacterial communities in the winter when bird numbers at feeders peak against in the summer when feeder usage is likely to be lowest (Cannon et al. 2005; Chamberlain et al. 2005; Chamberlain et al. 2007) would be particularly valuable in exploring the spread of pathogens at bird feeders.

All feeders were exposed to the same general environmental conditions but variation in individual exposure, particularly to sunlight, may have influenced final bacteria reads (Sinton et al. 2002; Vermeulen et al. 2008; Pereira et al. 2014). Manipulating these environmental conditions such as placement in shading or perhaps more importantly comparing across different seasons may result in changes in the bacterial communities. In particular further investigations in winter when birds use feeders at higher rates and are believed to be at higher risk of infection could yield important results (Nelson & Demas 1996; Chamberlain et al. 2005). The use of volunteers to fill the feeders may also have increased the risk of contamination but given the similar high levels of bacteria on the control feeders we suggest that this was minimal. The infrequent presence of Grey Squirrels may have confounded the results so excluding them may be advisable in future studies. However, it is possible they may act as a vector of some bacterial pathogens and they are common users of many UK garden feeding stations (Bonnington et al. 2014a; Chapter 2).

Aside from the potential contamination from the volunteers and the few animals that visited them, the main source of contamination on control feeders as well as a major contributor to bacterial communities on the experimental feeders is likely to be bacteria spread by aerosols colonising the feeders (Lindemann & Upper 1985; Brodie et al. 2007; Smith et al. 2013). Urban aerosols have been found to harbour diverse bacterial communities including pathogens with temporal meteorological conditions playing an important role in their spread (Brodie et al. 2007). In addition invertebrates, particularly insects alighting on the feeders may also act as microbial vectors, leaving bacteria on the feeder surfaces including potential pathogens (Hirano & Upper 2000; Nadarasah & Stavrinides 2011).

It is important to consider when viewing these results that bird feeders themselves may still represent a significant transmission risk for other pathogen types. Although bacteria represent a good model taxa for studying zoonotic transmission within birds and from birds to humans, other pathogens potentially transmitted on and around supplementary feeding stations may spread differently (Benskin et al. 2009). These other pathogen types include some major pathogens of conservation. For example, a strain of *Trichomonas gallinae* (a protist), affecting Greenfinches and to a lesser extend Chaffinches *Fringilla coelebs*, believed to be transmissible at bird feeders has contributed to significant population declines of these species across the UK (Lawson et al. 2011a; Lawson et al. 2011b; Lawson et al. 2012b). Bird feeders may also be linked to the spread of a form of the avian pox virus in tit (Paridae) species across the UK (Lawson et al. 2012a).

If transmission on hanging bird feeders is less common than supposed, it may instead occur elsewhere in the vicinity of feeding stations. Bird droppings along with dropped food can accumulate on the ground below feeders, and many common UK garden birds are primarily ground feeders (such as Chaffinches, Dunnocks, Robins and thrushes). Platform feeders and bird baths (Cabral 2010) may also generally represent a greater risk of infection than hanging feeders for similar reasons (Foster et al. 2006). In addition, over time faeces can build-up on hanging feeders to also increase transmission risk, although exposure to rain and sunlight may mitigate this.

A more direct way to explore the role of wild birds as microbial vectors around bird feeders would be to catch and take samples from them directly, such as by using cloacal swabs (Galbraith et al. 2017). Not only would this allow the comparison of individual birds and species microbial loads but also offer another way to explore the relationship between bird feeder use and bacterial load. Blood samples can also be used to detect the presence of some pathogens in bird populations (Wilcoxen et al. 2015) and again could be used to explore the prevalence and transmission of these pathogens at feeders.

Frequent users of supplementary food, such as finches (*Fringillidae*) and House Sparrows, have regularly been recorded with mortality-causing bacterial infections such as listeriosis, conjunctivitis, salmonellosis and staphylococcosis (Fischer et al. 1997; Pennycott et al. 2006), although a range of species can be affected (Benskin et al. 2009). Deaths from such outbreaks are often detected near feeding stations where infected birds often continue feeding until death and so potentially contaminate feeders and their surroundings (Hotchkiss et al. 2005). However, this is largely correlative, and may simply reflect the fact that disease is noted where birds are found at higher densities and more likely to be observed. Conclusive evidence is generally lacking as to whether feeders are a major source of infection (Benskin et al. 2009; this study) though there are identified exceptions, such as the spread of the bacterial pathogen *Mycoplasma gallisepticum* (a causative agent of conjunctivitis) in the House Finch (*Haemorhous mexicanus*) at North American bird feeders (Dhondt et al. 1998; Hotchkiss et al. 2005; Adelman et al. 2015).

The density of gathering and interactions between birds on and around supplementary feeding stations has few natural parallels for many of the bird species that typically use them (Chamberlain et al. 2005; Galbraith et al. 2015), with the possible exception of non-breeding season flocking and roosting behaviour in some species. This means that even if pathogens are not commonly present on or around supplementary feeders under typical conditions, the potential for their transmission within and between species at these unnatural point sources may be high when they are (Benskin et al. 2009; Lawson et al. 2014). As birds are more likely to gather at feeding stations in the winter when natural resources are low (Cannon et al. 2005; Chamberlain et al. 2005; Chamberlain et al. 2007) and their immunity function possibly depressed (Nelson & Demas 1996), the possibility of pathogen spread on and around feeders and the need to take remedial steps increases.

Monitoring such pathogens and outbreaks in wild bird populations offers an important source of information for wildlife conservation, as well as for human and domestic animal health (Murray et al. 2016). Salmonellosis provides a strong example of this as outbreaks in wild birds (including garden birds), domestic animals and humans have been associated in the past (Tauni & Österlund 2000; Andres et al. 2013; Lawson et al. 2014) though how important small wild birds are as a zoonotic salmonella reservoir is unclear and is probably low (Rouffaer et al. 2016). Other zoonotic pathogens such as avian influenza provide similar examples of why we must monitor pathogens in wild as well as domestic animals (Sanchez et al. 2016). Although we find minimal evidence for bird feeders being an infection risk for bacterial pathogens in the UK, it is important for bird feeding members of the public to be aware wild birds can carry zoonotic pathogens as well as ones that threaten birds themselves. Sensible routine hygiene precautions such as hand washing, regular feeding station cleaning and avoiding direct contact with bird faeces and carcasses should be carried out (Lawson et al. 2014) as well as considering removing feeders entirely during serious outbreaks (Murray et al. 2016).

We suggest that the normal prevalence of bacterial pathogens around bird feeders may be low, and that their diversity and abundance is in part driven by differences in feeder design. These results should not negate the possibility that bird feeders overall may represent an important point source of pathogen transmission in garden birds, and from them to humans. Further direct studies are required to establish the role of bird feeders in the transmission of both bacteria and other pathogens to assess the true risk of transmission on and around different types of bird feeders and food types. With the sheer prevalence and popularity of garden bird feeding in the UK and many other countries, it is vital to ensure that we not inadvertently putting the health of wild birds or the people who care for them at risk.

Chapter 5: Use of anthropogenic material affects bird nest arthropod community structure: influence of urbanisation, and consequences for ectoparasites and fledging success

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5.1 Abstract

Nests are a critically important factor in determining the breeding success of many species of birds. Nevertheless, we have surprisingly little understanding of how local environment helps shape materials used in construction, how this differs among related species using similar nest sites, or if materials used directly or indirectly influence the numbers of offspring successfully reared. We also have little understanding of any potential links between nest construction and the assemblage of invertebrates which inhabit the nest and in particular, with ectoparasites. We addressed these questions by monitoring the success rates of nest-box using Blue Tits and Great Tits, from rural, urban greenspace and urban garden settings. We collected used nests, identified arthropods present, and measured the proportions of highly processed anthropogenic materials used in their construction. Some 25% of Great Tit nest materials were of an anthropogenic source and this was consistent across habitats, while Blue Tits used little (1-2%) except in gardens (~16%), suggesting that Great Tits preferentially sought out these materials. In fledged nests, increasing use of anthropogenic material was associated with lower general arthropod diversity and ectoparasite predator abundance (Blue Tits only) but higher levels of Siphonapterans (fleas). Higher arthropod diversity was associated with lower flea numbers, suggesting that increased diversity played a role in limiting flea numbers. No direct link was found between breeding success and either anthropogenic material usage, or arthropod diversity and abundance. However, breeding success declined with increasing urbanisation in both species and increased with nest weight in Blue Tits. The interplay between urbanisation and bird ecology is complex; our work shows that subtle anthropogenic influences may have indirect and unexpected consequences for urban birds.

5.2. Introduction

Today, over half of the world's population lives in ever-growing towns and cities (UN 2011), and these urban areas are increasingly recognised as being of considerable value for bird diversity and abundance (Gregory & Baillie 1998; Davies et al. 2009; Evans et al. 2011; Aronson et al. 2014). The changes in habitat and resource availability associated with urbanisation have a marked effect on the life histories of urban birds (Chace & Walsh 2006). Urban-dwelling birds tend to lay eggs earlier, produce smaller clutches and lighter nestlings, and have lower average productivity per nesting attempt than their non-urban conspecifics (Chamberlain et al. 2009). The lower availability of natural foods in urbanised areas results in lower food provisioning to nestlings, and while supplementary feeding can be ubiquitous in urban areas (Davies et al. 2009, Orros and Fellowes 2015a, Hanmer et al submitted a), the benefits for bird productivity are not clear (Robb et al. 2008b; Harrison et al. 2010; Plummer et al. 2013a).

Many wild bird species utilise a diversity of urban habitats, and private suburban gardens are particularly important in this context (Cannon et al. 2005; Chamberlain et al. 2005). Aside from the provision of supplementary food, other resources provided by people helps support some urban bird populations. In the UK it is estimated that more than one in five gardens contains a bird nest box, equating to a minimum of 4.7 million nest boxes, nationally equivalent to the provision of one nest box for every six breeding pairs of cavity nesting birds (Davies et al. 2009). The availability of suitable nesting sites limits breeding density (Newton 1998) and with the removal of mature and dead trees typical of suburbia, there will be fewer natural nest sites in such areas (Wiebe 2011). Buildings may provide some cavities but modern or refurbished houses tend to have fewer potential nesting holes to compensate for this loss (Mason 2006; Shaw et al. 2008). As a result, the provision of nest boxes in urban areas may be a particularly valuable resource, allowing cavity nesters to prosper (Chace & Walsh 2006; Wiebe 2011) and providing an opportunity to investigate factors affecting urban bird breeding biology.

Despite the potential importance of nest site provisioning and the influence of urbanisation on wild bird populations, our understanding of the effect of urbanisation on bird nesting biology remains relatively limited (reviewed in Deeming and Reynolds 2015). Factors that potentially effect breeding success are of considerable interest, and species that utilise nest boxes offer a practical way to explore these effects (Croci et al. 2008). There are several possible ways that urbanisation can influence bird nests themselves. There is evidence for geographic variation within species in nest construction, with nests constructed in cooler regions typically being larger and better insulated (Deeming et al. 2012; Mainwaring et al. 2014a; Biddle et al. 2016). Due to the urban heat island (UHI) effect increasing local environmental temperatures, it is plausible that nests from more highly urbanised areas may need less insulation, leading to smaller, lighter nests requiring less energy investment to build.

However, there is little if any evidence that a change of the magnitude associated with the UHI effect influences bird reproduction (Deviche & Davies 2014).

Increased urbanisation may also be associated with a change in the proportion of anthropogenic material incorporated into nests (Reynolds et al. 2016). Given the general decline in biodiversity seen with increasing urbanisation (McKinney 2008), the availability of some key natural nesting materials may diminish, while the availability of potentially suitable anthropogenic alternatives is likely to increase. Depending on behavioural preferences and nest location this may cause some birds to expend more energy finding suitable natural nesting material or instead they may utilise whatever is readily available (Britt & Deeming 2011), and so with higher levels of urbanisation incorporate more anthropogenic material into their nests (Wang et al. 2009; Reynolds et al. 2016). Given the potentially high insulation value of some anthropogenic materials they may be preferred and such preferences (if any) may differ between species (Surgey et al. 2012; Suárez-Rodríguez et al. 2013). Anthropogenic material incorporated into nests may also be hazardous to bird survival and breeding success, particularly by causing entanglement (Votier et al. 2011; Townsend & Barker 2014), but possibly also through more subtle effects on bird health. For example, House Sparrows incorporating discarded cigarette butts into their nests reduce their ectoparasite load at the cost of exposure to toxins (Suárez-Rodríguez et al. 2017). For the purposes of this study we define anthropogenic material as highly processed anthropogenic material (e.g. polyester, nylon, highly processed cotton), although we are aware that hair from human-associated animals and material from exotic garden plants could be considered to be anthropogenic in origin.

Changes in nest construction may in turn influence the invertebrate assemblage present in nests, of which changes in the presence and abundance of bird ectoparasites is of primary interest in this context. The influence of nest construction on ectoparasite load has been explored in a number of studies (e.g. Moreno et al. 2009, Suárez-Rodríguez et al. 2013) but only one has previously occurred in the European urban environment (Reynolds et al. 2016), focusing on fleas and Blue Tits. Generalist nest-dwelling ectoparasites such as fleas (Siphonaptera) and biting mites (Acari, principally from the family Dermanyssidae) are common in passerine nests (Moreno et al. 2009; Cantarero et al. 2013), but the latter are rarely considered.

Ectoparasites may influence reproductive success in a number of ways, such as by reducing nestling growth and survival (Merino & Potti 1995) or by affecting adult health (Tomás et al. 2007), possibly leading to nest desertion (Oppliger et al. 1994). Nest composition may influence ectoparasite load by affecting larval mortality and growth through effects on nest humidity (Heeb et al. 2000) or through the attraction/repellence effects of the materials themselves (Remeš & Krist 2005; Mennerat et al. 2009a; Tomás et al. 2012). As nest construction and host defence behaviour may differ significantly between species utilising similar nest sites in a local area, ectoparasite loads may also differ (Moreno et al. 2009).

Bird nests are also potentially home to a diverse array of non-parasitic arthropods (Tryjanowski et al. 2001). To our knowledge, no studies have considered the influence of nest construction on this diversity in the context of urbanisation. In turn it is unclear what (if any) effect these arthropods have directly or indirectly on the breeding success of birds. Notably, Krištofík et al. (2017) found that adding saprophagous larvae of *Fannia* sp. to nests containing young European Bee-eaters *Merops apiaster* increases nestling condition, as the larvae consume nest and nestling waste and detritus and so improve conditions in the nest cavity. While unstudied, some invertebrates may also predate other nest-dwelling invertebrates, including ectoparasites, depressing their numbers and thus potentially increasing bird productivity. Just how urbanisation affects this diversity is not understood; it is possible that diversity will decline with increasing urbanisation, as more generally found with invertebrates (McKinney 2008; Jones & Leather 2012). Irrespective of the relationship, we hypothesise that increased diversity in the nest may be associated with increased nesting success.

Taken together, it is evident that nest material could influence breeding productivity, and may also influence ectoparasite load. What is not clear is if there is a consistent influence of urbanisation on these factors, if species show similar responses, or if the wider nest arthropod community also varies with urbanisation. To examine this we compared the a) nesting materials, b) ectoparasite load, c) the assemblage of other arthropods and d) fledging success, of two common British urban ‘adapter’ passerine species, the Blue Tit and Great Tit, at different levels of urbanisation in and around a large urban area.

5.3. Materials and Methods

5.3.1. Study areas

This study was conducted in and around the large urban district centred on Reading, South East England, between April and June 2016. Greater Reading covers approximately 72 km^2 and has a population of ~290 000 people (Office for National Statistics 2013; following Orros & Fellowes 2015b).

Volunteer garden owners were recruited across Reading through other studies previously run by the People and Wildlife research group, leafleting and word of mouth. Additional nest boxes were monitored on the grounds of the University of Reading, the Hill Primary School and Beale Wildlife Park and Gardens in addition to Maiden Erlegh Lake, Lavell’s Lake and Hosehill Lake local nature reserves (Figure 5.1).

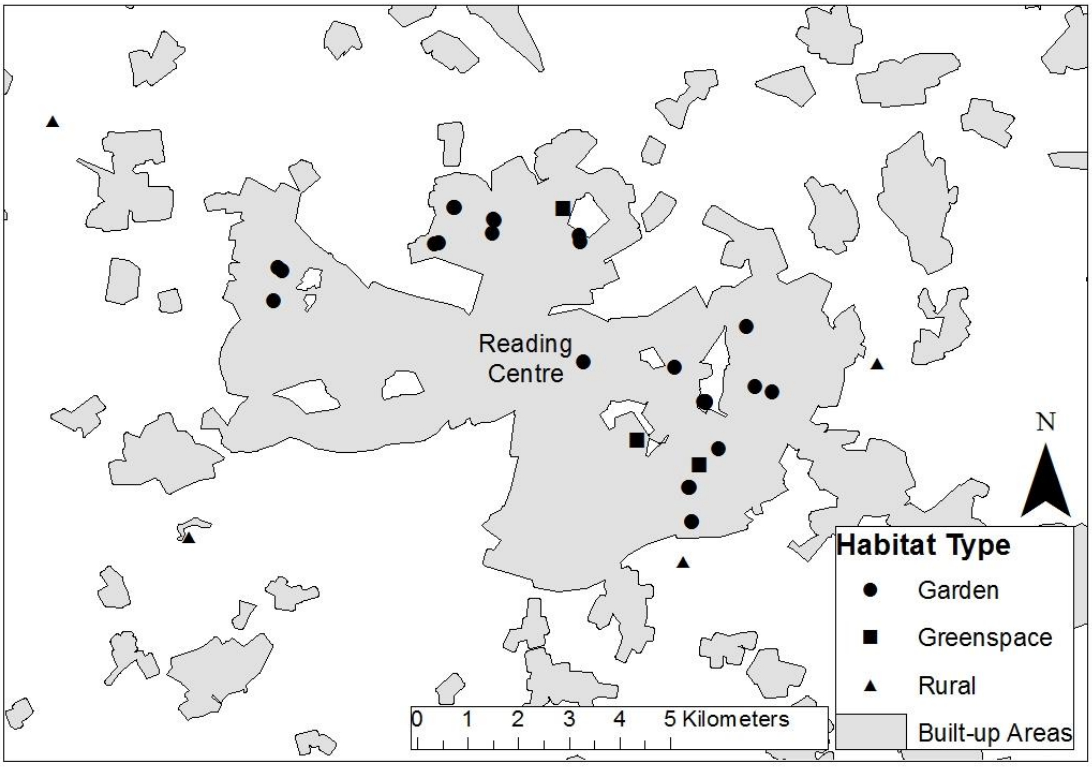

Figure 5.1. The distribution of study sites in and around the Greater Reading area marked by broad habitat type.

5.3.2. Nest monitoring

Nest boxes were monitored from early April until the final fledging in late June. Only one breeding attempt per nest box was monitored and all boxes were cleared of old nesting material prior to the breeding season. Approximately 350 potentially useable nest boxes were monitored for this study. Once a nesting attempt was found it was checked up to twice a week until fledging or confirmed failure following the British Trust for Ornithology (BTO) Nest Record Scheme (https://www.bto.org/volunteer-surveys/nrs). All surviving chicks were ringed at approximately 14 days old under BTO Ringing Permit C5258. Dead chicks were removed whenever found during monitoring. All nest boxes were measured to establish their internal dimensions and their locations plotted using a GPS (GPSMAP 60CSx, Garmin, USA). Within sites, boxes were of effectively the same design and size but there was some variation between sites which was controlled for in the analysis by the inclusion of site as a random factor in the mixed models.

5.3.3. Nest materials and arthropod load

Successful nests were removed between two days and three weeks of the estimated fledging date and sealed in plastic bags (Moreno et al. 2009). Failed nests that had grown chicks were removed when all chicks were found to have died or being predated. Nests that failed as eggs were removed when the nest had apparently been abandoned for at least a month beyond the estimated hatch date and there was no evidence of adult attendance. Fully predated nests were removed when they were found, provided significant damage had not been done to the nest that removed material. All remaining unhatched eggs and dead chicks were disposed of during removal. Nests were removed during the breeding season under Natural England license 2016-23468-SCI-SCI granted to H.J.H. All bagged nests were stored in a cold room at c.5°C for up to 4 weeks. They were then placed in Tullgren funnels equipped with 60W bulbs to extract invertebrates and dry the nests for 48hrs. Dried nests were weighed to the nearest 0.01 g on an electric balance. Nest materials were then broken down into apparently natural material from the environment (plant matter and natural fibres such as animal hair) and processed anthropogenic material (primarily dyed, treated cotton and artificial materials), and each element was weighed separately.

Extracted invertebrate samples from each nest were collected and stored in tubes containing 40 ml of 70% ethanol solution. Due to variation in collection time in failed and some fledged nests, invertebrate data was only collected from the successful nests removed within 3 weeks of fledging. Arthropods were sorted under a dissecting microscope (maximum magnification x100; Nikon SMZ645, Nikon, Japan) to Order and subsequently identified to lower taxonomic levels where practical, particularly in the case of likely ectoparasities. All arthropods were individually counted, with the exception of flea larvae where numbers were on rare occasions very large. In this situation a subsample of 25% of the material was counted, and total numbers of larvae then extrapolated. Shannon diversity indices at the Order level were calculated for each fledged nest examined for arthropods.

Habitat data for each collected nest was established for a 200m radius around each nest box in ArcGIS 10.0 (ESRI 2011) using data from the Ordnance Survey Mastermap collection (EDINA 2016, University of Edinburgh) land use data. Habitat/land use categories within 200 m of collected nests were grouped together to form four broad categories: constructed surfaces (buildings, roads, driveways and pavements), natural surfaces (trees, scrub and grassland), water bodies (primarily lakes and ponds) and private gardens (defined as garden mixed surfaces).

5.3.4. Analysis

All analyses were carried out within program R, version 3.3 (R Core Team 2016). Due to the low sample sizes, particularly for Great Tits leading to the selection of Null models in model selection, a mixed analysis approach was adopted, utilising both non-parametric and modelling approaches to explore the various relationships of interest. Given a larger sample size a purely modelling based approach would have been adopted. Mann Whitney U tests were used to compare between bird species and within species between broad habitat types (Garden, Greenspace and Rural) for productivity and nest construction. Spearman's rank correlation was used to examine the relationship between percentage habitat cover and nest construction across all collected nests. For the subset of fledged nests collected under a standardised methodology and fully examined for arthropods, Mann Whitney U tests were carried to compare between species overall and within species between broad site types for ectoparasite abundance, a measure of arthropod predator abundance (total numbers of Pseudoscorpionida, Staphylinidae and Histeridae) and arthropod diversity. For all multiple comparisons p was automatically corrected for the false discovery rate within R.

Separate mixed effects models for Blue Tits and Great Tits were carried out using R package lme4 (version 1.1-12; Bates et al. 2015) to examine effects of nest construction and habitat separately on the proportional usage of anthropogenic material and overall nest fate (both Binomial models) along with the number of eggs laid and number of chicks fledged in failed and successful nests (both Poisson models). Predated nests were excluded from models examining nest fate and the number of chicks fledged to control for the influence of direct nest predation on breeding success (Lambrechts et al. 2016a). Separate additional mixed effect models were run for the subset of nests examined for arthropod diversity and ectoparasite load. These examined Shannon diversity (linear model), overall flea abundance (Poisson model), overall Dermanyssidae mites abundance (Poisson model) and the presence/absence of Dermanyssidae mites (Binomial model). To explore influences on these factors along with nest construction and habitat, final models considered all potential factors influencing number of eggs laid and chicks fledged just for these nests.

In all mixed-effect models, individual study site (rather than broad site type) was treated as a random effect to account for the potential non-independence of nests from the same site and for the slight variation in box design between sites. In overdispersed models, individual nest identity was added as an additional random effect (Harrison 2014). Nest boxes within 200 m of each other, or on the same property/reserve were considered to be from the same site. Model selection was carried out on the global models using delta AIC_cs and model weights (Burnham & Anderson 2002). From the models within delta 2 AIC_c of the AIC_c selected model, predicted lines of best fit with 95% confidence intervals were calculated for plotting. With the exception of Shannon diversity models the proportion constructed surfaces was used as a measure of urbanisation. In the Shannon models the total proportion of green surfaces (natural surfaces and gardens) was found to produce more stable models and so was utilised instead whereas the reverse was true for models considering all other dependent variables. For models considering the number of chicks fledged, clutch size was used as a fixed factor to account for any relationship between the two.

5.4. Results

5.4.1. Overall nests

In total 98 nests (62 Blue Tit and 36 Great Tit) were fully monitored and deconstructed. Of them 60 (35 and 25 respectively) apparently fledged at least one chick while the other 38 (27 and 11 respectively) failed at either the egg or chick stage. Five Blue Tit and one Great Tit nest seemingly failed due to direct predation. Breeding and nest construction parameters for collected nests at different levels of urbanisation are summarised in Table 5.1.

Table 5.1. Summary of productivity parameters and nest construction for collected Blue Tit and Great Tit nests in the study. Median values with interquartile ranges are included to summarise variation in the data where appropriate.

Species	Habitat	Overall success rate	Eggs laid	Chicks fledged	Proportion Anthropogenic Material	Nest dry weight (g)	Nest box base surface area (cm^2)	N nests (sites)
Blue Tit	Rural	0.79	8.0 (7.0 – 8.5)	4.0 (2.0 – 6.0)	0.02 (0.00 – 0.08)	25.1 (22.9 – 27.1)	150 (149 – 221)	29 (4)
	Greenspace	0.42	8.0 (6.5 – 9.0)	0.0 (0.0 – 4.0)	0.01 (0.00 – 0.14)	20.2 (17.2 – 24.5)	150 (144 – 180)	27 (4)
	Garden	0.53	8.0 (7.0 – 8.3)	0.5 (0.0 – 2.3)	0.16 (0.01 – 0.25)	22.4 (18.9 – 25.7)	161 (128 – 190)	16 (15)
	Overall	**0.56**	**8.0** **(7.0 – 9.0)**	**2.0** **(0.0 – 4.8)**	**0.02** **(0.00 – 0.16)**	**22.7** **(18.3 – 25.9)**	**150** **(144 – 192)**	**62** **(23)**
Great Tit	Rural	1.00	7.0 (6.0 – 7.0)	5.0 (4.0 – 5.0)	0.23 (0.17 – 0.33)	30.4 (24.5 – 38.8)	221 (150 – 221)	9 (5)
	Greenspace	0.67	6.0 (4.0 – 6.0)	1.0 (0.0 – 3.0)	0.25 (0.05 – 0.31)	22.7 (17.3 – 31.7)	150 (150 – 192)	21 (4)
	Garden	0.44	6.5 (5.3 – 7.0)	0.5 (0.0 – 1.8)	0.25 (0.21 – 0.27)	27.0 (20.2 – 29.2)	166 (159 – 207)	6 (3)
	Overall	**0.69**	**6.0** **(5.0 – 7.0)**	**2.0** **(0.0 – 4.0)**	**0.24** **(0.12 – 0.32)**	**25.0** **(18.7 – 34.0)**	**157** **(150 – 192)**	**36** **(12)**

5.4.2. Nest composition

In Blue Tits rural nests were significantly heavier than urban greenspace nests (W = 368, $p = 0.04$, other comparisons $p > 0.1$; Table 5.1) while Great Tits showed no significant differences between habitat types (all $p > 0.1$; Table 5.1). There was no significant difference in nest box size (using interior base surface area) between broad habitat types in either species (both $p > 0.1$; Table 5.1).

Nest materials included mosses, grasses, leaves, twigs, feathers, animal hair (both domestic and wild) and anthropogenic materials, which were largely treated cotton and artificial stuffing materials.

Anthropogenic material was found in 77% and 94% of Blue Tit and Great Tit nests respectively (84% of all nests). Blue Tit nests contained proportionally less anthropogenic material and showed considerably more variation in rates of use than Great Tits ($W = 590.5$, $p = 0.001$; Table 5.1). There was no effect of habitat type on the use of anthropogenic materials for either species ($p > 0.09$ for all comparisons). In a logistic mixed model regression and controlling for site, neither species showed a significant association between either broad habitat type or the actual level of urbanisation as a proportion of constructed surfaces and the proportion of anthropogenic materials used.

5.4.3. Nest arthropod diversity and ectoparasite load

Due to the more standardised collection of nests and the loss of several invertebrate samples, only 42 fledged nests (23 Blue Tit and 19 Great Tit) from 15 different sites were explored for their arthropod diversity and numbers. Arthropods from 19 different orders were found in nests (Table 5.2). Parasitic Dermanyssidae mites were found in 55% of nests. Adult Siphonaptera (fleas) or their larvae were found in all but one nest. All adults were identified as members of the *Ceratophyllus* genus and were most likely Hen Fleas *Ceratophyllus gallinae* (Harper et al. 1992), with the exception of one individual *Dasypsyllus gallinulae*. As they are functionally alike and flea larvae could not readily be separated to species, and a number of nests contained high numbers of larvae but no adults, all fleas were combined together into a single category to form an overall measure of flea abundance in nests. Mallophaga (biting/bird lice) and Analgoidea (feather mites) were only found in single nests and so were not included in the ectoparasite analysis. Amongst the other arthropods found, potential predators of mites or fleas were identified in 52% of nests (adult predators only). Staphylinidae (Rove Beetles) were the most frequently recorded coleopterans, and these prey on other insects and mites. Other potential predators included Histeridae beetles, Pseudoscorpions (Pseudoscorpiones) and some predatory mites of the suborder Prostigmata (Table 5.2).

Table 5.2. All arthropods detected in Blue Tit and Great Tits nests identified to at least Order taxonomic level with summary statistics for both Blue Tits and Great Tits. Families and notes on predatory/ectoparasites are included where known.

Class	Order	Total numbers in Blue Tit nests *Median* (IQR)	Total numbers in Great Tit nests *Median* (IQR)	Identified Families	Notes
Arachnida - Subclass Acari (Mites)	Orabatida	42 *0* (0 – 1)	11 *0* (0 – 1)		
	Trombidiformes (Suborder Prostigmata)	800 *0* (0 – 1)	7 *0* (0 – 0)	Tetranychidae (Spider Mites)	Some predators
				Cheyletidae?	Some predators and Ectoparasites
	Mesostigmata	1103 *14* (2.5 – 43.5)	1435 *38* (4 – 82)	Dermanyssidae (Biting Mites)	Ectoparasites
				Laelapidae	
	Sarcoptiformes	2593*47* (3 – 130.5)	4597 *21* (0.5 – 72)	Acaridae	
				Analgoidea (Feather Mites)	Ectoparasites
				Glycyphagidae	
Other Arachnida	Araneae (Spiders)	4 *0* (0 – 0)	9 *0* (0 – 0.5)		
	Pseudoscorpiondia (Pseudoscorpions)	3 *0* (0 – 0)	0		Potential ectoparasite predators
Malacostraca	Isopoda (Woodlice)	21 *0* (0 – 0)	14 *0* (0 – 0)		
Collembola (Springtails)	Entomobryomorpha	80 *0* (0 – 3.5)	37 *2* (0 – 2.5)	Entomobryoidea	
	Poduromorpha	2 *0* (0 – 0)	0	Poduroidea	
Insecta (Insects)	Coleoptera (Beetles)	325 *1* (0 – 15.5)	670 *1* (0 – 7.5)	Staphylinidae (Rove Beetles)	Potential ectoparasite predators
				Latriididae	
				Corylophidae	
				Histeridae (Clown Beetles)	Potential ectoparasite predators
	Dermaptera (Earwigs)	0	1 *0* (0 – 0)		
	Diptera (Flies)	134 *0* (0 – 2)	216 *0* (0 – 1.5)	Psychodidae (Drain/moth flies)	
	Hymenoptera	7 *0* (0 – 0)	30 *0* (0 – 0)	Formicidae (Ants)	

	Hemiptera (True Bugs)	7 *0* (0 – 0)	1 *0* (0 – 0)	Aphidoidea (Aphids)	
				Aleyrodidae (White Fly)	
	Lepidoptera (Moths)	530 *3* (1 – 10)	314 *7* (2 – 21)		
	Psocoptera (Booklice)	62 *0* (0 – 0)	32 *0* (0 – 0)		
	Thysanoptera (Thrips)	1 *0* (0 – 0)	0		
	Phthiraptera (Lice) (Suborder Mallophaga - Bird Lice)	3 *0* (0 – 0)	0		Ectoparasites
	Siphonaptera (Fleas)	9110 *318* (46 – 611.5)	7531 *297* (159 – 515)	Ceratophyllidae	Ectoparasites: *Ceratophyllus gallinae* (Hen Flea) *Dasypsyllus gallinulae* (Moorhen Flea)

There was no difference in Shannon diversity at the order level between fledged Blue Tit and Great Tit nests ($H_s = 1.29$ and $H_s = 1.28$ respectively) and within species no significant difference between the broad site types ($p > 0.1$ in all cases; Table 5.3). In Blue Tit nests the AIC_c selected logistic regression mixed effect model for factors influencing Shannon diversity, found that the proportion of green surfaces within 200m (used instead of constructed surfaces due to poor model stability) to be positively associated with increased diversity ($\chi^2(1) = 5.34$, $p = 0.024$, following Bates et al. 2015; Figure 5.2, Table 5.4). Two possible outliers were identified to have unusually high Shannon diversity but a low proportion of green surfaces in the surrounding area (Figure 5.2). The removal of these data points and subsequent reanalysis found both the proportion of green surfaces within 200m and the nest dry weight to be positively associated with increased Shannon diversity in the AIC_c selected model ($\chi^2(2) = 20.13$, $p < 0.0001$; Figure 5.2). No effect was found in Great Tits.

Table 5.3. Summary of the arthropod Shannon diversity, ectoparasite load, productivity and nest construction for the subset of fledged nests examined for arthropod numbers and diversity. All values are medians with interquartile ranges with the exception of nests with mites which shows the proportion of those nests that contained Dermanyssidae mites and rural Great Tits which uses the mean and range instead.

Species	Habitat	Shannon diversity	Fleas N	Nests with Mites	Eggs N	Chicks fledged N	Proportion Anthropogenic Material	Nest dry weight (g)	N nests (sites)
Blue Tit	Rural	0.76 (0.42 – 0.86)	442 (49 – 669)	43%	7.0 (7.0 – 10.0)	5.0 (3.0 – 5.5)	0.10 (0.04 – 0.13)	21.2 (16.4 – 25.6)	7 (2)
	Greenspace	0.93 (0.70 – 1.23)	336 (67 – 626)	70%	7.5 (7.0 – 8.0)	4.5 (4.0 – 5.8)	0.11 (0.00 – 0.23)	21.0 (19.0 – 25.0)	10 (4)
	Garden	1.09 (0.74 – 1.16)	135 (34 – 325)	50%	7.5 (7.0 – 8.8)	2.5 (1.25 – 3.8)	0.07 (0.00 – 0.29)	17.6 (13.2 – 28.1)	6 (6)
	Overall	**0.91** **(0.65 – 1.15)**	**318.0** **(46 – 612)**	**57%**	**7.0** **(7.0 – 9.0)**	**4.0** **(3.0 – 5.0)**	**0.10** **(0.01 – 0.17)**	**22.2** **(18.1 – 26.2)**	**23** **(12)**
Great Tit	Rural	0.50 (0.40 – 0.60)	770 (657 – 883)	100%	9.5 (7.0 – 12.0)	3.0 (2.0 – 4.0)	0.17 (0.02 – 0.32)	27.1 (24.5 – 29.7)	2 (1)
	Greenspace	0.86 (0.68 – 0.95)	297 (208 – 515)	55%	5.0 (4.0 – 6.5)	3.0 (2.0 – 4.0)	0.30 (0.23 – 0. 43)	19.3 (11.8 – 26.1)	11 (4)
	Garden	0.83 (0.67 – 1.09)	124 (30 – 265)	33%	6.5 (6.0 – 7.0)	2.0 (2.0 – 3.5)	0.18 (0.04 – 0.22)	30.6 (26.2 – 36.3)	6 (6)
	Overall	**0.84** **(0.62 – 0.95)**	**297** **(159 – 515)**	**53%**	**6.0** **(5.0 – 7.0)**	**3.0** **(2.0 – 4.0)**	**0.29** **(0.09 – 0.32)**	**24.5** **(18.3 – 30.7)**	**19** **(11)**

Table 5.4. Summary of linear mixed model effects factors on Shannon diversity of arthropods in Blue Tit nests. ANOVAs were carried out between candidate models and the null model to determine model significance.

Model		Covariates	Estimate	SE	χ^2	p	Delta AIC_c	Model weight	d.f
Initial Models (including outliers)	Null	Intercept only	0.8648	0.0831	N/a	N/a	2.38	0.106	20
	Global	Anthropogenic material	-0.5346	0.5123	7.81	0.0988	8.77	0.004	16
		Green surfaces	1.926	0.7368					
		Chicks fledged	-0.0083	0.0376					
		Nest dry weight	0.0074	0.0071					
	Model 2	Green surfaces	1.670	0.7074	6.71	0.0349	1.93	0.132	18
		Nest dry weight	0.0085	0.0071					
	AIC_c selected	**Green surfaces**	**1.773**	**0.7235**	**5.34**	**0.0209**	**0.00**	**0.347**	**19**
Alternative Models (excluding outliers)	Null	Intercept only	0.8480	0.0993	N/a	N/a	13.54	0.001	18
	Global	Anthropogenic material	-0.4880	0.3706	22.21	0.0002	6.52	0.017	14
		Green surfaces	3.8237	0.6625					
		Chicks fledged	0.0178	0.0278					
		Nest dry weight	0.0127	0.0054					
	Model 2	Green surfaces	3.5832	0.7658	14.99	0.0001	1.63	0.192	17
	AIC_c selected	**Green surfaces**	**3.6346**	**0.6780**	**20.13**	**<0.0001**	**0.00**	**0.436**	**16**
		Nest dry weight	**0.0134**	**0.0056**					

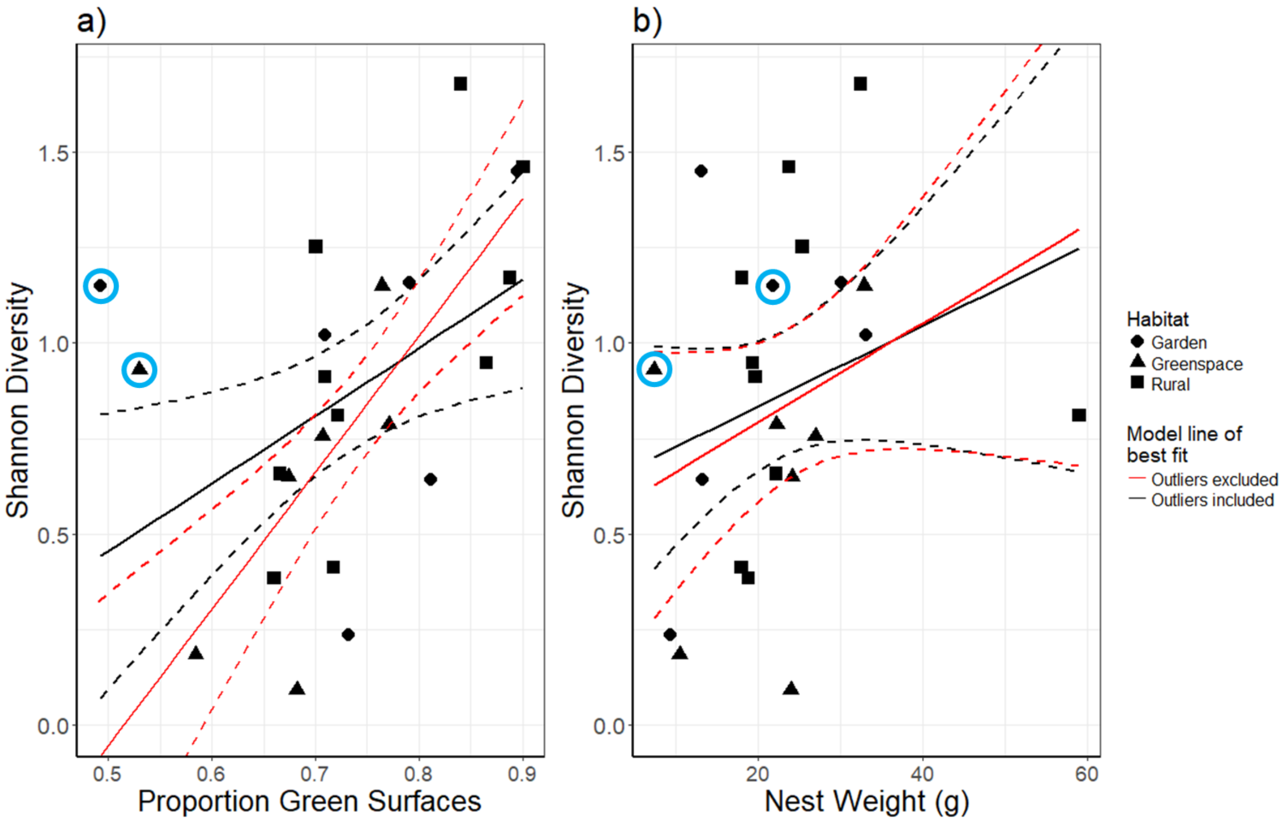

Figure 5.2. The influence of a) the proportion green surfaces (natural surfaces and gardens) and b) dry nest weight on nest arthropod Shannon Diversity index. The plotted lines of best fit (with 95% confidence intervals) are based on predictions extracted from the linear mixed effect models with Shannon diversity as the dependent variable. The black line of best fit is from the model including the outliers and the red line from the model excluding them. Site and nest box were random factors. Point type indicates the broad habitat type around the nest box. The two circled in blue were identified as potential outliers.

An increase in potential predator abundance (total Pseudoscorpiondia, Staphylinidae and Histeridae) was associated with a decrease in the proportion of anthropogenic nest material in the Blue Tits nests (r_s= -0.52, p = 0.012; Figure 5.3). There was a high outlier in the predator numbers and the correlation was still highly significant following its removal (r_s= -0.55, p = 0.008; see Figure 5.3). Predator abundance or presence/absence was not significantly associated with or affected by any other variables including ectoparasite abundance (all p > 0.09). No relationship was found between predator abundance or presence/absence and any other measured variable in Great Tits (p > 0.1).

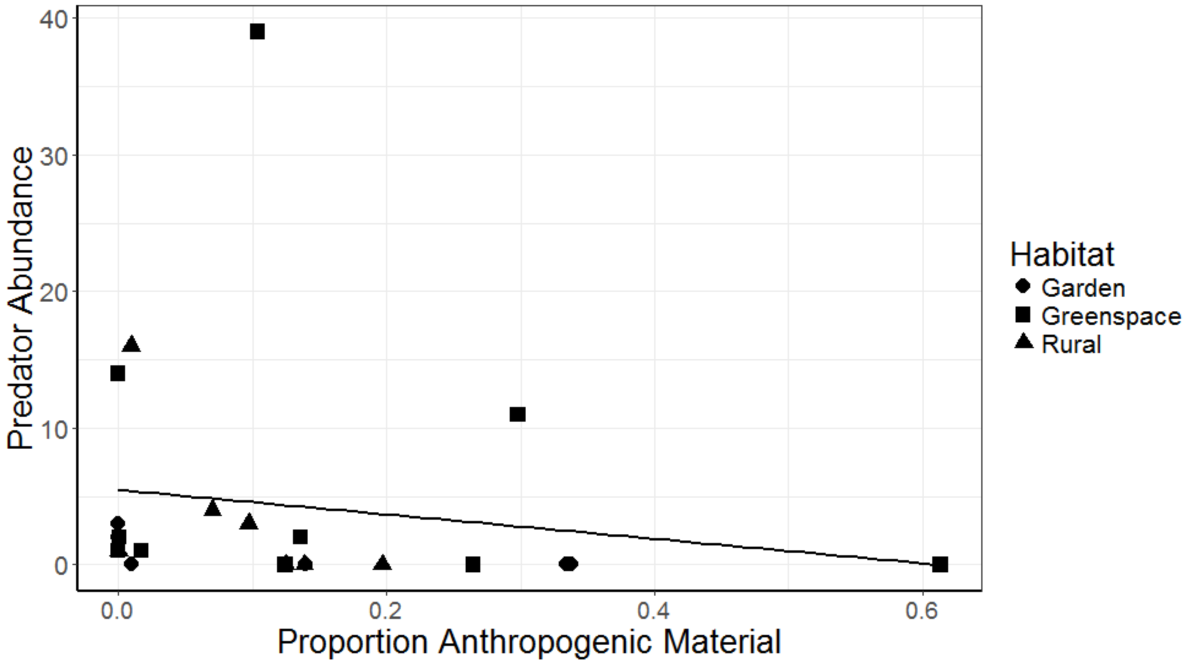

Figure 5.3. The influence of the proportion of anthropogenic nest material on the abundance of predators (total abundance of Pseudoscorpiondia, Staphylinidae and Histeridae) living in Blue Tit nests. Fitted with a linear line of best fit. Point type indicates the broad habitat type around the nest box.

In Blue Tits the AIC_c selected model for flea abundance could not be distinguished from the null model ($\Delta AIC_c < 2$). In Great Tits increasing levels of urbanisation (constructed surfaces) led to lower flea abundance and another model within ΔAIC_c 2 additionally found a significant positive relationship between the proportion of anthropogenic material (p = 0.001 and p = 0.052 respectively; Figure 5.4, Table 5.5). No model was found containing a significant predictor following selection for the abundance or presence of Dermanyssidae mites in the nests of either species. No relationship was found for either ectoparasite type with the weight of the nests, numbers of eggs laid and number of chicks fledged.

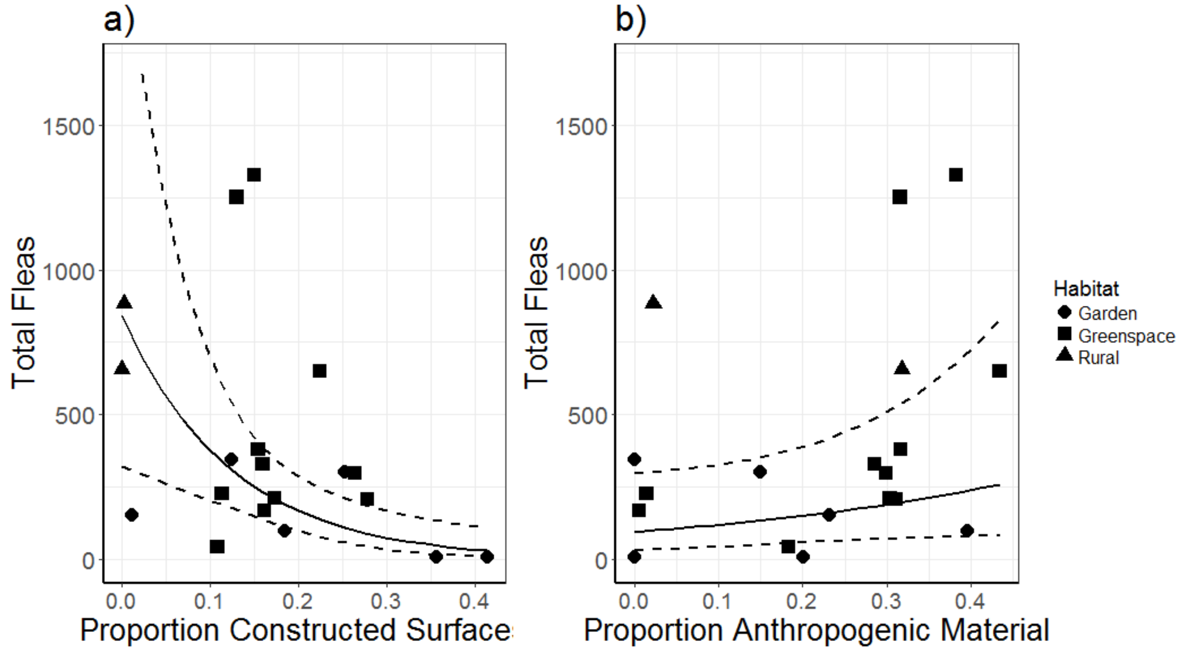

Figure 5.4. The influence of a) the proportion of constructed surfaces within 200m of the nest box and b) the proportion of anthropogenic material making up nests on overall flea abundance in fledged Great Tit nests. The plotted lines of best fit (with 95% confidence intervals) were based on predictions extracted from the respective mixed effect model for these variables. Site and nest box were random factors. Point type indicates the broad habitat type around the nest box.

Table 5.5. Summary of Poisson mixed model effects factors on flea (Siphonaptera) abundance in fledged Great Tit nests with delta AIC_c and model weights. For P value significance: • p = 0.1 - 0.05, * p < 0.01, ** p < 0.001, *** p < 0.0001.

Model	Covariates	Estimate	SE	P	Delta AIC_c	Model weight	d.f
Null	Intercept only	5.0590	0.5128	<0.0001 ***	3.40	0.047	16
Global	Anthropogenic material	3.5570	1.8450	0.0539 •	14.1	0.000	11
	Constructed surfaces	-8.8670	2.2790	<0.0001 ***			
	Chicks fledged	-0.1754	0.1715	0.3065			
	Shannon diversity	-0.2375	0.6959	0.7330			
	Nest dry weight	-0.0076	0.0273	0.7806			
Model 2	Anthropogenic material	3.2330	1.6660	0.0523 •	0.32	0.219	14
	Constructed surfaces	-8.1170	2.2610	0.0003 ***			
AIC_c selected	**Constructed surfaces**	**-8.0940**	**2.4710**	**0.0011 ****	**0.00**	**0.257**	**15**

5.4.4. Influences on breeding success

Overall, Blue Tits laid significantly more eggs that Great Tits ($W = 1711.5$, $p < 0.001$; Table 5.1) per breeding attempt, but there was no overall difference in the number of chicks they fledged, nor in the proportion of nests that fledged at least one chick. In successful nests there was no significant correlation between the number of eggs laid and the number of chicks fledged in either species (both $p > 0.1$). The proportion of anthropogenic material was not a significant predictor of any measure of breeding performance.

There was no significant difference in the number of eggs laid in either species across sites, but rural breeding birds fledged significantly more chicks per breeding attempt than urban greenspace and garden breeding birds for both Blue Tits ($W = 368$, $p = 0.032$ and $W = 201.5$, $p = 0.028$ respectively; Table 5.1) and Great Tits ($W = 132$, $p = 0.001$ and $W = 39$, $p = 0.007$ respectively; Table 5.1). Increasing proportions of constructed surfaces as a measure of level of urbanisation did not significantly influence the number of eggs laid but it did lead to fewer chicks being fledged in both species ($r_s = -0.32$, $p = 0.01$ and $r_s = -0.45$, $p = 0.006$ for Blue Tits and Great Tits respectively).

For Blue Tits, increased levels of urbanisation was associated with reduced overall breeding success, ($p = 0.022$; Figure 5.5). Heavier nests were associated with more eggs being laid ($p = 0.02$; Figure 5.6a, Table 5.6) and more chicks fledged ($p = 0.008$; Figure 5.6b, Table 5.6). Increased urbanisation also resulted in fewer chicks fledging ($p = 0.002$; Figure 6c, Table 5.6).

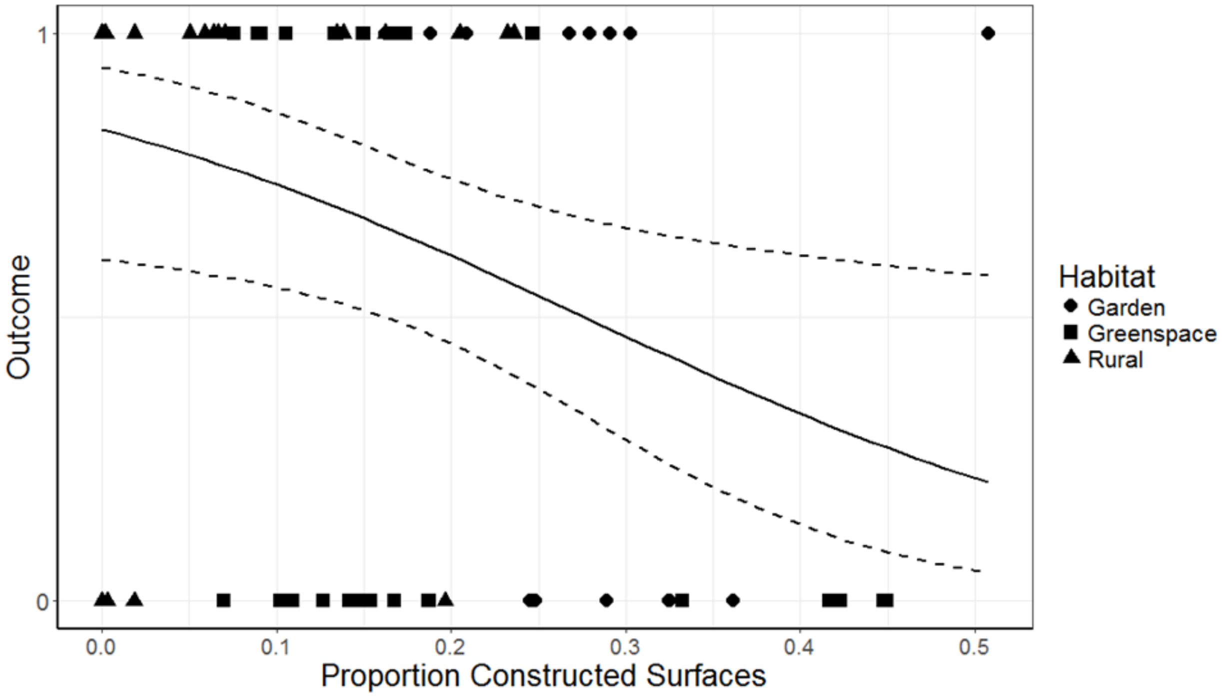

Figure 5.5. The influence of the proportion of constructed surfaces within 200m of the nest box on the outcome of Blue Tit breeding success, where 1 indicates fledging at least one chick and 0 indicates failure. The plotted line of best fit (with 95% confidence intervals) was based on predictions extracted from the Binomial mixed effect model for nest outcome. Site and nest box were random factors. Point type indicates the broad habitat type around the nest box. Nests that failed through predation were excluded from this model.

There was an indication of a negative association between level of urbanisation and the number of chicks fledged in Great Tits ($p = 0.05$; Figure 5.6d) but the null model was within delta 2 AIC_c of that AIC_c selected model, indicating low model support. While only nests that successfully fledged one chick or more were studied, no evidence of an effect of arthropod or ectoparasite numbers, nest construction or level of urbanisation affecting the number of chicks fledged was found.

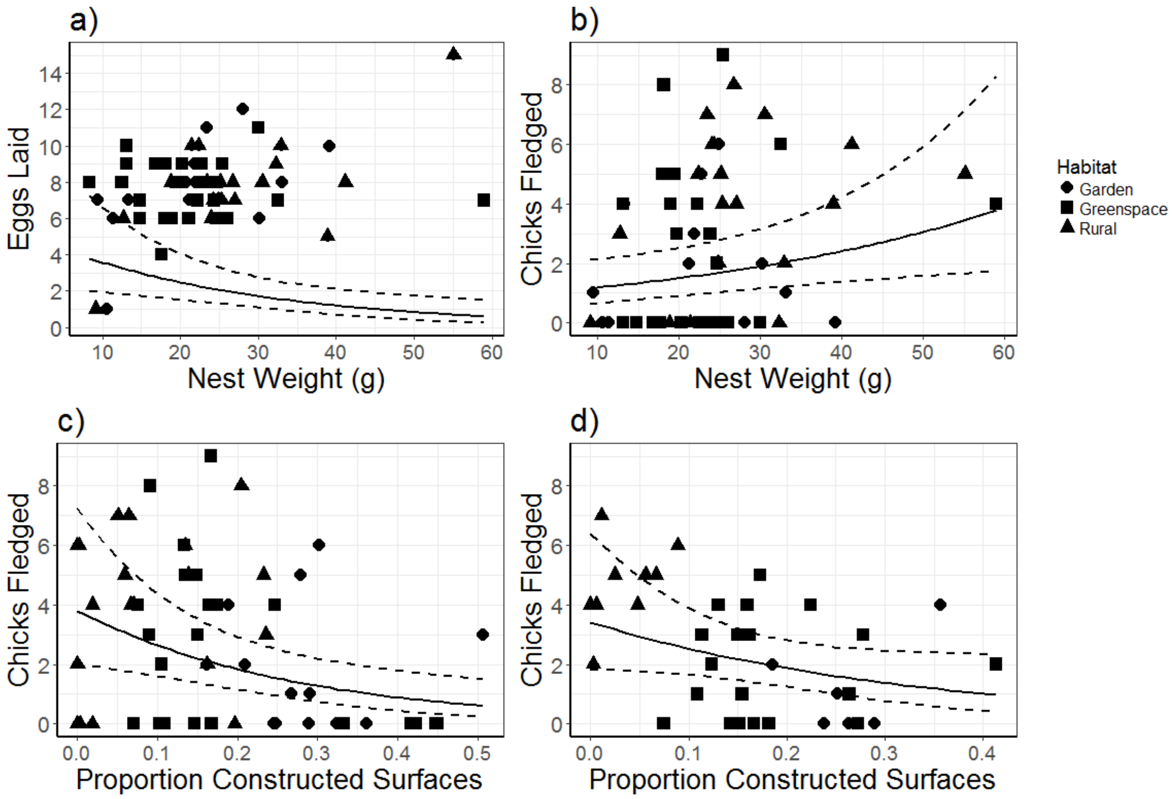

Figure 5.6. The influence of dry nest weight on a) the number of eggs laid and b) the number of chicks fledged by Blue Tits. The influence of the proportion of constructed surfaces within 200m of the nest box on the number of chicks fledged by c) Blue Tits and d) Great Tits. The plotted lines of best fit (with 95% confidence intervals) were based on predictions extracted from the respective mixed effect model for these variables. Site and nest box were random factors. Point type indicates the broad habitat type around the nest box. Predated nests were excluded from the models considering the number of chicks fledged.

Table 5.6. Summary of mixed model effects factors on the productivity of Blue Tit nests with delta AIC$_c$ and model weights. For P value significance: • p = 0.1 - 0.05, * p < 0.01, ** p < 0.001, *** p < 0.0001. For the Binomial Outcome and Chicks Fledged models, nests that failed through predation were excluded.

Dependent variable	Model	Covariates	Estimate	SE	p	Delta AIC$_c$	Model weight	d.f
Binomial Outcome (Failed / Fledged)	Null	Intercept Only	0.4761	0.3623	0.1890	4.70	0.038	55
	Global	Nest dry weight	0.0770	0.0479	0.1075	1.95	0.152	52
		Anthropogenic material	-1.1960	1.8070	0.5083			
		Constructed surfaces	-5.942	2.7830	0.0327 *			
	Model 1	Constructed surfaces	-5.7500	2.5020	0.0215 *	1.61	0.180	54
	AIC$_c$ selected	**Nest dry weight**	**0.0725**	**0.0449**	**0.1067**	**0.00**	**0.402**	**53**
		Constructed surfaces	**-6.1510**	**2.6770**	**0.0216 ***			
Eggs	Null	Intercept Only	2.0400	0.0458	<0.0001 ***	2.99	0.092	60
	Global	Nest dry weight	0.01059	0.0046	0.0201 *	3.75	0.063	57
		Anthropogenic material	0.0800	0.2324	0.7308			
		Constructed surfaces	0.3131	0.3721	0.4000			
	Model 1	Nest dry weight	0.0104	0.0045	0.0213 *	1.50	0.194	58
		Constructed surfaces	0.3282	0.3687	0.3734			
	AIC$_c$ selected	**Nest dry weight**	**0.0105**	**0.0045**	**0.0195 ***	**0.00**	**0.411**	**59**
Chicks Fledged	Null	Intercept Only	0.5148	0.2615	0.0490 *	11.57	0.002	54
	Global	Number of eggs laid	0.0096	0.0455	0.8330	4.54	0. 049	51
		Nest dry weight	0.0234	0.0107	0.0295 *			
		Constructed surfaces	-3.7080	1.2750	0.0036 **			
		Anthropogenic material	-0.3484	0.6426	0.5877			
	AIC$_c$ selected	**Nest dry weight**	**0.0254**	**0.0096**	**0.0080 ****	**0.00**	**0.478**	**53**
		Constructed surfaces	**-3.7910**	**1.2510**	**0.0024 ****			

5.5. Discussion

Our work supports the view that increased urbanisation is generally associated with a reduction in the overall breeding success of wild birds (reviewed in Chamberlain et al. 2009). We were surprised to find that while the species differed in their use of anthropogenic materials to construct nests (Great Tit > Blue Tit), this was not associated with urbanisation, suggesting perhaps an element of choice in nesting materials beyond simple availability of materials. There was no difference in nest mass among habitats for Great Tits, but Blue Tit nests in rural areas were significantly heavier, and overall, heavier nests were associated with greater fledging rates. Both bird ectoparasites and nest-dwelling arthropods more generally showed evidence of declining with increasing loss of green space. However, there was a negative correlation between flea load and overall arthropod diversity in nests, suggesting that arthropods may be predating flea larvae and/or eggs, or acting as competitors for resources. At the same time, while overall arthropod diversity and predator numbers were both negatively associated with increased proportional use of anthropogenic nesting material in nests, flea numbers conversely increased. We speculate that the reduction in use of natural nesting materials reduces overall diversity in the arthropod nest box assemblage, which in turn reduces the effects of predation and/or competition on flea abundance.

Our understanding of the role of nests has increased considerably in recent years but the nest building phase of breeding success is relatively understudied (Deeming & Reynolds 2015). Nests represent a major energy investment (Mainwaring & Hartley 2013) and understanding them, particularly in the light of urbanisation, may help us understand changes in productivity across habitat gradients and their conservation implications. In addition to finding the broad decline in reproductive output associated with urbanisation found elsewhere (Chace & Walsh 2006; Chamberlain et al. 2009) we also similarly found heavier nests to be linked with higher reproductive output. This concurs with a number of past nest box studies and may be linked to adult quality (Alvarez et al. 2013; Gladalski et al. 2016; Lambrechts et al. 2016a) though not with all (Lambrechts et al. 2016b). Such differences in turn may be linked to differences in nesting behaviour and reproductive output between these species, as Blue Tits typically build proportionally heavier nests and have a higher average reproductive output per breeding attempt than the physically larger Great Tit (Lambrechts et al. 2014; Lambrechts et al. 2015; Gladalski et al. 2016).

While the majority of nesting material is intended to provide insulation and structure, nest components may also provide additional benefits. Aromatic plants may offer an anti-ectoparasite or even anti-bacterial function in nests (Mennerat et al. 2009a; Tomás et al. 2012; Ruiz-Castellano et al. 2016). Fewer native aromatic plants may be available at higher levels of urbanisation even though the overall plant diversity can be higher due to the planting of exotic plant species in gardens and other areas (McKinney 2008). The prevalence and importance of aromatic plants in the nests of UK breeding Blue Tits and Great Tits is unknown. However, Blue Tits have been found to utilise them elsewhere in their range (Mennerat et al. 2009a; Mennerat et al. 2009b; Tomás et al. 2012). Artificial nesting materials will not offer defences against macro- or micro-parasites, and so their benefits are in terms of nest structure and insulation. Furthermore, as processed anthropogenic materials are largely artificial in origin, they will also not provide food resources for consumers (principally arthropods) and decomposers (mainly bacteria and fungi), and hence may affect the complexity of the structure of the assemblage of species (including predatory species) that inhabit the nest boxes.

We found variation in the use of anthropogenic nest components similar to that found in other studies on Blue Tit and related species here in the UK and in Europe more generally (Moreno et al. 2009, Britt and Deeming 2011, Reynolds et al. 2016; although this variation is understudied, Deeming and Mainwaring 2015). Like Reynolds et al. (2016) we found that anthropogenic material was present throughout the site types and in the majority of nests irrespective of their local level of urbanisation. Great Tit nests contained a median of 24% anthropogenic material and this varied little across habitats, suggesting that they may preferentially seek these when nest building, particularly when these materials are uncommon (Surgey et al. 2012). That may be due to a preference for its insulation properties and so fitness benefits (Reynolds et al. 2016). In contrast, Blue Tit nests contained an overall median of 2% anthropogenic material, and while not statistically significant due to considerable variation among nests, we note that this increased to 16% in urban gardens, suggesting that Blue Tits are more opportunistic in their use of non-natural materials. This may be due to the decline of natural nesting material availability or an increase in the general availability of artificial substitutes in urban areas (Wang et al. 2009).

In contrast to Reynolds et al. (2016), we do find a possible effect of anthropogenic materials on the presence of ectoparasites and other arthropods. In Blue Tits a higher proportion of anthropogenic nest material is associated with lower arthropod diversity. While the majority of non-parasitic arthropods appeared to be opportunistic in nature, their numbers did also include potential predators of flea larvae and eggs. These also appeared to decline with increasing use of anthropogenic materials. While a relationship between predator and flea numbers was not found, increased arthropod diversity was correlated with a decline in flea numbers. This may result from competition for resources (consuming adult flea frass which would otherwise be consumed by flea larvae (Tripet & Richner 1999), in a manner analogous to that found by Krištofík et al. 2017) or predation of flea eggs and larvae.

Such changes in the degree of interspecific interactions may provide a functional explanation of the increase in flea numbers associated with an increase in the proportion of anthropogenic materials used in nests. We suggest that nests constructed of more natural materials supports a more structurally diverse arthropod community (including more predators) which therefore reduces flea numbers irrespective of the level of urbanisation. Given this, it would be logical to expect birds to prefer natural materials where possible. This makes the possible preference for anthropogenic materials shown by Great Tits unexpected if they are less exposed to them and more energy is expended in finding these materials (Surgey et al. 2012). As they appeared to seek it out regardless of overall availability in the local environment, we speculate that they may derive other advantages from utilising anthropogenic materials.

Such a relationship between anthropogenic materials and parasite load, even if indirect, may help explain findings by others on variation in nest ectoparasite loads with different materials (Moreno et al. 2009; Tomás et al. 2012; Cantarero et al. 2013; Reynolds et al. 2016). Nevertheless, it is not clear if nest material choice and associated changes in arthropod assemblage helps explain variation in breeding success associated with urbanisation. This may simply be due to food availability being the most important factor driving the reduction in fledgling success seen in urban areas (Chace & Walsh 2006; Chamberlain et al. 2009) or that the effects of parasites are frequently hidden until nestlings become highly stressed (Simon et al. 2004; Arriero et al. 2008; Bańbura et al. 2011).

We acknowledge that our sampling approach was constrained; as nests could not be removed until after fledging we cannot be certain that the biodiversity recorded in removed nests represents that present in nests as they are being used (although previous work suggests the loss of fleas should have been low, Wesołowski and Stańska 2001). Furthermore, Tullgren funnels may not be the most effective way of sampling adult flea abundance (Harper et al. 1992; Moreno et al. 2009), thus explaining the comparatively low numbers of adults found in this study compared to others that used freezing and manual deconstruction of nests to find them (Reynolds et al. 2016). Nevertheless, the counting of flea larvae does provides a measure of nest flea abundance in the absence of adults and this approach did allow us to collect the other nest arthropods present, which for species such as mites would have been very challenging to sample using other approaches (Moreno et al. 2009).

Cavity nesters that take easily to artificial nests sites provide an important research tool for exploring the effects of various factors on breeding success (Vaugoyeau et al. 2016), but it is important to bear in mind that nest box based studies may not be directly comparable to nests in natural cavities (Wesołowski & Stańska 2001; Maziarz et al. 2017). Nevertheless, in urban areas these may be the main nesting cavities available to these bird species (Davies et al. 2009). Given the different responses detected in this study and by others of these two related species, it is important to consider that bird species may respond differently to similar pressures (Lambrechts et al. 2015; Gladalski et al. 2016) and so we must be mindful of drawing broad conclusions from single species studies (Reynolds et al. 2016; Vaugoyeau et al. 2016). Due to the relatively poor breeding season experienced during our fieldwork sample numbers were lower than anticipated, which reduces our statistical power. A larger/multiple year study also considering the effects on nest failure would allow for a more considered reflection on how these factors interact to affect the breeding success of urban birds.

Being an urban adapter brings novel opportunities (e.g. supplementary food: Orros & Fellowes 2015b, Hanmer et al. 2017, submitted a, b) and challenges (e.g. domestic cats: Thomas et al. 2014, Hanmer et al submitted c). Nest boxes provide a clear opportunity when breeding sites are limited, but it is evident that increased urbanisation is associated with a decrease in the number of offspring successfully fledged by nest box using species such as Blue and Great Tits (Cowie and Hinsley 1987, Chamberlain et al. 2009; this study). We examined how potential variation in nest construction may contribute to this reduction in breeding success, both directly (nesting materials affecting successful breeding) or indirectly (nests and nest boxes as homes to ectoparasites and other arthropods). Blue Tit nests in less urbanised areas tended to be heavier, with heavier nests leading to more eggs being laid and more chicks fledged, whereas no effect of urbanisation on nest weight was found in Great Tits. We found that Blue and Great Tits differ in how they utilise anthropogenic materials, with Great Tits showing higher rates of use, but no effect of urbanisation, whereas Blue Tits show some evidence of increased use in urban gardens where such material is likely to be more common. We find no evidence that the use of anthropogenic materials directly affected breeding success. However, while arthropod diversity and predator numbers decline with increasing use of anthropogenic nest materials, the number of fleas increased, suggesting that there may be indirect links between materials used in nest construction and parasite (flea) load. Nest-boxes are clearly ecological communities in their own right; we suggest that they may be more intriguing than they appear at first sight, and worthy of consideration for further investigation.

Chapter 6: Urbanisation affects range size of the Domestic Cat (*Felis catus*): consequences for conservation

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6.1. Abstract

Domestic cats (*Felis catus*) are the most abundant predator in many urban ecosystems, and their ranging behaviour will help determine predation rates. To investigate how degree of urbanisation affects cat ranging behaviour, we used GPS trackers to follow 38 cats in three (urban, suburban and peri-urban) residential areas in the large town of Reading, UK. Median home range (95% KE) was 1.28 ha, but varied from 0.9 ha in the urban habitat, to 1.56 ha in the suburban habitat and 1.60 ha in the peri-urban region, with a maximum range size of 6.61 ha. The median maximum distance reached from home was 99 m, and again varied with urbanisation (urban: 79 m; suburban: 141 m; peri-urban: 148 m; maximum 278 m). For home and core (50% KE) ranges there were no significant differences with respect to study areas, cat sexes, cats living in the same household, or core day/night range. A decreased proportion of constructed surfaces (a proxy for urbanisation) was associated with an increase in cat range size; cats in peri-urban areas range further than those in urban areas. As urban areas grow, many areas containing species of conservation importance are encroached upon by residential zones on urban fringes. To protect these species we suggest that boundary habitats should be managed to reduce rates of cat access to these areas, or that buffer zones of 300-400m should be formed between housing and areas containing vulnerable species. These management options may help mitigate the ecological consequences of cat predation.

6.2. Introduction

As opportunistic, generalist predators (Barratt 1997b; Thomas et al. 2012; Loyd et al. 2013), domestic cats (*Felis catus*) are considered to be among the greatest threats to global biodiversity (Nogales et al. 2004; Medina et al. 2011; Loss et al. 2013; Doherty et al. 2016). It is thought that cats introduced to islands have caused the extinction of 63 animal species including 40 birds (Doherty et al. 2016) and domestic cats are the primary threat to over 8% of threatened reptiles, birds and mammals (Medina et al. 2011; Doherty et al. 2016). In many urbanised countries, domestic cats are commonly kept as companion animals, where they are fed and cared for. For example, the UK is home to more than 10 million pet cats (Murray et al. 2010) and >800,000 feral cats, making them the most common mammalian predator, outnumbering all others combined (Harris et al. 1995; Battersby 2005). While in the USA and Canada it is estimated that there are 84 million and 8.5 million owned cats respectively, with similar sized feral cat populations (Blancher 2013; Loss et al. 2013).

Levels of cat ownership are highest in urban areas, resulting in extremely large local cat populations (>>100 individuals km^{-2}; Baker et al. 2008; Sims et al. 2008; Thomas et al. 2012). Predation studies suggest that more than 180 million prey individuals (55 million birds, 119 million mammals) are killed annually by domestic cats in the UK (Thomas et al. 2012). Estimates of annual numbers of prey taken in the USA (>1 billion birds and 6 billion mammals; Loss et al. 2013) and Canada (100-350 million birds, ~2-7% of all birds in southern Canada; Blancher 2013) implicate cats as one of the most important anthropogenic causes of bird mortality (Loss et al. 2015). In addition, cats need not actively hunt to have a negative effect on wild birds, as their presence alone may further depress wild bird populations (Beckerman et al. 2007; Bonnington et al. 2013). Despite such losses, whether such direct and indirect affects have population level consequences for their prey is a topic of considerable debate (Baker et al. 2005; Baker et al. 2008; McDonald et al. 2015), but given the enormity of the estimated losses the precautionary principle suggests that we should act to mitigate cat predation (Lilith et al. 2006).

As the World becomes increasingly urbanised (UN 2011), biodiverse areas are increasingly encroached upon by development (McKinney 2002; McKinney 2008). Typically, suburban areas grow on the peripheral zones of urban areas, potentially resulting in increased numbers of domestic cats accessing areas of conservation concern (Morgan et al. 2009; McDonald et al. 2015). Town planners and conservation biologists have suggested that one possible mechanism to reduce potential cat predation is to introduce buffer zones around areas of greater conservation value, where either housing development would be prevented or through prohibiting the ownership of domestic cats for people choosing to live within a set distance of the protected area (Lilith et al. 2006; Lilith et al. 2008; Metsers et al. 2010; Thomas et al. 2014).

Such buffer zones around protected areas have been proposed to keep cats away (Metsers et al. 2010) particularly for new housing developments (Thomas et al. 2014), although how enforceable such restrictions are is open to question (Hall et al. 2016a). A cat-free buffer zone of 300-400 m between housing developments and areas of higher biodiversity value has been suggested for Australia (Lilith et al. 2008) and the UK (Thomas et al. 2014), but in rural New Zealand a distance as great as 2.4km has been proposed (Metsers et al. 2010). Such cat exclusion zones could be incorporated into the planning of developments near protected areas but must also be scaled appropriately to the landscape for effective management (Hall et al. 2016b). Night-time curfews are also a potentially useful cat management technique as cats have sometimes been found to range further at night than during the day (Metsers et al. 2010; Thomas et al. 2014). Some prey types, such as small mammals, are more active then (Woods et al. 2003) and make up a significant proportion of domestic cat prey (Thomas et al. 2012).

Monitoring the ranging behaviour of domestic cats using conventional telemetry radio tracking approaches has proved challenging to conduct in some habitats such as urban areas (Schmutz & White 1990) and combined Global Positioning System (GPS) and radio setups can be relatively heavy and expensive (Coughlin & van Heezik 2014). More recently, the development of light-weight, relatively inexpensive GPS trackers for human use such as iGotU GPS tags (Hervías et al. 2014; Coughlin and van Heezik 2014; this study) or similar devices (Thomas et al. 2014; Kitts-Morgan et al. 2015) has changed how cat ranging behaviour is studied. While such cheaper GPS trackers may sacrifice some accuracy and precision compared to specialised GPS trackers from wildlife telemetry suppliers, they make large scale simultaneous tracking studies feasible (Adams et al. 2013; Coughlin & van Heezik 2014; Forin-Wiart et al. 2015).

The landscapes and countries in which tracking studies have taken place have varied, resulting in a wide range of domestic cat home ranges being calculated (Hall et al. 2016b), in part confounded by the use of differing methods and time scales (e.g. Morgan et al. 2009; Metsers et al. 2010; van Heezik et al. 2010; Wierzbowska et al. 2012; Coughlin and van Heezik 2014; Thomas et al. 2014; Hervías et al. 2014; Kitts-Morgan et al. 2015). Generally, rural cats (Wierzbowska et al. 2012; Kitts-Morgan et al. 2015) appear to range further than urban cats (Morgan et al. 2009; van Heezik et al. 2010; Thomas et al. 2014; Hall et al. 2016b) but studies directly comparing them in the same general geographical area are few in number (Metsers et al. 2010; Thomas et al. 2014) and the applicability of studies from one distinct biogeographic area such as New Zealand (Metsers et al. 2010; van Heezik et al. 2010) to another such as the UK is debatable even without considerations of local landscape structure. In the UK, the only previous published study only considered suburban domestic cats (Thomas et al. 2014) so how appropriate its findings are to more or less urbanised areas has yet to be determined. In particular while domestic cats living on the edge of farmland, parkland or nature reserves in the urban environment may have the opportunity to extend their ranges into these areas to hunt, it is unclear if such areas are preferred by domestic cats (van Heezik et al. 2010).

If we are to develop appropriate management and planning recommendations then understanding how urbanisation level affects cat roaming behaviour is critical. Here, we address this using GPS tracking of free-ranging domestic cats in a large UK town, asking if the range size of cats was affected by level of urbanisation, habitat availability, cat sex, and wearing a collar. In addition, we also explored if there were any differences between day and night ranging, and if the ranging behaviour of cats living in the same household differed, as this has implications for approaches to management.

6.3. Materials and Methods

6.3.1. Study areas

The study took place in and around Greater Reading (Figure 6.1), south east UK (51°27’N, 0°58’W) during May 2016. The area is approximately 40 km west of London and has an overall population of around 230,000 people (Office for National Statistics 2013). Three sites were chosen to represent typical areas of housing present in the UK; core urban terraced housing with small gardens and little nearby green space (the inner town district of Katesgrove, ~27.8 households/ha, build cover > 50%) surrounded entirely by similar housing and within 400m of the town centre; suburban, primarily detached and semi-detached housing with generally large gardens, some of which are adjacent to an urban local nature reserve (Maiden Erlegh, in the district of Earley, ~10.7 households/ha, build cover 30 - 50%) surrounded entirely by similar housing; and a peri-urban area (Shinfield village south of Reading, ~7.3 households/ha) similar to the suburban area in terms of housing type and build cover within the settlement, but with open farmland and natural habitats within 200 m of the majority of the housing including the homes of all recruited cats. The households per hectare information is for the entire settlement area (Office for National Statistics 2013) and build cover derived from the Ordnance Survey Mastermap collection (EDINA 2016, University of Edinburgh).

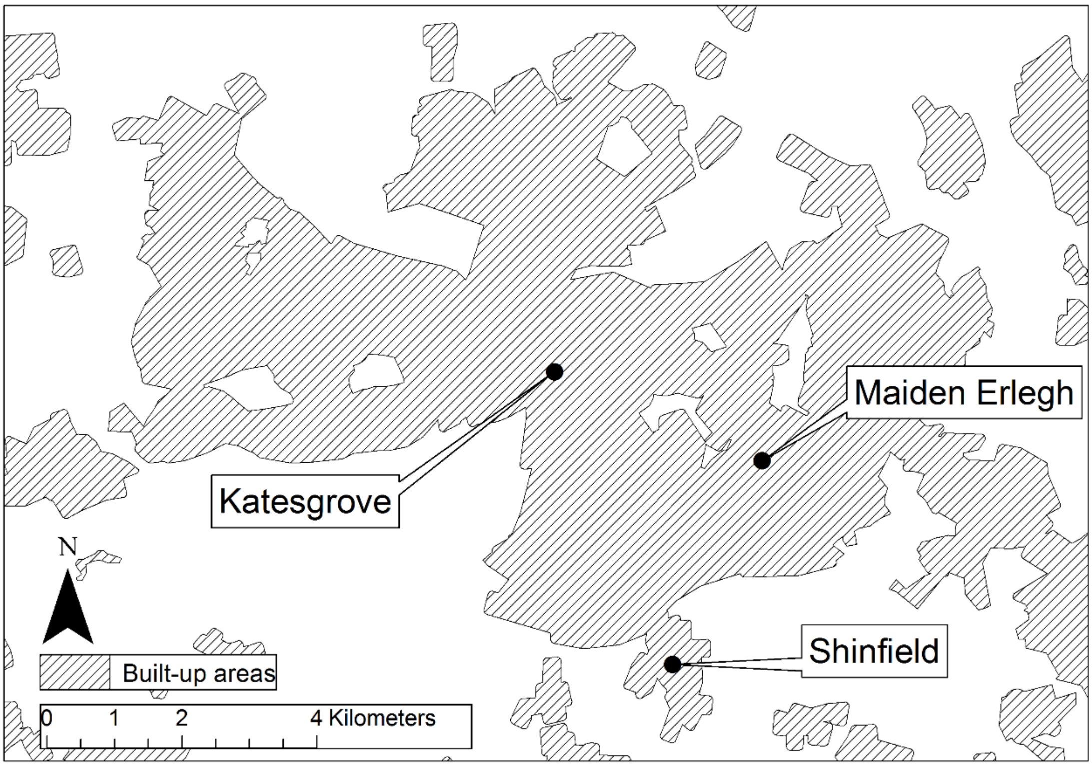

Figure 6.1. The three study sites within the general Greater Reading area, UK.

6.3.2. Cat Recruitment

Recruitment was carried out primarily through leaflets posted through letter boxes, and door-knocking was carried out when necessary. Volunteers were asked to encourage friends and neighbours to take part. The study was approved by the School of Biological Sciences ethical review panel.

Just over half of the successfully tracked cats (53%) came from households with more than one cat participating in the study, which may violate the assumption of spatial independence due to cats ranging in identical habitat (Millspaugh et al. 1998). However, cats are independent animals and those residing in homes with two or more other cats live in a socially complex society where access to resources and behaviour vary (Crowell-Davis et al. 2004).

All cats were at least one-year-old (fully grown) and in good health. The following information was recorded for each cat: age (to the nearest year with estimates for several former rescue cats), neutered status, sex, weight (on last veterinary visit if not more recently) and whether they had previously worn a collar on a regular basis prior to the study. Owners were asked to monitor the health of their cats throughout the study and record any prey items brought home during the tracking period. All cats generally had unrestricted access to the outdoors and were fed daily by their owners.

All cats not already usually wearing collars (29 of 49 cats recruited) were provided with standard collars (Ancol Safety Buckle Cat Collar, Ancol, UK) approximately two weeks beforehand to attempt to get cats accustomed to them and to reduce the probability of tracker loss or rejection during the actual tracking period.

6.3.3. The GPS units

The GPS units were iGotU GT-120 USB GPS Travel Loggers (4.4 × 2.7 × 1.3 cm; Mobile Action Technology, Taiwan), set to acquire a fix once every 15 min, which theoretically enabled 10 days of recording battery life. The weight of the GPS unit including its gel cover was 26 g. Volunteers were provided with standard quick release collars weighing 7.2 g to attach them to, though a number of volunteers/cats preferred to use their current collars weighing up to 10 g. For standardisation provided collars were not fitted with bells. GPS fixes from the first hour of tracking were removed to allow time for the cats to get used to the trackers. The tracking period was intended to last c.7 days, effectively simultaneously across all cats though due to tracker losses and owner commitments two cats started and finished early and three cats started and finished late, while another ran for nine days due to the unit being accidently left on the cat.

The collars with the GPS units were not counter weighted for simplicity and to increase recruitment and reduce rejection by cats. This is likely to have increased the number of erroneous and missing GPS fixes (Coughlin & van Heezik 2014). Prior to analysis the data were conservatively filtered to remove incorrect fixes on the basis of unrealistic distance/speed travelled. The number of filtered apparently erroneous fixes was used as a measure of logging errors in the analysis.

Trackers lost in the first half of the study period were replaced on the first loss instance within eight hours of it being reported by the owners. Several lost trackers were found and returned by members of the public allowing the data to be retrieved. The GPS tracks from these returned trackers were either added to the tracks taken by replacements if lost in the first half of the study period or treated as a full track if retrieved with more than 100 fixes spanning more than three full days of tracking (after filtering).

Accuracy and precision of GPS fixes can be influenced by the habitat the cat is in. Signal strength is reduced under dense foliage (D'Eon 2003) and within buildings so cat use of these areas is likely to be under-estimated (Coughlin & van Heezik 2014). The proximity to buildings can also influence GPS satellite signal acquisition and location precision is affected by the position and number of satellites available (van Heezik et al. 2010). Past studies using these same devices utilised in this study have found positional errors in the order of 10.03m when placed upright with direct line of sight to the satellites, increasing to 29.96m when placed under a mature tree with an open canopy (Coughlin & van Heezik 2014). Such errors are likely to be increased in more highly urbanised areas or within thick vegetation due to interference with the GPS signal and therefore should be treated as a minimum possible error (Coughlin & van Heezik 2014).

6.3.4. Data analysis

6.3.4.1. Home range size

We used 95% kernel contour estimates (isopleth) to calculate cat home ranges and 50% kernel contour estimates to calculate cat core ranges (referred to as home range and core range respectively in this paper). To allow for direct comparisons between this study and older studies we have also included 95% Minimum Convex Polygon (MCP) home range estimations. In addition, each fix was classified as being during the day or night, calculated using local daily sunrise and sunset times. These were then split and used to calculate overall 95% and 50% kernel density estimates to look at any differences between night and day ranging. To allow for the differences in day and night length (day length ~15 hours at the time of the study) these results were standardised based on comparative day and night length to compare the proportional difference in day and night time ranging.

All home range estimation analysis was carried out in program R (R Core Team 2016) using the 'adehabitatHR' package (Calenge 2016; version 0.4.14). Proportional range overlaps of cats living in the same household were calculated by estimating the proportion of animal i's home range that is overlapped by animal j's home range to create a median overlap value with interquartile ranges (Calenge 2006; Katajisto & Moilanen 2006; Walter & Fischer 2017). Polygons of the kernel estimate home and core ranges were then projected into ArcGIS 10 (ESRI 2011) via the R 'maptools' package (Bivand and Lewin-Koh 2016; version 0.8-39) on to Ordnance Survey Mastermap collection (EDINA 2016, University of Edinburgh) land use data to determine habitat usage. Each projected kernel polygon was cut from the Mastermap layer, and the resulting areas for each habitat category extracted for each range. Fifteen habitat/land use categories occurred within cat ranges which were combined to form three broad categories: all constructed surfaces (buildings, roads etc.), natural surfaces (grassland, trees and scrub) and private gardens (mixed surfaces). Of these, constructed surfaces was included in further analyses as a measure of the level of urbanisation as it was present in all cat ranges, unlike natural surfaces which were not present in some urban areas. Incremental analyses using isopleth range increments of 5 in chronologically ordered location data was used to determine whether home ranges (95% KDE) were fully revealed within the study timeframe. A cat range was considered to be fully revealed if the 90% KDE isopleth was within 10% of their total estimated home (95% KDE) range size (i.e., approaching the asymptote) (Harris et al. 1990; Barg et al. 2005; Plotz et al. 2016).

Maximum distance travelled from home was measured from the cat owner's home to the furthest point in their 95% Kernel home range estimates, and recorded to the nearest metre. A recommended exclusion zone was calculated for each site by taking the cat with the maximum recorded distance from home in each site and incorporating a 20% increase as a safety margin for protecting wildlife sites and to allow a margin of error when ranges were not fully revealed (following Lilith et al. 2008). Habitat selection was evaluated for all cats and specifically for cats living adjacent to green spaces and natural habitat fragments (within 50m) using selection ratios (Manly et al. 2002): both habitat use (based on location fixes) and availability were measured within 100% MCPs to better account for the available habitat in the local area.

6.3.4.2. Statistical analyses

As the data were not normally distributed, Kruskal-Wallis tests were used to compare across all three sites together, while unpaired Wilcoxon tests were used to compare between individual sites for logging errors (in the form of number apparently erroneous fixes filtered from the data as detailed above), ranges (home and core) and maximum distance from home. To allow for potential Type II error from multiple comparisons p was adjusted for the false discovery rate where appropriate (Benjamini & Hochberg 1995). Day and night effects on home and core range area were compared using separate paired sample Wilcoxon tests to first test for differences in the recorded ranges directly and then compare the proportional difference in range size when accounting for day length. The size and proportion of overlap in ranges for cats within the same household was compared using paired sample T-test or Wilcoxon tests as appropriate to their distribution.

To normalise data for linear mixed-effects model analysis, kernel home and core range estimates along with maximum distance from home were log transformed prior to analysis, with individual cat identity as a random factor to account for individual variation. We used R with the ‘nlme’ package (Pinheiro et al. 2016; version 3.1-127) to separately evaluate effectors on these three different measures of cat roaming. Factors considered in the range size models were: proportion of constructed surfaces (as a measure of the level of urbanisation) within the appropriate kernel estimate, cat age (rounded to the nearest year), cat sex and whether the cat usually wore a collar prior to the study. Cat age, sex and whether they usually wore a collar has been found to be associated with cat ranging behaviour in past studies and hence were included here (Coughlin & van Heezik 2014; Hall et al. 2016b). The same factors were used in models investigating effectors of the maximum distance reached from home. Model selection was carried out using an information theory approach based on the models’ associated AIC_c values and model weights (Burnham & Anderson 2002). We chose a set of candidate models on the basis of a ΔAIC_c of 2. Study site was not included in any of these models due to its high correlation with the proportion of constructed surfaces used as a measure of urbanisation.

6.4. Results

6.4.1. Tracking

Of 49 cats originally recruited for the study, two were withdrawn due to unrelated health concerns and four were too uncooperative to fit with collars. Of the remaining 43 cats, nine lost trackers at some point during the study but six of those were retrieved or replaced. Overall five cats produced fewer than 100 fixes in total due to tracker loses or malfunctions and were excluded from the analyses. This left 38 individual cats (14 females and 24 males; all neutered) ranging in weight from 2.0 to 7.5 kg (mean = 4.9 kg, median = 4.8 kg), varying in age from 1 to 15 years (mean = 6.6 years, median = 7), and 19 had worn a collar prior to the study. There was some variation in the number of valid GPS points (median = 230, range = 143 – 527). The median tracking period was 7.1 days (mean = 6.8, s.e = 0.2, range = 3.3 – 9.4). Owners reported four cats bringing back five individual prey items during the tracking period: three mice *Mus*/*Apodemus* spp., one rat *Rattus norvegicus* and one robin . This suggests the GPS trackers did not restrict normal predatory behaviour.

6.4.2. Logging errors

There were no significant differences in numbers of unfiltered, filtered or numbers of GPS fixes between study areas. However, there was a significant difference in the number of erroneous GPS fixes filtered from the data ($H = 16.9$, $p < 0.001$) among study areas. Significantly more GPS fixes were removed from the urban area (median = 23.5) compared to the suburban and peri-urban areas (median = 8.0, $W = 12$, $p < 0.001$ and median = 6.0, $W = 20.5$, $p = 0.012$ respectively) whereas there was no significant difference between the suburban and peri-urban areas ($W = 53$, $p = 0.4$).

6.4.3. Ranging characteristics

The median 95% kernel density estimate for home range size was 1.28 ha (mean = 1.66 ha, median 95% MCP = 0.95 ha; Table 6.1). The median core range estimate (50% kernel density estimate) was 0.17 ha (mean = 0.23 ha). Repeated incremental analysis utilising 90% KDE as the maximum home range showed fully revealed ranges, but at 95% KDE this was not so, suggesting that ranges were not fully revealed due to the influence of extreme locations on the range size estimates. Therefore, we consider that there is no habitat bias in our study, and that our range size estimates should be considered to be conservative.

Home range size was only borderline significantly different between study sites overall ($H = 5.604$, $p = 0.061$) and pairwise comparisons found a borderline significant difference between the urban and suburban site ($W = 159$, $p = 0.054$, corrected for the false discovery rate) but not in other comparisons between sites. There was no significant difference between core range sizes, either overall or between individual sites ($p > 0.1$). The maximum estimated distance ranged was 278.0 m (with a high degree of variation between individual cats; Table 6.1). Cats in the peri-urban area ranged the furthest on average, and also showed the greatest degree of variation in maximum distance travelled, followed by cats dwelling in the suburban, then the urban area (Table 6.1). Overall there was a significant degree of variation across the different sites (H = 10.7, p = 0.005) and in individual comparisons between sites there was a significant difference between both the suburban and peri-urban (borderline) sites with the urban site but not with each other (W = 182, p = 0.003 and p = 0.053 respectively, corrected for the false discovery rate). Recommended exclusion zones based on maximum distance from home were 146 m for the urban area, 204 m for the suburban area and 334 m for the peri-urban area.

Table 6.1. Mean and Median home and core range (ha) for cats across three levels of urbanisation along with maximum straight-line distance from home (m) and sample sizes. Areas determined by kernel density (KE) and minimum convex polygon (MCP) estimation.

Area	Mean home-range area ± s.e. *Median* (min – max)		Mean 50% KE (core area) ± s.e. *Median* (min – max)	Mean maximum distance ranged ± s.e. *Median* (min – max)	Number of cats (female, male)
	95% KE	95% MCP			
Urban	1.05 ± 0.13 *0.90* (0.32 – 1.92)	0.75 ± 0.10 *0.62* (0.22 – 1.42)	0.18 ± 0.03 *0.15* (0.05 – 0.36)	85 ± 5 *79* (58 – 122)	14 (6,8)
Suburban	1.79 ± 0.24 *1.56* (0.73 – 3.90)	1.31 ± 0.17 *1.16* (0.51 – 2.67)	0.25 ± 0.04 *0.18* (0.07 – 0.58)	127 ± 8 *141* (81 – 170)	15 (4, 11)
Peri-urban	2.41 ± 0.73 *1.60* (0.40 – 6.61)	1.63 ± 0.42 *1.32* (0.27 – 3.96)	0.28 ± 0.09 *0.17* (0.06 – 0.75)	153 ± 27 *148* (62 – 278)	9 (4, 5)
Overall	**1.66 ± 0.21** ***1.28*** **(0.32 – 6.61)**	**1.18 ± 0.13** ***0.95*** **(0.22 – 3.96)**	**0.23 ± 0.03** ***0.17*** **(0.05 – 0.75)**	**118 ± 8** ***99*** **(58 – 278)**	**38** **(14, 24)**

Samples were limited due to loses/insufficient data being generated by some cats among multiple cat households but no significant difference was found between the size of cat home or core ranges within households (t = 0.468, p = 0.652 and W = 34, p = 0.192 respectively, n = 15 cats, 7 households). The median proportional home range overlap between cats living in the same household was 0.824 (IQR = 0.460 – 0.861)

6.4.4. Habitat Selection

For cats living adjacent to large greenspaces and natural habitat fragments (n = 11) standardised average habitat selection ratios were 0.553 for garden habitat, 0.311 for anthropogenic surfaces and 0.136 for natural habitat. Cats further away from these large greenspaces and natural habitat fragments (n = 27) had standardised average habitat selection ratios of 0.599 for garden habitat, 0.345

for anthropogenic surfaces and 0.056 for natural habitat. Despite these differences and their proximity to more natural habitat border cats still showed a clear selection preference for garden habitat.

6.4.5. Daytime/night time roaming

There was no difference between cat ranging during the day and night for home and core ranges (p > 0.1 for both). However, Cats ranged proportionally further at night for both home (W = 724, p < 0.001) and core ranges (W = 571, p = 0.003) when differences between the length of day and night were accounted for. This suggests that when day and night length are equal cats will range significantly further at night. Incremental analysis suggested that day and night home ranges had not been fully revealed.

Table 6.2. Mean and median day and night home and core ranges (ha) for cats across three levels of urbanisation determined by kernel density estimation (KE).

Area	Mean 95% KE home-range area ± s.e. *Median* (min – max)		Mean 50% KE core area ± s.e. *Median* (min – max)	
	Day	Night	Day	Night
Urban	1.00 ± 0.13 *0.82* (0.32 – 1.85)	1.10 ± 0.15 *0.98* (0.32 – 2.58)	0.11 ± 0.02 *0.06* (0.03 – 0.27)	0.09 ± 0.01 *0.10* (0.03 – 0.16)
Suburban	1.65 ± 0.20 *1.30* (0.63 – 2.98)	1.76 ± 0.29 *1.29* (0.64 – 3.93)	0.16 ± 0.04 *0.11* (0.04 – 0.61)	0.16 ± 0.04 *0.10* (0.03 – 0.48)
Peri-urban	1.84 ± 0.51 *1.02* (0.38 – 4.48)	3.11 ± 1.12 *2.50* (0.46 – 10.64)	0.16 ± 0.06 *0.07* (0.03 – 0.56)	0.12 ± 0.03 *0.08* (0.03 – 0.29)
Overall	**1.46 ± 0.13** ***1.12*** **(0.32 – 4.48)**	**1.84 ± 0.31** ***1.14*** **(0.32 – 10.64)**	**0.12 ± 0.02** ***0.09*** **(0.03 – 0.61)**	**0.12 ± 0.02** ***0.10*** **(0.03 – 0.48)**

6.4.6. Factors effecting cat ranging

In the AIC_c selected model for the home range size the proportion of constructed habitat was significantly negatively associated with territory size across all selected models (p < 0.001). Whether the cat had worn a collar before was a borderline significant predictor (p = 0.099) with increased ranging associated with not usually wearing a collar (Table 6.3).

The same predictors featured in cat core range AIC_c selected model. Proportion of constructed habitat (p = 0.047), and collar (p = 0.044; Figure 6.2) were significant predictors though these factors were only borderline significant in the other AIC_c selected models (Table 6.3).

For the maximum distance reached from home AIC$_c$ selected model the proportion of constructed habitat was significantly negatively associated with territory size ($p < 0.001$) with no other significant factors found (Table 6.3).

Sex (Figure 6.3) and age were not found to be significant predicators in any models fitted.

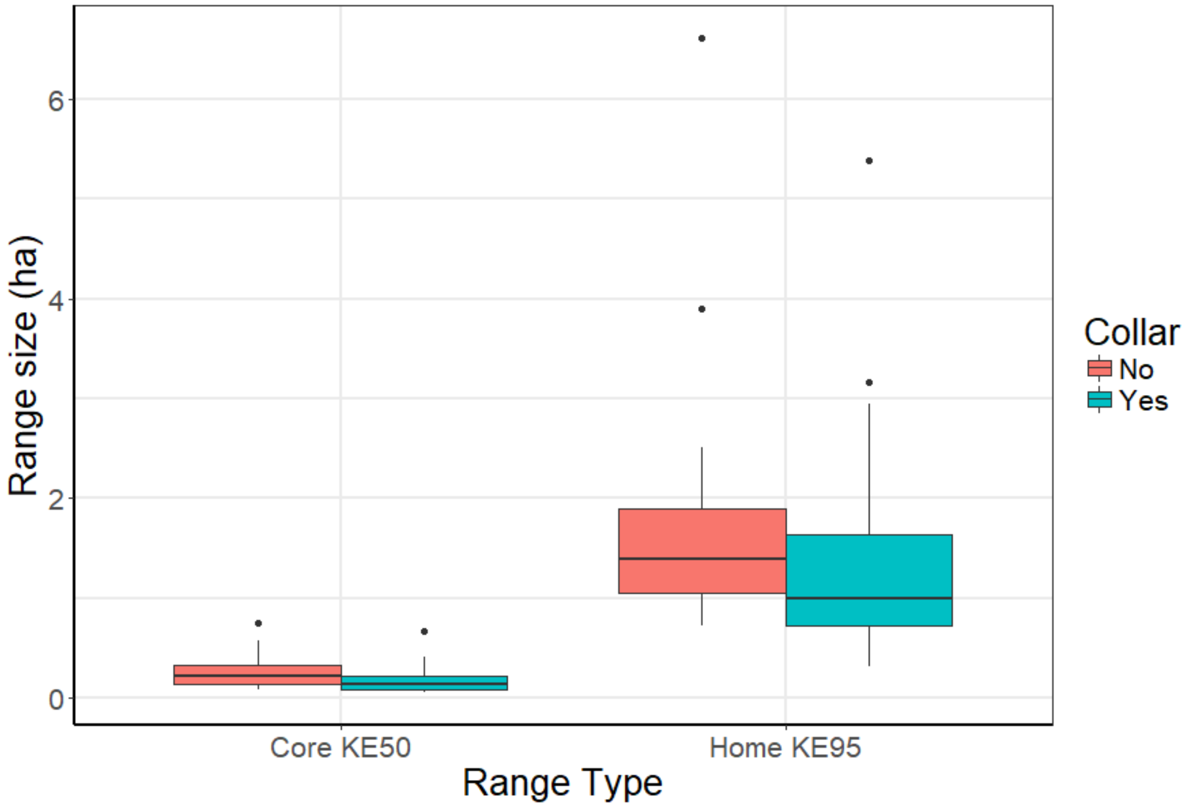

Figure 6.2. Median (+/- IQR) core (KE50) and home (KE95) range sizes by if a Domestic Cat normally wore a collar.

Table 6.3. Set of candidate models for 95% (home) and 50% (core) KDE home ranges and maximum distance reached from home of domestic cats using linear mixed-model analysis showing all variable contrasts with model weights, Delta AIC_c and R^2 values. '%Constructed' refers to the proportion of constructed surfaces within a cat's range, 'Sex' refers to cat sex (female set to intercept), 'Collar' refers to whether the cat normally wore a collar (no usual collar set to intercept). All other models had $\Delta AIC_c > 2$. For P value significance: ● p = 0.1 - 0.05, * p < 0.01, ** p < 0.001, *** p < 0.0001.

Dependent variable	Model	Variables	F	S.E.	P	Delta AIC_c	Model weight	d.f
95% KDE	Global Model	Intercept	0.9695	0.3625	0.0115 *	4.31	0.029	33
		%Constructed	-2.1518	0.593	0.0010 **			
		Sex	0.2304	0.204	0.2670			
		Collar	-0.2609	0.1898	0.1784			
		Age	0.0001	0.0300	0.9980			
	Model 1	Intercept	0.9701	0.2774	0.0013 **	1.28	0.133	34
		%Constructed	-2.152	0.577	0.0007 ***			
		Sex	0.2302	0.1934	0.2421			
		Collar	-0.2609	0.1866	0.1710			
	Model 2	Intercept	0.7889	0.2486	0.0031 **	0.57	0.190	35
		%Constructed	-2.1116	0.5840	0.0009 ***			
		Sex	0.2898	0.1912	0.1386			
	Model 3	Intercept	0.9843	0.2164	0.0001 ***	0.33	0.215	34
		%Constructed	-2.1492	0.5939	0.0009 ***			
	AIC_c Selected Model	**Intercept**	**1.1518**	**0.2330**	**<0.0001 *** **	**0.00**	**0.253**	**35**
		%Constructed	**-2.1875**	**0.5795**	**0.0006 *** **			
		Collar	**-0.3098**	**0.1830**	**0.0994 ●**			
50% KDE	Global Model	Intercept	-1.2527	0.3935	0.0032 **	4.21	0.027	33
		%Constructed	-1.0911	0.5753	0.0667 ●			
		Sex	0.2526	0.2299	0.2797			
		Collar	-0.3777	0.2136	0.0863 ●			
		Age	-0.0071	0.0373	0.8498			
	Model 1	Intercept	-1.3017	0.2941	0.0001 ***	1.22	0.120	34
		%Constructed	-1.1119	0.557	0.0540 ●			
		Sex	0.2646	0.2181	0.2335			
		Collar	-0.3748	0.2100	0.0833 ●			
	AIC_c Selected Model	**Intercept**	**-1.0931**	**0.2403**	**0.0001 *** **	**0.00**	**0.222**	**35**
		%Constructed	**-1.1518**	**0.5597**	**0.0471 ***			
		Collar	**-0.4304**	**0.2064**	**0.0444 ***			
Maximum distance from home	Global Model	Intercept	5.3246	0.1998	<0.0001 ***	6.13	0.016	33
		%Constructed	-1.5593	0.32678	<0.0001 ***			
		Sex	0.0175	0.1121	0.8773			
		Collar	-0.1267	0.0152	0.2343			

		Age	-0.0113	0.1058	0.5358			
	Model 1	Intercept	5.2748	0.1268	<0.0001 ***	0.85	0.230	35
		%Constructed	-1.5972	0.3153	<0.0001 ***			
		Collar	-0.1302	0.0996	0.1995			
	AIC$_c$ Selected Model	**Intercept**	**5.2044**	**0.1159**	**<0.0001 *****	**0.00**	**0.352**	**36**
		%Constructed	**-1.5812**	**0.3182**	**<0.0001 *****			

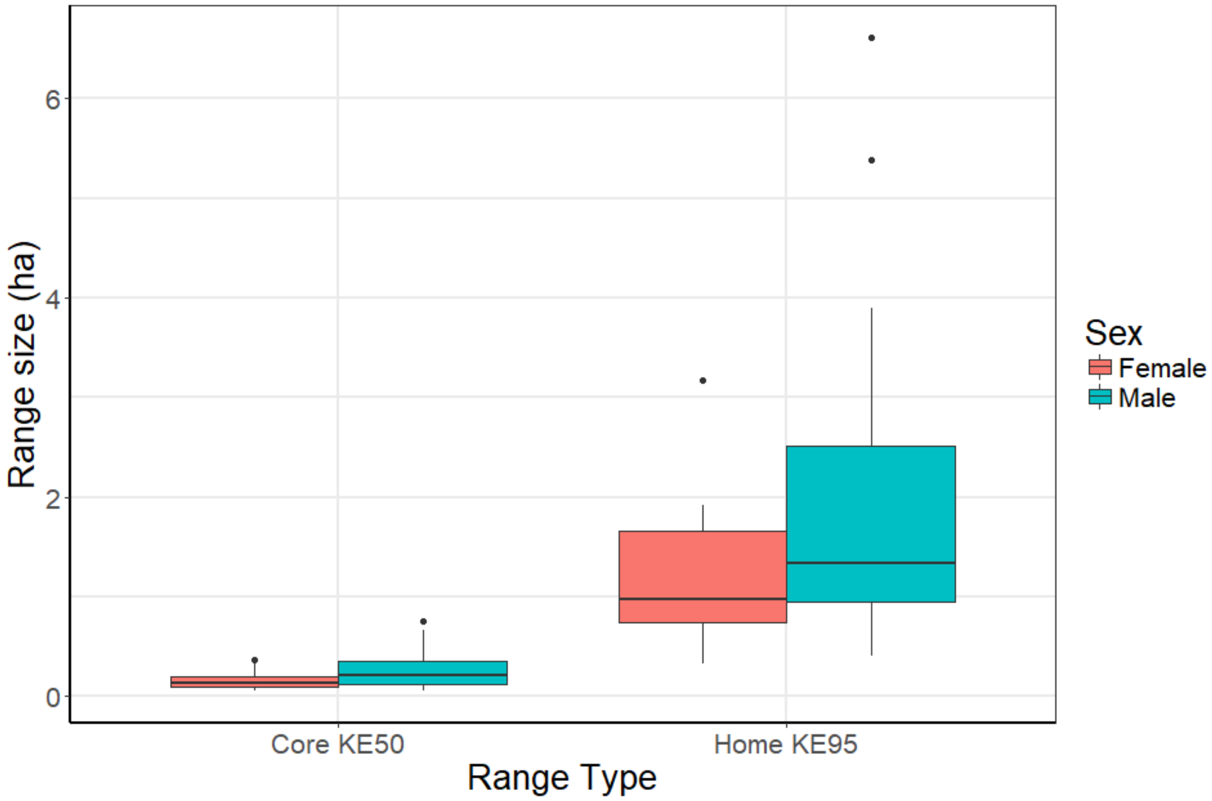

Figure 6.3. Median (+/-IQR) core (KE50) and home (KE95) Domestic Cat range sizes by sex.

6.5. Discussion

We find strong evidence for an effect of urbanisation on cat roaming behaviour. Cats residing in areas with a smaller proportion of constructed surfaces (buildings, artificial surfaces etc i.e. less urban) ranged further than those in more urbanised habitats. Although some of the home ranges produced in this study are smaller than many previous studies which have generally taken place in entirely separate biogeographical areas they are still broadly comparable and here we provide one of the largest cat tracking samples to date and one of the few across different habitats in the same local landscape. Cats did have proportionally larger range sizes at night given day length at the time of the study, but there was no difference between the sexes; cats that wore collars typically had smaller range sizes. Overall, our results suggest a buffer zone of ~335m between peri-urban housing and areas of conservation concern would be appropriate. This finding may also help urban planners and conservation biologists consider the possible local effect of cat predation at different levels of urbanisation. In suburban areas, similar ‘effect’ zones would be ~200m and in urban areas ~145m in radius.

Cat ranges in the peri-urban area were particularly variable although they also had the smallest sample size. Some of the study cats came from similar habitats to that found in the suburban areas (large gardens and semidetached/detached housing), whereas others lived on or close to the edge of the housing areas bordering on farmland habitats. Among those were the cats with the largest ranges, and they therefore may represent the greatest risk to wildlife though this may not always be the case (Metsers et al. 2010). In turn, cats in more rural landscapes are likely to range significantly further than those tested in this study (Metsers et al. 2010; Wierzbowska et al. 2012; Kitts-Morgan et al. 2015; Hall et al. 2016b). Given the potential biogeographical differences between these areas and the UK, further comparable tracking studies to the present study would be necessary to determine the magnitude of such an effect and its significance to inform additional management recommendations applicable to the UK. For example, comparing UK cat ranging with that of countries were large predators may be present in the same habitat such as coyotes *Canis latrans* in North America (Gehrt et al. 2013) and dingoes *Canis dingo* in Australia (Johnson et al. 2007) may be inappropriate as domestic cat behaviour may be influenced by their presence (Ritchie & Johnson 2009). Likewise the presence of non-comparable prey (Barratt 1997b; Lilith et al. 2008) and/or habitats (Morgan et al. 2009; Kitts-Morgan et al. 2015; Wood et al. 2016) may also influence cat ranging behaviour both within and between general biogeographical areas. However, the dominant habitat selection of cats living on the edge of green spaces was still for garden habitat, indicating that they did not necessarily exploit these areas despite bordering them (Kays & DeWan 2004; Metsers et al. 2010). This further reinforces the importance of understanding variation in ranging behaviour among individual cats (Dickman & Newsome 2015).

Understanding the range size of domestic cats provides insights into where they are likely to be a threat to wildlife (Hall et al. 2016b). The concept of a buffer zone between housing and areas of conservation value is quite straight-forward (Lilith et al. 2008), but data on range size also allows us to consider the role of cats in two other ways. First, for individuals responsible for managing reserves and parks in more urban areas, habitat and cat access could be managed (e.g. through the planting of dense vegetation, or using waterways as barriers) in order to keep roaming cats apart from vulnerable species of interest (Kays & DeWan 2004; Metsers et al. 2010). Second, we suggest that cat roaming behaviour extends the ecological footprint of urbanisation out into the surrounding countryside beyond direct influences on habitats and wildlife (Thompson & Jones 1999; Marzluff 2001;

McKinney 2006). Most simplistically, consider a hypothetical town with a periurban periphery comprised of dwellings. The incidence of predation by domestic cats on surrounding wildlife may be considerable (Barratt 1997a; Metsers et al. 2010; Hall et al. 2016b), and is evidently not confined to the urban area *senso strictu*; in a town 40km^2 in area, cat predation and other indirect negative effects may extend to cover an additional area of ~8km^2.

Overall, we found that cats did range proportionally further at night in the time available suggesting that when day and night length are equal cats will range further at night, in keeping with the findings of previous research (Barratt 1997a; Metsers et al. 2010; Thomas et al. 2014), although it is likely that domestic cats show more diurnal activity than feral cats (Alterio & Moller 1997). This difference in roaming behaviour may be linked to reduced road traffic (Barratt 1997a) and increased activity by some prey at night (Woods et al. 2003). Largely nocturnal species, such as small mammals (Vickery & Bider 1981; Wolton 1983; Galsworthy et al. 2005) make up a significant proportion of cat prey (Thomas et al. 2012).

It is important to note that incremental analyses suggested that all the examined home ranges had not been fully revealed, though 90% KDEs were fully revealed indicating the effect of extreme location fixes on the home range estimates (Harris et al. 1990). Clearly this suggests that the tracking period of 7 days was not long enough to provide a true estimate of the cat home ranges in this study. The main reason for this limitation was the battery life of the tracking device used. Thus, a device with a better battery life should produce a better home range estimate though, this must be traded off against the likely higher cost of such a device and the increased opportunity for it be lost in a longer tracking period. Therefore, the home range estimates presented here should be treated as a conservative guide only. However, they are in keeping with past studies in similar habitats and tracking periods (e.g. Kays and DeWan 2004; van Heezik et al. 2010; Coughlin and van Heezik 2014; Thomas et al. 2014;) suggesting they are still of relevance for comparisons between studies and making management recommendations.

A curfew keeping cats inside at night may be considered a more acceptable form of cat management than exclusion zones by owners to reduce their effect on some vulnerable prey populations (Grayson et al. 2002; Lilith et al. 2006) with nocturnally active mammals likely to be the main beneficiary (Woods et al. 2003; Galsworthy et al. 2005; Thomas et al. 2014) rather than birds. In addition to conservation concerns there are clear welfare advantages to keeping cats indoors at night (Lilith et al. 2006; Toukhsati et al. 2012; McDonald et al. 2015). Such advantages include lowering the risk of road traffic accidents, infectious disease transmission and reducing injures from fighting with both other cats and wildlife which may undermine cat welfare and contribute to cat mortality (Moreau et al. 2003; Rochlitz 2004; Egenvall et al. 2010; Calver et al. 2013).

We found no difference between the ranging behaviours of male and female domestic cats, supporting several broadly comparable studies (Metsers et al. 2010; van Heezik et al. 2010; Coughlin & van Heezik 2014; Thomas et al. 2014) and unlike the meta-analysis carried out by Hall et al. (2016b) which considered 24 separate studies. All study cats were neutered which reflects typical cat fertility status in the UK where over 91% of domestic cats are believed to be sterilised (Murray et al. 2009; Thomas et al. 2012). Unneutered individuals, particularly males, have been suggested to range further though Hall et al. (2016b) did not find any overall significant influence on domestic cat ranging due to desexing considering data across seven separate studies featuring both neutered and unneutered individuals. Domestic cats generally show reduced territoriality due to the ready availability of supplementary food (Liberg 1984), which combined with neutering may reduce behaviours associated with roaming and territory defence.

Perhaps surprisingly age was not a significant predictor of cat ranging behaviour in contrast to findings by other authors (Morgan et al. 2009; Hervías et al. 2014; Hall et al. 2016b) though only three cats in the study were under two years old, meaning the study was biased towards older cats.

Similarly to Coughlin & van Heezik (2014), we found cats that did not usually wear a collar had significantly larger core ranges than those that did, though there was no difference between home ranges or maximum distance reached from home. In an attempt to counter this known effect (Coughlin & van Heezik 2014) and reduce the number of tracker losses, collars were provided beforehand in an attempt to get cats used to them. This difference is most likely due to cats adjusting differently to the presence of the added weight of the collar even though it made up less than 2% of their body mass in all cats as recommended in previous studies (e.g. Casper 2009; Coughlin and Van Heezik 2014). The effect of wearing collars may disappear if cats wore them for longer. However, this difference in roaming behaviour between cats which normally wear a collar and those which do not may be a result of differences in cat personality (Dickman & Newsome 2015), with bolder individuals that may range more (Barratt 1997a) being less likely to accept collars. Further work is required to elucidate this. Nevertheless, collars with bells have been found to reduce cat predation success (Ruxton et al. 2002; Gordon et al. 2010) so from a conservation and animal welfare perspective it is advisable to fit free ranging cats with belled collars. Some cat owners remain concerned about potential health impacts collars may have on their cats (Harrod et al. 2016) but the risks appear to be minimal compared to the many other hazards present in their environment (Calver et al. 2013).

We found no significant difference between cat ranges for those living in the same house and unsurprisingly in all cases their home ranges overlapped considerably. It is interesting to note that the cats whose home ranges that lay entirely within another cat living in the same house’s range were all female within related male ranges, suggesting at least for these household’s males ranged further than their female kin. There is evidence in feral cats that male cat home ranges are in part a result of them seeking access to females, whereas female home ranges largely reflect their access to resources (Bengsen et al. 2016). This may explain this apparent difference been males and females though given all cats were neutered and fed daily applying this to owned cats is problematic. Although tracking cats from the same household may violate spatial independence assumptions (Millspaugh et al. 1998) this represents the reality for many domestic cats (Metsers et al. 2010) with many households having multiple cats (Hall et al. 2016a). Due to the spread of volunteered cats and shortcomings of the GPS devices it is difficult to directly look at overlaps between cats in separate households in this study. However, how domestic cats interact in local areas may affect their ranging and predatory habitats and is worthy of future consideration. At higher housing densities cats are more likely to encounter other cats, dogs or other deterrents to widespread roaming. Therefore, housing density can be considered a surrogate for cat density and likely the real cause of changes in cat ranging behaviour with urbanisation (Hall et al. 2016a; Hall et al. 2016b).

Understanding cat behaviour is central to reducing their predation rates, particularly in areas of higher conservation value. Insights into ranging behaviour are a first step towards developing recommendations for the provision of buffer zones, and other means of limiting the consequences of cat predation at a local scale (Hall et al. 2016b). From our study, we find that the level of urbanisation was significant predictor of cat range size and suggest minimum exclusion zone distances between houses and areas of conservation concern (Lilith et al. 2008; Metsers et al. 2010) could be adjusted to the level of urbanisation in the landscape. The minimum exclusion zone distance for the most urbanised area was less than half the size of the peri-urban area (distances of 146 m, 204 m and 334 m for urban, suburban and peri-urban sites respectively). The exclusion zone calculated for the peri-urban area is similar to that found by Thomas et al. (2014). Exclusion zones for protected areas within urbanised areas could be tailored to the level of urbanisation in the local landscape, which in turn may be both easier to enforce and increase cat owner collaboration with cat management for conservation which can be problematic (Thomas et al. 2012; McDonald et al. 2015; Gramza et al. 2016; Hall et al. 2016a). Irrespective of management implications, such data also provide helpful insights into how estimates of the likely assemblages of prey taken by cats are calculated.

Cat exclusion zones can be incorporated into planning requirements for new residential developments and possibly into existing ones near protected areas with vulnerable species of conservation concern. In addition, management actions could be taken to restrict cat ranging at night as reduced nocturnal roaming may reduce predation pressure on some vulnerable prey types. However, only exclusion zones could fully reduce both the direct and indirect negative effects of cats on prey populations. Further studies should consider cat use of nature reserves and adjacent areas in UK at different levels of urbanisation and with different habitats to further inform these potential management actions. Furthermore, it is important to consider how cats adjacent to exclusion zones respond to the presence of cat-free areas. If cat density is the driver of range size (Hall et al. 2016b) then creating cat free areas may encourage them to enter the exclusion zones and potentially range further into the areas we wish to keep them from. The Thames Basin Heaths Special Protected Area (SPA) in the UK incorporates buffer zones limiting and even prohibiting new developments to protect rare species such as the Dartford Warbler *Sylvia undata*. One of the stated aims of these SPA buffer zones is to exclude predatory domestic cats with buffers prohibiting new developments and hence owned cats within 400 m (Thames Basin Heaths Joint Strategic Partnership Board 2009). This is broadly in keeping with our own recommendations, though distances as large as 1000 m or more have been suggested by some to account for the increased ranging potential in the low density cat areas created by exclusion zones as well as the inclusion of physical barriers such as fences (Underhill-Day 2011) and development is controlled in a 5 km buffer around the Thames Basin Heaths SPA (Thames Basin Heaths Joint Strategic Partnership Board 2009). It is clear we must err on the side of caution (Lilith et al. 2006; Calver et al. 2011) and consider larger exclusion zones than the tracking data may suggest (Lilith et al. 2008; Underhill-Day 2011). It would be valuable to explore cat behaviour around fenced and unfenced exclusion zones to see not only how cats respond to these zones but also to see how potential prey populations respond. This would not only help confirm the effectiveness of unfenced exclusion zones but also help confirm if cats are an important predation threat in these areas.

Domestic cats occur at exceptionally high densities in the UK, particularly in urban areas. This introduced predator represents a high predation risk to many species living in and around urban areas. Buffer zones where free ranging cat ownership is limited or night-time cat curfews represent potentially important management tools that could be used to limit their effect on species inhabiting protected areas. In this study, the second GPS tracking study in the UK and is the first to look at cat ranging across different levels of urbanisation within the same geographical area, we find cat ranges are larger in less urbanized habitats and that cats range proportionally further at night. We suggest cat management measures such as buffer zones should be scaled with the level of urbanisation in the local landscape which may increase their effectiveness for protecting wildlife.

Chapter 7: Discussion

We intentionally and unintentionally affect the survival and diversity of birds living around us in many ways. In urban areas we intentionally provide supplementary food and nest sites, and these direct, apparently beneficial actions can be mitigated by unexpected negative effects. My work suggests that there are practical ways to partially reduce these negatives, and perhaps some may be less serious than generally thought. It is key that we take effective action to maximise benefits to bird diversity, for the benefit of both birds and ourselves in this increasingly urbanising world. Below I review the outcome of my research, placing it in context, and then draw it together to emphasise the value of this approach.

7.1. Garden bird feeders and the Grey Squirrel (Chapter 2)

Supplementary bird feeding has the potential to support large populations of wild birds (Orros & Fellowes 2015b), and in return those feeding gain a vital connection to wildlife with associated benefits to health and well-being (Cox & Gaston 2016; Cox et al. 2017b). However, the presence of Grey Squirrels and other non-target animals that outcompete and potentially depress target bird populations may subvert this system away from its intended purpose (Bonnington et al. 2014b). I found some evidence that the presence and use of feeders by the introduced Grey Squirrels reduces the use of garden bird feeders by urban birds (Chapter 2). The presence of a Grey Squirrel effectively excluded all birds from a feeding station and at a rough estimate across the whole study, the energy provided could plausibly support the full energy requirements of more than two adult Grey Squirrels based on their average use of feeders 44.3% of the time (Harris & Yalden 2008; Orros & Fellowes 2015b). Even when not physically present, bird use of feeders may be depressed by regular Grey Squirrel usage and there was evidence of a behavioural change in the timing of first bird visitation to feeders, with some species responding more than others. By allowing Grey Squirrels free access to supplementary food we as a bird feeding nation are directly helping to support a large population of a highly competitive introduced species (Bonnington et al. 2014a; Bonnington et al. 2014b; Bonnington et al. 2014c; Orros & Fellowes 2015b) that is in addition a direct and indirect nest predation risk to our native wildlife (Chapter 3).

Excluding Grey Squirrels using cage style feeder guards reduces the amount they are able to benefit from supplementary food but at the cost of also discouraging some of the very bird species that supplementary feeding seeks to support. This is likely to be a response to the guards themselves possibly presenting a real or perceived barrier to escape behaviour and/or predator detection (Devereux et al. 2006; Cresswell et al. 2009). Other exclusion methods such as baffles and feeders that control access based on weight could be used, though we should be careful not to accidently encourage other predators/competitors instead. Such measures can be expensive, which may discourage some garden owners from purchasing them though the reduced food usage by larger animals with higher energy requirements may counteract this to some extent (Orros & Fellowes 2015b).

This study shows that careful consideration must be given not only to allowing non-target species to benefit from the supplementary food (further examined in Chapter 3) and to the effects of any exclusionary steps we may take in response.

7.2. Nest predation around bird feeders (Chapter 3)

As we have seen, Grey Squirrels directly compete with target species for resources, potentially helping to build up their populations. Alongside Grey Squirrels, corvids are common nest predators in urban areas (Eaton et al. 2013; Bonnington et al. 2014a) and frequent supplementary feeding stations (Chamberlain et al. 2005; Väisänen 2008; Bonnington et al. 2014a; Chapter 2). Urban gardens are home to nationally important populations of some bird species (Gregory & Baillie 1998; Bland et al. 2004) and many, particularly open cup nesters, are vulnerable to nest predation (Ricklefs 1969; Martin & Li 1992; Máthé & Batáry 2015). Unintended predation effects have previously been found around supplementary feeding sites, with predators being encouraged into the vicinity of these point sources and foraging in the local area (Cooper & Ginnett 2000; Orros & Fellowes 2012; Selva et al. 2014; Orros et al. 2015). This effect had previously not been considered with nest predation; if potential nest predators are attracted to supplementary feeding stations, we may unwittingly be encouraging nest predation.

I found that artificial nests adjacent to filled bird feeders suffered greatly increased predation rates, with the survivorship of nests adjacent to unguarded feeders being less than 20% of that seen in similarly placed artificial nests near empty feeders (Chapter 3; published as Hanmer et al. 2017). The direct exclusion of larger animals including potential nest predators using bird feeder guards did not significantly counteract this effect, although it did reduce it, suggesting the link between bird feeder usage and nest predation is more complex than it first appears. The role of Grey Squirrels was particularly interesting, as aside from being a nest predator themselves, their presence at bird feeders appeared to influence the behaviour of Magpies and Jays, other local nest predators. The mechanism for this warrants further study, particularly in the area around the bird feeders. I suggest that they may be attracted by the increased presence of other omnivores, associating it with increased feeding potential, even if they themselves are not primary users of the bird feeders. Second, the presence of Grey Squirrels on feeders may exclude other omnivorous predators as well as small birds (Chapter 2), resulting in increased foraging in the vicinity of the feeders. These mechanisms could work plausibly together to increase local nest predation even if indirectly.

Clearly if this predation effect occurs in UK gardens during the breeding season and we are providing energy to support large populations of Grey Squirrels and other nest predators (Chapter 2) then we may be compounding the effects of local nest predation (Chapter 3). Even if the effect is highly localised around a feeder (Malpass et al. 2017), given how widespread supplementary feeding is (over 45% of households feed birds; Davies et al. 2009; Orros & Fellowes 2015b) this could have potentially serious and overlooked implications for national populations of some garden bird species even ignoring the additional risks of pathogen transmission at feeding stations (Chapter 4).

7.3. Bacteria and bird feeders (Chapter 4)

It has long been assumed that garden supplementary feeding represents a major pathogen transmission risk, both between birds and from birds to humans. The concentrations of birds and interactions found on and around the point sources of food supplementary feeders present are unusual in nature for many of the bird species using them (Galbraith et al. 2015; Chapter 2). As such the transmission of pathogens is likely to be increased on and around supplementary feeding stations (Benskin et al. 2009; Murray et al. 2016), particularly in the winter when usage is increased (Chamberlain et al. 2005; Chamberlain et al. 2007). While bacteria are not the perfect models for pathogen transmission (Swinton et al. 2002; Benskin et al. 2009), developments in DNA sequencing techniques allows closer investigation of the communities and pathogens present in the environment, including on bird feeders. In the first study of its kind, I used NGS to identify the bacterial communities inhabiting typical feeders placed in the field.

Peanut feeders had significantly higher reads (a proxy for abundance) of bacteria but lower OTU diversity than seed feeders (Chapter 4). Neither type of experimental feeder differed significantly from their respective controls in terms of overall bacterial reads, richness or diversity. This means that there was no clear effect of animal usage on the bacterial communities, including pathogens, on bird feeders with most of what was detected apparently coming from the local environment (e.g. soil bacteria). What is noteworthy is that feeder type was more important than other factors in determining bacterial communities, and thus the risk of pathogen transmission may be influenced by feeder design.

As only bacteria where considered, the presence and transmission of other pathogens on bird feeders cannot be ruled out in this study, nor that of any type of pathogen in area around the bird feeders. Therefore these findings should not discourage people putting out food for birds and other wildlife from following good hygiene practices to combat the spread of pathogens (Lawson et al. 2014). However, my results do suggest that the risk of pathogen transmission directly on supplementary bird feeders, used in a typical suburban garden setting, may be lower than previously feared.

7.4. Nest boxes, materials, arthropods and urbanisation (Chapter 5)

Aside from supplementary food (Chapters 2 – 4) we provide other resources to birds both intentionally and unintentionally. In particular in the UK we provide millions of garden and urban greenspace nest boxes, allowing common cavity nesting birds such as Blue Tits and Great Tits to heavily utilise urban areas as breeding as well as foraging habitat (Davies et al. 2009). This allows the investigation of the effects of urbanisation on breeding biology on these particular birds in ways generally impractical with other species (Vaugoyeau et al. 2016). The decline in breeding success with urbanisation is particularly interesting and while food availability and predation is likely to play a key role in this decline (Chamberlain et al. 2009), other poorly explored factors may also contribute. For example, reductions in the availability of natural nest-building material in more urbanised areas may lead to an increasing use of anthropogenic materials as a substitute, with effects on nest-dwelling arthropods, including ectoparasites (Reynolds et al. 2016). In turn this may have a hidden influence on the breeding success of urban birds.

I found that anthropogenic material was common in nests regardless of the level of urbanisation in both Blue Tits and Great Tits (Reynolds et al. 2016; Chapter 5). Great Tits made much more use of it and in a more uniform way regardless of habitat, whereas Blue Tits only increased their use of it in the most urbanised habitats. This relatively uniform incorporation of anthropogenic materials across the urbanisation gradient in Great Tits suggests they may preferentially seek it out while Blue Tits only use it when the availability of natural materials is lower (Wang et al. 2009; Surgey et al. 2012). In fledged nests increasing use of anthropogenic material was associated with lower general arthropod diversity and ectoparasite predator abundance but higher levels of Siphonapterans (fleas). Higher arthropod diversity was linked to lower flea numbers implying supporting a more complex arthropod community reduced the abundance of nest ectoparasites. No direct association was found between anthropogenic material usage or nest-dwelling arthropods with breeding success. Breeding success declined with increasing urbanisation in both species (Chamberlain et al. 2009) and increased with nest weight in Blue Tits (Gladalski et al. 2016; Lambrechts et al. 2016a).

As has been noted before we should not assume the patterns found in bird nests inside nest boxes accurately represent those found in birds of the same species nesting in natural cavities (Wesołowski & Stańska 2001; Maziarz et al. 2017). However, given the possible importance of these artificial sites in urban areas (Davies et al. 2009) this should not undermine the relevance of nest box studies in studying the effects of urbanisation of wild birds, and indeed as mesocosms for community ecology research. While no firm conclusions can be drawn from this study it appears that hidden factors may play a role in determining breeding success across the urbanisation gradient (Chamberlain et al. 2009; Chapter 5).

7.5. Cat ranging and management (Chapter 6)

Aside from the supplementary resources we provide to urban birds (Chapters 2 – 5) we also add additional challenges to the urban environment beyond altering habitat and resource availability. Domestic Cats are the most abundant predator in many urban ecosystems and in the UK their national population far outnumbers that of fully native wild predators (Harris et al. 1995; Battersby 2005; Murray et al. 2010). They occur at densities far beyond those supported by natural prey populations (Baker et al. 2008; Sims et al. 2008; Thomas et al. 2012) but despite the apparently huge numbers of animals killed by cat predation (Thomas et al. 2012; Blancher 2013; Loss et al. 2013) and any associated indirect effects (Beckerman et al. 2007; Bonnington et al. 2013), it is unclear what impact they have on prey populations. However, the precautionary principal suggests that we should consider taking action to minimise the risk of predation on species of concern, particularly in and around protected areas (Lilith et al. 2006). Exclusion zones where cat ownership is discouraged/banned is a key way we might be able to limit cat predation around such areas but to implement them effectively it is necessary to establish how far cats range in the landscapes of interest so appropriate buffer zones can be calculated (Lilith et al. 2006; Lilith et al. 2008; Metsers et al. 2010; Thomas et al. 2014). Local levels of urbanisation in particular may be an important factor in determining cat ranging (Hall et al. 2016b).

I found that if it were determined that ranging cats could have a negative effect on wildlife populations in a given protected area (such as predating a vulnerable protected species), meriting their exclusion, then a buffer zone of at least 335m (including a 20% error margin) would be needed from the edge of urban developments (Chapter 6). In suburban areas, similar buffer zones would be ~200m and in urban areas ~145m. In turn for more isolated developments such as a farm or hamlet, a larger buffer zone would be likely to be needed (Metsers et al. 2010; Wierzbowska et al. 2012; Kitts-Morgan et al. 2015; Hall et al. 2016b) and additional local tracking studies required to determine the size of such a zone. Short of an outright ban on roaming cats which is likely to prove publicly unacceptable for existing developments, determining and managing the effect of cat predation remains difficult (Thomas et al. 2012; Hall et al. 2016a), particularly in a small highly urbanised country such as the UK. If a night time curfew system were deemed more acceptable, then my results combined with that of others does suggest that this may reduce the area threatened by roaming cats (Barratt 1997a; Metsers et al. 2010; Thomas et al. 2014). In turn this may reduce the rates of predation, particularly of small mammals, but also of birds and other prey. Given the effect of urbanisation on these estimates it is vital that we consider the level of urbanisation as well as individual variation (Dickman & Newsome 2015) in calculating such exclusionary buffers.

7.6. Unsuccessful research components

Two important components of this PhD as initially intended proved unsuccessful.

In Chapter 2 in addition to recording the number of animals utilising bird feeders I originally sought to quantify the amount of food by weight being consumed and hence estimate the energy consumed. Combined with visit records this could have allowed the estimation of how much each species of animal was consuming, and so provide an alternative measure of supplementary feeder usage and the animals supported by it. However, given the feeding stations were only physically visited up to twice a week to minimise disruption to the volunteer garden owners, it was difficult to measure food consumption effectively and then relate it to feeder use and so this component was dropped from the study. Daily checks could potentially have been carried out to measure food consumption by weight combined with complete daily video visit records to quantify consumption by each animal species but this would have been difficult logistically, particularly over an extended study period.

As detailed briefly in the thesis introduction Chapter 6 was initially conceived to investigate if Domestic Cats frequented gardens and other areas containing supplementary feeding stations, as well as more generally investigating influences on cat ranging behaviour. However, it proved more difficult than anticipated to gain a complete enough picture of the locations of feeding stations within cat territories through door step questionnaires and perhaps more importantly the analysis of home ranges raised concerns over the ability of the GPS devices used to pinpoint such a highly localised area. Hence Chapter 6 instead focused on the management implications of cat ranging across different levels of urbanisation. Possibly a network of camera traps would have offered a better way to investigate if cats frequent the vicinities of supplementary feeding stations though this would have limited the possible sample size.

7.7. Further Research

My thesis shows how interwoven the various factors influencing urban bird success can be and how difficult it can be to isolate these effects in the environment itself. More research is required to fill in our various knowledge gaps and so further link the complex interacting effects of urbanisation and associated human actions on various stages of wild bird life histories.

Given both the apparent direct predatory effect of Grey Squirrels (Chapter 3) and the exclusion effect they have on bird supplementary feeding (Chapter 2 and 3) I suggest they may affect local bird populations, though isolating such an effect would be extremely challenging. However, there is little empirical evidence that this is the case and so more work should be done establish if this is so. Utilising an exclusory system to keep them and preferably other predatory species out, while not discouraging target small bird usage may yield important evidence, particularly combined with a larger sample size and carried out over a longer period of time when seasonal changes in real bird populations can be monitored in the local environment. Directly quantifying how much of the supplementary food is consumed by different species, particularly by Grey Squirrels would give a clearer idea of how much food is subverted away from the target bird species and indicate how dependent different species may be on this artificial energy resource (Orros & Fellowes 2015b). Additionally, I found indications that birds responded behaviourally to feeder use by Grey Squirrels (Chapter 2) and so it may be worthwhile exploring this further to determine how birds can adapt to this competitive exclusion such as through changes in visit timing and utilisation of alternative food sources. Such changes may largely mitigate against the exclusionary effects of Grey Squirrels on specific supplementary feeders for species though perhaps not in others. This could also offer an interesting way of exploring differences between animal species using bird feeders in the timing of their visits to bird feeders more generally, particularly across different seasons (Ockendon et al. 2009a; Ockendon et al. 2009b).

Carrying out a similar study to Chapter 3 using feeders placed near real rather than artificial nests in the urban environment may be particularly valuable though careful consideration must be given to the practical and ethical implications of such an experiment. Since the publication of this experimental chapter (Hanmer et al. 2017) a potentially complementary field study has been published from North America linking supplementary feeding to nest predation. However, it should be noted that the environment the experiment took place in, and some of the species studied, lack direct analogues in the UK (Malpass et al. 2017). Combining aspects from these two studies in the UK urban environment would be challenging, even ignoring the potential ethical implications of placing real nests at risk. The ubiquitous nature of UK supplementary feeding makes it extremely difficult to effectively control experimentally. Given the apparent importance of Grey Squirrels in this system the study could also be replicated in an area where they absent but the other species present to see how the system functions without them. Given how numerous and widespread Grey Squirrels are in the UK and difficulty of controlling their spread (Battersby 2005; Baker & Harris 2007; Aebischer et al. 2011; Bertolino et al. 2014) it would challenging to find an otherwise directly comparable system without them. However, further investigation could be rewarding and confirm if through supplementary feeding at bird feeders we are unintentionally causing local nest predation on a wide scale and thus whether we should reconsider how supplementary food is provided during the breeding season (Chapter 3) as well as more generally (Chapter 2).

In is clear from Chapter 4 that there are differences between the bacterial communities on different bird feeders and that these communities appear to be primarily driven by environmental factors rather than animal usage despite potential differences in the animal communities supported by different bird feeders (Chapter 2; Chapter 4). Few pathogens were found and those that were showed no discernible relationship with animal usage, although sample size may have limited our statistical power to investigate this further and thus requires more observed feeder samples (Chapter 4). However, only bacteria were investigated in this study and while they provide a useful model for investigating pathogen spread, many important bird and zoonotic pathogens, including those likely to be transmittable on and around bird feeders, will spread differently (viruses, protists and fungi); these may well have been present but undetectable in this study (Swinton et al. 2002; Benskin et al. 2009). Clearly an approach sampling across other potential pathogens should be explored in any further research. Given the lack of relationship with direct bird feeder use other potential pathogen transmission surfaces/media should also be experimented with and sampled such as bird tables and bird baths. This could include taking faecal or blood samples from the birds using the feeders themselves to establish what pathogens are present in the bird population using the feeders (Wilcoxen et al. 2015; Galbraith et al. 2017). Experimentally excluding Grey Squirrels may also be valuable to establish if they confound the results or indeed act as pathogen carriers on feeders. Different hygiene regimes could be used to experimentally examine the build-up of bacterial/pathogen communities on bird feeders. A larger study using a combined approach and preferably across the seasons may yield important further information and perhaps give more weight to encouraging good hygiene practices by the bird feeding members of the public than my current findings.

Unlike open cup nesting birds, cavity nesters tend to be less vulnerable to predation (Ricklefs 1969) and so are perhaps less likely to suffer from the apparent effect of supplementary food I observed in Chapter 3. However, their nests and nestlings may be effected by urbanisation in other ways, such as through the influence of urbanisation on another overlooked threat, nest ectoparasites. I found evidence for interlinking effects of nest arthropods and nest construction on nest ectoparasites but lacked the statistical power to investigate further or to determine if there is any effect on breeding success (Chapter 5). A larger more detailed multi-year study is required to determine the magnitude of the detected effect and if it is a contributor to the decline in breeding success with urbanisation, as well as allowing for the normal variation in reproductive success between breeding seasons that may confound single season field studies. A more exhaustive breakdown of the nest material into its component parts should also be performed (Britt & Deeming 2011; Alvarez et al. 2013; Mainwaring et al. 2014b; Reynolds et al. 2016) and if a standardised box design were used, potentially nest thermal properties measured (Deeming & Biddle 2015; Deeming & Mainwaring 2015; Deeming &

Gray 2016a; Deeming & Gray 2016b). This would allow the exploration of the relationships between these factors with urbanisation and any consequential effects on breeding success.

While we may be inadvertently encouraging nest predation and competition around supplementary feeders (Chapters 2 and 3), we are also knowingly supporting a large population of predators in our homes whose effects appear largely ignored by the public (Chapter 6). With increasing urbanisation, housing developments are often built close to important nature reserves and thus potentially brings more predatory Domestic Cats into these areas (Thames Basin Heaths Joint Strategic Partnership Board 2009). However, we do not know how far cats range into these areas, their specific habitat utilisation or their true impact on local prey populations. We also know little about the effect the implementation of exclusionary buffer zones may have on the ranging behaviour of cats living adjacent to them (Lilith et al. 2006; Calver et al. 2011). Using GPS tracking combined with trail cameras it may be possible to determine how far cats range into nature reserves, other natural habitat patches and intended buffer zones compared to urban and rural areas more generally (Chapter 6). Camera traps also allow the estimation of cat densities and the relative abundances of other predators and through prey surveys and return studies, the impact on local prey populations potentially determined. Exploring how tracked cats frequent areas with monitored supplementary feeding stations as originally intended in this chapter may also be rewarding, potentially allowing us to determine how their presence influences feeder usage alongside that of Grey Squirrels (Chapter 2) and their contribution to real nest predation (Chapter 3). This would most likely be done using a combination of extensive questionnaires to determine the locations of bird feeders, cat GPS tracking, preferably using a more precise device, and camera traps to detect cats near feeding stations and the birds using them. Better understanding these ecological aspects may assist in developing habitat management plans that minimise conflicts between cat ownership and our need to protect biodiversity.

7.8. Implications, Recommendations and Conclusions

It is clear that despite its myriad challenges, urban areas present enormous opportunities for those wild bird species able to adapt to the artificial landscape humans have created. However, notwithstanding its proximity to us, we still know relatively little about many of the processes occurring in the urban environment that affect wild bird populations. What we do know is that it is the people dwelling in urban areas that make the decisions that influence which species can thrive alongside us.

We spend over £200M a year on supplementary food for birds (BTO. 2006), yet the direct benefits to birds are not always clear (Robb et al. 2008b; Harrison et al. 2010; Robb et al. 2011; Plummer et al. 2013a). However, if through providing food larger denser populations of wild birds are supported

(Evans et al. 2011), particularly in a habitat where natural resources are scarce (McKinney 2008), then any individual downsides such as through reductions in individual condition and productivity (Plummer et al. 2013a; Plummer et al. 2013b) should be outweighed. Feeding birds provides a vital connection between people and wildlife, something of increasing importance in an urbanising world (Cox & Gaston 2016; Cox et al. 2017a), with the bonus of potentially enhancing human health and well-being (Cox & Gaston 2015; Cox et al. 2017b). Therefore, to ensure the garden supplementary feeding carried by a significant proportion of the UK and other countries populations is truly beneficial, steps must be taken to limit its potential negative effects both direct and indirect on birds, some of which are explored in this thesis.

Most obviously, supporting large populations of non-target competitive and predatory species via supplementary feeding may directly act against our good intentions to support garden bird populations (Bonnington et al. 2014b), particularly when one of the key species is a non-native that threatens a native species (Bertolino et al. 2008; Bertolino et al. 2014). The extent that introduced Grey Squirrels appears to dominate and exploit garden supplementary feeders potentially at the expense of target birds is quite clear (Chapter 2; Chapter 3) and I have found evidence that they influence nest predation around bird feeders, both directly by predating nests themselves but also by potentially influencing the behaviour of other nest predators (Chapter 3). This suggests nationally we not only unintentionally support a large population of an introduced highly competitive species at bird feeders, reducing target bird access to food and so possibly depressing their populations (Bonnington et al. 2014a; Orros & Fellowes 2015b; Chapter 2) but we may also be indirectly depressing local bird breeding success to further depress their populations (Malpass et al. 2017; Chapter 3).

This means it may be necessary to reconsider the advice from the RSPB, the pet trade and other organisations encouraging year round supplementary feeding, including during the breeding season (RSPB 2009a; BTO 2017b). In particular, garden owners should be wary of placing feeding stations near potential nesting sites, and take active steps to limit the intake of food by nest predators, particularly Grey Squirrels so their populations are not supported as a by-product of bird feeding. Although feeder guards and other possibly better alternatives (baffles, counter-weighted feeders) may add expense to supplementary feeding, in many cases this should be in part be counteracted by the reduced costs of food consumed by unwanted species (Orros & Fellowes 2015; Chapter 2). In this way, we not only potentially reduce the risk of local nest predation but also in the longer term provide less energy support to predator populations and thus more generally reduce a negative effect on local and national native bird populations. How target birds adapt behaviourally to the presence of Grey Squirrels and indeed other larger competitive/predatory species on and around supplementary feeders beyond avoidance when they present is still unclear (Bonnington et al. 2014b). If birds adjust their foraging behaviours so they can still benefit from supplementary food despite the regular presence of Grey Squirrels then their negative effect under normal circumstances outside the breeding season may be limited. I did find some evidence for birds adjusting their feeding habits (Chapter 2) but this requires further investigation to determine how different bird respond and if Grey Squirrels truly depress local target bird populations beyond reducing breeding success (Chapter 3).

Beyond supporting nontarget species there are further potential unintentional negative consequences of bird feeding with the increased possibility of disease transmission that can occur when birds come together at unusually high densities still being underexplored. My experimental study into bacteria on bird feeders in a typical suburban setting suggests that they may not be as a major a source of bacterial pathogen transmission under normal circumstances as previously thought (Chapter 4). However, some pathogenic taxa were present and the general low level of pathogens I found should not undermine the need for good hygiene practices to limit the possibility of transmission, particularly of other pathogen types not investigated in this study or at other kinds of supplementary feeding points. Other possible points of transmission and the animals using these areas themselves need to be investigated (Galbraith et al. 2017) to explore if and how extensively pathogens are transmitted on and around supplementary feeding stations and other supplementary resources. Regular cleaning and disinfection of feeding stations, as well as the removal of debris and waste below feeders and other possible transmission points, should be carried out as suggested and encouraged by organisations such as the RSPB and researchers (Benskin et al. 2009; RSPB 2009a; Robinson et al. 2010; Lawson et al. 2012b; Garden Wildlife Health 2014; Lawson et al. 2014). In addition, the availability of hanging bird feeders that are not only hard wearing also but easily disassembled and reassembled for cleaning may be particularly important and should be encouraged among manufacturers. Given my findings in Chapter 2 and 3 these feeders should also be designed to exclude nontarget species to the more general benefit of our urban birds and may require innovative design solutions to be effective. Making cleaning bird feeders easier and more effective may encourage more people to do it regularly and thus combat this unwanted negative effect.

Food as I have already detailed is not the only supplementary resource we intentionally provide in our attempts to support our urban bird populations. Artificial nest boxes are an important resource for some species in urban areas (Davies et al. 2009), many of which such as the Blue Tit and Great Tit also frequent the supplementary food resources we provide (Chapter 2; Chapter 5). Both urbanisation, due to reductions in the availability of natural food and supplementary feeding, possibly due to the supply of inappropriate nutrients, have been linked to reduced individual breeding success (Chamberlain et al. 2009). However, we unintentionally provide an additional common and widespread supplementary resource that is particularly concentrated in urban areas rarely considered in this context, that of artificial materials in the environment (Wang et al. 2009; Reynolds et al. 2016). Manufactured materials such as wool-like materials can be incorporated into nests by birds (Reynolds et al. 2016) and such material may have beneficial insulation properties to the point it may even be preferred by some species (Chapter 5). However, as Chapter 5 shows it may like food also have unexpected side-effects.

My analysis of the effect of urbanisation on nest construction and parasites (Chapter 5) possibly indicates the use of artificial material in nests is a subtler contributing factor to the decline in breeding success with increasing urbanisation than that of natural food availability (Chamberlain et al. 2009). The increased use of artificial materials appears to be associated with increased nest ectoparasites which may be a contributing factor to reductions in breeding success with increased urbanisation (Chamberlain et al. 2009), though more research would be required for conformation. This perhaps highlights the need to preserve natural habitat patches and provide native plant species in domestic gardens regardless of the level of urbanisation to ensure that natural nest materials are available in the environment for birds that prefer them. This would be more generally beneficial to urban birds due to the likely increase in the availability of natural food to breeding and non-breeding birds alike (McKinney 2008) as an alternative to supplementary food as well as providing additional natural nest sites. It may also be important to encourage well-meaning garden owners and other landowners putting up boxes as an additional supplementary resource to clear out nest boxes following breeding attempts. This is recommended by various sources as well as the scientific literature as it combats the potentially deleterious effects of higher ectoparasite loads associated with the presence of old nesting material and thus possibly increases the chances of uptake (Tomás et al. 2007; RSPB 2009b; Gonzalez-Braojos et al. 2012; Cantarero et al. 2013; BTO 2017a). There are still many nest boxes and designs available that do not include access to do this and so conservation organisations should be clearer on their advice over this. This study like other parts of my research also serves to remind us that even apparently very similar species such as the Blue Tit and Great Tit can respond quite differently to the same environment and resources (Chapter 2; Chapter 5) and so we should be careful of assuming a one size fits all approach to urban bird conservation.

Finally, more action is required to manage and mitigate against Domestic Cat predation on native animals, particularly with regard to protected areas and species of conservation concern, a threat we have directly added to human associated environments. How they interact with the supplementary resources we provide is still unexplored and requires thorough investigation but my research does indicate that urbanisation influences cat ranging behaviour and so may have important implications for devising management strategies for important protected areas in and near developed areas, both in the UK and elsewhere in the world (Hall et al. 2016b; Chapter 6). Confining companion Domestic Cats indoors is a common practice in many countries, particularly with large predatory native wildlife or the presence of diseases (Toukhsati et al. 2012; Loss et al. 2013; Hall et al. 2016a). However, this is not the case in the UK, where studies found the concept of restricting cat roaming to be unpopular with owners (Thomas et al. 2012; Hall et al. 2016a), despite the evidence that allowing them out, especially at night, carries considerable risks to their health (Lilith et al. 2006; Toukhsati et al. 2012; Calver et al. 2013; McDonald et al. 2015).

To combat this reluctance buffer zones prohibiting the ownership of free roaming could be used to protect areas of importance. From investigating cat ranging on the edge of a large UK urban area I suggest that an exclusionary buffer zone in the region of 300-400m should limit the risk of predation in nearby protected areas in keeping with the recommendations of others (Thames Basin Heaths Joint Strategic Partnership Board 2009; Thomas et al. 2014) and such zones could feasibly be scaled to the level of urbanisation in the local landscape (Chapter 6). Even the implementation of just a night time curfew based on a zone could be locally beneficial. Even outside the bounds of buffer zones more must also be done to encourage owners to keep Domestic Cats indoors, with in particular more leadership on management required from conservation organisations like the RSPB and Wildlife Trusts. Not only does this reduce their potential negative effects on prey populations (Thomas et al. 2012; Blancher 2013; Loss et al. 2013) but it also reduces their exposure to the many risks present in the environment to a roaming cat (Calver et al. 2013). Experimenting with excluding them from sites may also be of interest, though we should be careful about restricting the natural movement of wild animals. We should also explore how the implementation of exclusion zones of a given size would affect the ranging behaviour of cats in adjacent areas to confirm they actually have the desired effect of keeping cats away from protected areas (Lilith et al. 2006; Calver et al. 2011). In addition, efforts should also be made to establish if roaming Domestic Cats frequent areas around supplementary feeding stations and if they impact their usage and/or increase local predation in a more direct way than Grey Squirrels (Chapter 2; Chapter 3). Any evidence of an association and negative impact on usage by target bird species would further the case for restricting cat roaming behaviour. At the very least if attempts to encourage owners to keep their cats indoors are unsuccessful all owners should be encouraged to fit their cats with belled collars as this has been shown to reduce bird predation (Ruxton et al. 2002; Gordon et al. 2010) and compared to the other hazards to free roaming Domestic Cats the health risk feared by some owners is minimal (Calver et al. 2013; Harrod et al. 2016).

7.9. Final Thoughts

In some ways, this thesis is a story of negatives, showing that despite our very best intentions to help our feathered neighbours, there are unintended consequences. As a society, we feed birds on a vast scale, and gain great pleasure and benefits from doing so, but yet as we do, we support invasive species, encourage nest predators and provide opportunities for threatening diseases to spread. We provide nest sites, but those with nests containing more of the material we produce have more parasites, and those clutches laid in our gardens produce fewer young than those far away from the people who wish to help. We love birds, feel compassion for suffering animals, want to protect biodiversity, and yet one our closest companions kill millions of birds and other wild animals every year; we know this and witness it daily, but yet we do little to prevent it. If as it appears despite all these factors we still support higher bird populations than would otherwise be present, then it is worth considering what could we could support on the same resource levels if these negative effects were reduced, or some cases possibly even eliminated entirely. By teasing out these contradictions, I hope to have provided insights into ways that we can begin to think about how those negatives can be made right, for the benefit of birds and the many people who would miss them if they were gone.

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Appendices

Appendix 1.