The Use of Supplementary Food Sources by Bird Communities and Individuals.

Submitted by

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Thesis Abstract

Food availability has a considerable impact on the survival and reproductive output of individuals within a population. In order to support natural populations, supplementary food can be provided to natural populations with the aim of improving reproduction or survival of individuals. In a less scientific way, supplementary food is also provided to garden birds as a leisure pursuit. The provision of a supplementary food source to garden birds is a widespread and popular activity throughout the UK, but the full impact of this still requires extensive research. Relatively little is known about how a wide range of species use garden bird feeders, but there are also some gaps in our understanding of which individuals within a species are utilising a supplementary food source, particularly in relation to varying ambient temperature.

In this thesis I explored whether there were differences in feeding behaviour between and within species at a supplementary food source with the overall aim of gaining understanding whether there were particular species or individuals which were more likely to utilise supplementary food, and whether this was influenced by the type of food provided and ambient

In order to study behavioural differences between species, European Greenfinch (*Chloris chloris*) (hereafter Greenfinch), Common Chaffinch (*Fringilla coelebs*) (hereafter Chaffinch), European Robin (*Erithacus rubecula*) (hereafter Robin), Great Tit (*Parus major*), Eurasian Blue Tit (*Cyanistes caeruleus*) (hereafter Blue Tit) and Coal Tit (*Periparus ater*) were observed for a period of four months at feeding stations which provided two types of food. There were differences in feeding frequency and duration between species, and this was influenced by both body mass and ambient temperature. Larger species tended to spend longer at the feeders at lower temperatures, whereas smaller species such as Blue Tit and Coal Tit, spent longer at higher temperatures. Additionally, smaller species tended to visit more often. It was also conclusive that a food type with a shorter handling time was preferred overall. This reveals that garden bird feeders are utilised differently by species and therefore the impact of supplementary food may differ between species. Furthermore, ambient temperature should also be considered when exploring supplementary food use.

To study within species-differences in feeding behaviour, Blue Tits were studied. Individuals were fitted with Passive Integrated Transponder (PIT) tags which allowed individuals to be logged at bird feeders which were modified to support Radio Frequency Identification (RFID) technology. Data were gathered to inform which individuals were using supplementary food sources, the time of day they visited and how often they visited. This revealed that there were differences in feeding frequency which can be partially explained by body mass, showing that lighter individuals visited more frequently. Despite predictions that individuals with greater access to supplementary food would have brighter feathers due to the increased availability of dietary carotenoids, the yellow chroma of the breast feathers did not reflect the use of a supplementary food source, but this would benefit from further investigation. The time of day also influenced which individuals were likely to be using a supplementary food source; in this study lighter individuals tended to visit more frequently in the early morning and midday than their heavier counterparts. This indicates that conspecifics do not use food sources equally and that lighter individuals are probably being supported by supplementary feeding to a greater extent.

In conclusion, the continued study of garden birds and their behaviours at supplementary food sources is necessary to understand how a range of species are using an ever changing environment. Individual-level studies should be considered hand-in-hand with population level studies as both levels of detail are useful and necessary to gain a more comprehensive understanding of the impacts of supplementary feeding. With a more complete idea of how feeding may impact garden birds, it is possible to create more informed guidelines for the public who provide supplementary food. This could be beneficial for maintaining species numbers while continuing to engage the public with nature.

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1.1 Introduction

Food availability has a considerable impact on population ecology; food limitation can delay life-history events (Skogland, 1983), change population dynamics (Ford and Pitelka, 1984) and influence community composition (Ilarri et al., 2008; Galbraith et al., 2015). Natural food sources often have a patchy distribution and can be unpredictable (Benhamou, 1992; Weimerskirch, 2006); therefore an animal's ability to forage effectively is key to its survival. This is particularly true during the winter months when food availability is further restricted (Jansson et al., 1981) and any effect of food limitation can be augmented at this time (Martin, 1987). However, the effects of food limitation can be buffered, or even reversed, by supplementary feeding. These food sources tend to be more predictable, which reduces search effort and will therefore increase an individual's net energy intake with the potential to increase individual fitness. In household gardens, people often feed birds as a way of supporting bird populations numbers (Horn and Johansen, 2013), and in the UK it is estimated that around 48% of households provide supplementary food for birds at some point through the year (Davies et al., 2009). This is a large scale phenomenon, particularly in urban areas where food is more likely to be provided (Tryjanowski et al., 2015). Supplementary feeding can have considerable effects on wild populations including advancing the time of reproduction (Schoech and Hahn, 2007), increasing reproductive output (Soler and Soler, 1996) and increasing survival (Korslund and Steen, 2006). This could aid a population which may be in decline, or support a population through seasons with low food availability. Feeding is not consistent year-round; the public are more likely to provision in the winter than any other season (Cowie and Hinsley, 1988a; Bromley and Geis, 1998; Jones and Reynolds, 2008) and only 29% of households in the UK are thought to provide food on a weekly basis (Davies et al., 2012).

However, not all individuals within a population are likely to exploit a supplementary food source equally (Durell, 2000). There is the potential for resources to become monopolised by older, larger or more dominant individuals (Gustafsson, 1988; Polo and Bautista, 2002: Shelley et al., 2004), or information transfer occurring more readily between certain individuals may lead to some members of a population being

less able to access or locate resources (Weimerskirch et al., 2010; Aplin et al., 2012; Schnoell and Fichtel, 2012). This may lead to a bias in which individuals are being supported by supplemented food. Ultimately, individual differences in the use of a supplementary food source may produce a mean population wide response which differs from a second geographically distinct population.

It is important to understand the effects of supplementary feeding at the population and community levels so we can better understand how species respond to supplementary food and how it affects the wider community. However, we also need to understand the effects of supplementary feeding at the individual level so we can get a more detailed picture of how and why certain individuals within a population are using a food source. This may help to inform us of the mechanisms by which a population responds to a supplementary food source. With both individual-level and community-level information we can begin to understand the effects of supplementary feeding better.

1.2 Supplementary Feeding Effects at the Population Level
1.2.1 Survival and Reproduction
At the population level, it has been shown in several passerine species that supplementary food can aid survival over the winter period (Jansson et al., 1981; Brittingham and Temple, 1988; Lahti et al., 1998). Although, it has also been shown that supplementary food has a greater impact on survival in particularly cold winters (Kallander, 1981), which may explain some of the confounding evidence regarding the impacts of feeding as weather is rarely accounted for in such studies. Therefore, it is clearly important to analyse further the causes of population persistence.

In a variety of bird species, research shows that supplementary feeding can cause an advancement of lay date (Kallander, 1974; von Bromssen and Jansson, 1980; Clamens and Isenmann, 1989; Svensson and Nilsson, 1995;), an increase in clutch size (Hogstedt, 1981; Arcese and Smith, 1988; Clifford and Anderson, 2001 but see also Harrison et al., 2010) and greater chick survival (Peach et al., 2014). However, improved reproductive performance is not always seen, and studies show inconstencies in fledging success (von Bromssen and Jansson, 1980; Clamens and Isenmann; 1989; Svensson and Nilsson, 1995; Robb et al., 2008b) with some even showing a decrease (Jansson et al., 1981; Plummer et al., 2013a). At the population

level it is difficult to disentangle the reasons for these contrasting results because as data are averaged across the population the extreme ends of the scale can be obscured and the overall picture is potentially misrepresented. Additionally, population demographics may vary between different study sites which could explain some of the conflicting results but without further information on the individuals within the population, it is not possible to identify whether this is true.

The Kakapo (*Strigops habroptilus*) is a classic example of food supplementation being used to support endangered populations. Supplementary feeding was used to aid breeding (Powlesland and Lloyd, 1994). However, it was found that feeding did not induce breeding, but is thought to have brought the females to a body condition threshold (Elliot et al., 2001). The feeding programme has increased adult survival, but very few young have been raised to independence (five male and one female) (Clout and Merton, 2010). Unlike the Kakapo, supplementary feeding in Hihi (*Notiomystis cincta*) has not produced an increase in adult survival (Armstrong and Perrot, 2000; Armstrong et al., 2007), but has increased reproductive success (Castro et al., 2003). This highlights that providing food may not have a predictable impact on a population or an individual.

The effects of supplementary feeding on survival and reproduction are varied; for example, Robb et al. (2008b) found that feeding increased fledging success, whereas Plummer et al. (2013a) found a decrease in fledging success. This indicates that there may be other factors which need to be considered. It is possible that there is individual variation in the use of provisional food sources which could be causing some of the differences seen between the studies, as well as geographic and climatic differences.

1.2.2 Alteration of Behaviours
It was thought that supplementary food sources have caused an increase in the number of Eurasian Blackcaps (*Sylvia atricapilla*) overwintering in Britain since the 1950s (Leach, 1981; Berthold and Terrill, 1988). More recent research shows that the provision of food is working synergistically with climate change to produce the observed effect of increasing blackcap numbers in the UK (Plummer et al., 2015).

 Foraging behaviours and territoriality have both been shown to be affected by food provisioning. The use of 'vulture restaurants' have been shown to cause the home

range of the vultures to decrease as well as decreasing foraging time (Gilbert et al., 2007). In Bearded Vultures (*Gypaetus barbatus*), the provision of food caused an increase in population, which resulted in greater territoriality, decreased territory size and reduced average quality of territory being used (Carrete et al., 2006); this is potentially because lower ranking individuals are surviving when they wouldn't normally, and are using smaller territories. These changes could potentially have long term effects on the status of populations and the whole ecosystem balance.

1.2.3 Effects on Food Webs

Exposure to supplementary food is likely to cause an increase in population numbers (Fuller et al., 2008; Oro et al., 2013), particularly in urban areas where food provisioning is high and predation risk is relatively low (Shochat, 2004). A larger populationcan in turn impact the numbers of prey or predators of the supplemented population. In birds, arthropod prey availability was significantly reduced in gardens where bird feeders were present (Orros and Fellowes, 2012). Alternatively, supplementary feeding can sustain predator populations when prey numbers are low, allowing the prey population to recover (Lopez-Bao et al., 2008). However, the impact of provisional feeding on whole ecosystems and food webs has received comparatively little attention and should be taken into consideration in the future.

1.2.4 Problems with Population-Level Studies

The studies discussed so far have taken a population-level approach to researching the effects of supplementary feeding; however, there are some problems with this, primarily due to the fact that food consumption occurs at an individual level. Population-level studies may mask any individual variation in food uptake or feeding behaviours which may limit the ability to infer the underlying mechanisms which lead to population-level changes. There may be niche separation which leads to certain individuals being more likely to feed in particular locations or on particular prey (Bryan and Larkin, 1972; Araujo et al., 2011; Thiemman et al., 2011) or physiological differences, such as sex, which enable some individuals to access additional food sources (Bearhop et al., 2006). Additionally, there may be differences in foraging strategies and abilities (Cherel et al., 2009), as well as unequal distillation of knowledge through a population regarding resources and how to access them (Langen, 1996; Senar and Escobar, 2002). Furthermore, interactions between individuals may influence how or if they utilise a resource (Janson, 1985).   It is

largely unknown if there are particular individuals which are more likely to exploit a supplementary food source, or what predisposes these individuals to such behaviours. When all these individual variations are averaged to draw a population-level conclusion, it is possible that there is enough variation between individuals to create differences between populations, further emphasising the need for individual-level studies to complement our current knowledge at the population level.

1.3 Individual-Level Effects of Supplementary Feeding
1.3.1 Dependency
It has been of concern that birds will become dependent on supplementary food sources, and possibly even lose their ability to forage effectively. However, there is very little evidence of this occurring (Jones and Reynolds, 2008).   For example, Brittingham and Temple (1992) found that Black-capped Chickadees (*Poecile atricapillus*) in a rural area did not become dependent on feeders and maintained survival rates when feeders were removed.However, dependency may be more likely in urban habitats where there is less natural food available.   Furthermore, these studies have only been analysed at the population level which could be masking any dependency which is seen in only a select few individuals and it is possible that there are traits which predispose an individual to greater dependency.

1.3.2 Ecological Traps
Ecological traps occur when animals choose to settle in habitats which are of low quality, despite better quality habitat being available, with detrimental implications for reproduction and survival (Battin, 2004). This quite frequently occurs in habitats which have been altered by humans. An example of this are Mayflies (*Ephemeroptera* spp.) which choose to lay eggs on dry asphalt instead of water surfaces due a similar reflection-polarisation of both surfaces (Kriska et al., 1998). There are a multitude of other ways which man has manipulated habitats which has produced ecological traps resulting in reduced offspring and adult survival, (reviewed by Schlaepfer et al., 2002).

In birds, it is possible that food being provisioned in the pre-breeding season may result in an ecological trap. First, because supplementary feeding is likely to cause an advancement in lay date which, once the provisioned food is no longer available, could result in insufficient natural food availability to support the chicks (Robb et al., 2008b). Secondly, the presence of feeders may cause an increase in population

which is not naturally sustainable in a given area (Robb et al., 2008a). This is particularly problematic where supplementary feeding is not continued throughout the year (75% of households provide food in winter, whereas only 40% provide in summer (Cowie and Hinsley, 1988a) and ultimately this could lead to a reduction in reproductive success and survival (Jansson et al., 1981; Plummer et al., 2013a). However, further research into the individual utilisation of supplementary sources is required before it can be confirmed that ecological traps occur due to supplementary food.

1.3.3 Carry-Over Effects
Carry-over effects have been defined as events or processes that affect the condition of an individual in one season in such a way that it subsequently affects that individual's performance in a following season (Harrison et al., 2011). These carry-over effects happen due to differences in an individual's access to, or usage of, a resource (Harrison et al., 2011).

It has been demonstrated that food availability and quality in one season can produce carry-over effects which affect the success and body condition of birds in the following season (Sorensen et al., 2009; Inger et al., 2010). Additionally, it was shown that because individuals use habitats differently, there is a difference in magnitude of carry-over effects which vary with age and sex (Drake, 2013). As such, it was predicted that supplementary feeding could potentially produce a carry-over effect (Plummer et al., 2013b; Robb et al., 2008b), but a recent study found that consumption of supplementary food by an individual did not directly result in any carry-over effects (Crates et al., 2016). If there is sufficient natural food available, it is unlikely that supplementary feeding will produce significant carry-over effects, as carry-over effects will have a greater impact in years of unfavourable conditions, such as poor weather or decreased prey availability (Legagneux, 2012). However, there is a gap in our knowledge of carry-over effects as the majority of studies which describe carry-over effects have researched migratory populations (Norris et al., 2004; Saino et al., 2004; Sorensen et al., 2009; Inger et al., 2010). It is therefore important to assess resident populations at the individual level to understand better how supplementary feeding is affecting a wild population.

1.4 Individual Variation in Food Use

Many studies have researched the effects of supplementary feeding at the population level as discussed above, but it is likely that many of the mechanisms which cause the observed effects are being overlooked by ignoring individual differences. Population-level studies treat conspecifics as equals, when in fact there are many behavioural, physiological and social differences between individuals (Bolnick et al., 2003). Therefore, it can be presumed that individuals will differ in their usage of provisional food sources. This could be because they have different amounts of access to a feeder or natural food sources, potientially caused by dominance hierarchies within a population (Schneider, 1984; De Laet, 1985) or due to different levels of dependency on the provisioned source, as well as differences in the quality of food provided.

1.4.1 Variation in Use of Natural Resources

There are age and sex-related differences in feeding behaviour which, for example, can be caused by differences in morphology (by Marchetti and Price, 1989; Ligon, 1968) or social status (Slotow and Rothstein, 1995). However, there is also variation which cannot be explained by age or sex, including individual specialisations to habitat or diet (Mittlebach et al., 1999; Sargeant et al., 2006; Robertson et al., 2014), differences in acquired skills (Estes et al., 2003) and differences in ability to alter behaviour according to available food resources (Fewell and Page, 1993; Ehlinger, 1989); reviewed by Durell, (2000).

Age differences have been shown in more detail in Common Blackbirds (*Turdus merula*), and Herring Gulls (*Larus argentatus*), whereby foraging success increases with age (Greig et al., 1983; Desrochers, 1992), and in Willow Tits (*Poecile montanus*) where adults were dominant over first year birds, allowing them preferential access to higher parts of a tree (Ekman and Askenmo, 1984). In Little Blue Herons (*Egretta caerulea*) it was also shown that lack of experience reduced foraging efficiency (Recher and Recher, 1969).

In Common Blackbirds, there was no-sex related difference in foraging behaviour (Desrochers, 1992) but in Black-capped Chickadees, males had preferential use of habitat over females (Desrochers, 1989). Sex-related differences in time spent foraging was also found in Squirrel Monkeys (*Saimiri oerstedii*) (Boinski, 1988) and in White-tailed Deer (*Odocoileus virginianus*) (Bartoskewitz et al., 2003).

Furthermore, it has been shown that body mass can influence foraging behaviours. At the individual level this has been shown in Carrion Crows (*Corvus corone*), where larger members of the population were able to spend longer at a food patch than smaller conspecifics, (Richner, 1989). Additionally, French and Smith (2005) showed that larger body mass positively correlated with time spent feeding, as well as amount of food eaten per visit in a range of species. In Thick-billed Murres (*Uria lomvia*), larger birds were able to dive deeper, but also tended to dive during the day, whereas smaller birds foraged nocturnally (Orben et al., 2015).

Beyond the physiological differences which may influence an individuals' use of supplementary food, abiotic factors are also likely to impact behaviour. For example, the time of day or the ambient temperature. In Great tits it was shown that dominant birds tended to arrive at a food source earlier in the morning than subordinates (De Laet, 1984). However, the time of optimal feeding may also be influenced by perceived predation risk (MacLeod et al., 2005). In Australian magpies (*Gymnorhina tibicen*), foraging effort decreased at high temperatures (Edwards et al., 2015) but in Great Tits, the number of prey caught increased with temperature (Avery and Krebs, 1984). As there is a greater energetic demand at low temperatures (Ockendon et al., 2009) it is thought that supplementary food will be used to a greater extent at low temperatures, but this could be over-ridden by variables such as individual dominance or predation. These differences indicate that it could be important to consider abiotic factors within a study which aims to quantify the use of supplementary food.

These studies highlight some of the differences which may exist between individuals, and none investigate how individual differences in foraging behaviour may affect the use of supplementary food. This information could potentially change the way we view supplementary feeding of a wild population.

1.4.2 Variation in Use of Supplementary Food Sources

It has been considered whether dominance affects access to, and use of, a supplementary food resource. Robb et al. (2011) showed through stable isotope analysis that there is a difference in individual uptake in supplementary food in Blue Tits which could not be explained by age or sex. In Black-capped Chickadees, it was shown that there was significant individual variation in feeder use, but this was not

correlated with dominance rank and that time spent at the feeding station did not vary between individuals (Ficken et al., 1990). In Willow Tits and White-throated Sparrows (*Zonotrichia albicollis*), it was shown that dominance rank affects an individuals' access to a food source (Schneider, 1984; Ekman and Lillendahl, 1993). The reason for this conflicting information is not known; it may be due to species-level variation or there may be other factors which were not considered such as natural food resources of higher quality being available to high ranking individuals.

However, it has been predicted that there is a correlation between variation in plumage colouration and dominance, even when birds are in winter plumage (Rohwer, 1975). But it was found that the UV crown of Blue Tits does not correlate with dominance over winter (Korsten et al., 2007). However, individuals which are "more yellow" have greater foraging ability, (Senar and Escobar, 2002 and it has therefore been considered whether the yellow carotenoid-based feathers fulfil the role of status signalling during the winter. This hypothesis has been rejected in House Finches (McGraw and Hill, 2000 and Belthoff and Dufty, 1994), but in territorial American Redstarts, there is a positive correlation with male carotenoid-based winter-plumage brightness and territory quality (Reudink et al., 2009).

Relatively little work has been done to quantify individual variation in feeder use; particularly which individuals are most likely to use supplementary food (but see Cowie and Hinsley, 1988b and Crates et al., 2016). It may be important to research this because by overlooking individual variation the mechanisms behind population-level responses may not be able to be interpreted. There is the possibility that some individuals may exploit supplementary food to a greater extent due to limited access to natural food resources, potentially allowing an increased survival of individuals who would not otherwise survive, and therefore disrupting the process of natural selection (Plummer et al., 2013b). Alternatively, dominant individuals may monopolise a supplementary food source, potentially limiting survival and reproduction of less dominant individuals. The impacts of supplementary feeding on a population may have far reaching consequences which go beyond the population being investigated, as populations of species interact within a community. However, further research is required as it is not known which individuals are being supported and to what extent.

1.5 Conclusions

From the reviewed body of work, it can be clearly demonstrated that supplementary feeding has many, far-reaching consequences for populations. The effects of feeding can be seen between seasons, years and generations. Moreover, it is uncertain how supplementary feeding is likely to affect particular individuals within a population. Many of the consequences of supplementary feeding are little understood and the implications of this are not obvious; this could be of concern when the scale of garden bird feeding is taken into consideration.

1.6 Aims of This Study

My research will be a two part study; the first part will be a broad study of how supplementary feeding is used by a range of species and the second part will take a more fine-scale approach, focusing on the foraging behaviour of Blue Tits at a feeder. Both parts of the study will try to identify phenotypic and environmental variables which could influence feeding behaviour at a supplementary source.

I aim to compare and contrast a range of several species to test whether body size and dominance affects the frequency and duration of feeding at a supplementary food source. I will also test whether ambient temperature affects the feeding behaviour of different species. At the individual level, I aim to identify whether body mass or feather colouration predict feeder visitation rates and whether this is influenced by the ambient temperature or time of day.

This study could determine whether there are particular species or individuals which are more likely to use supplementary food. This could highlight which birds are most likely to be affected by any impacts of garden bird feeding, such as survival, dependency or ecological traps.

Chapter 2

The Frequency and Duration of Feeding at a Garden Bird Feeder by a Range of Common Species.

2.1 Abstract

Bird feeding is a hugely widespread activity, particularly in the UK. However, there is relatively little information available regarding how garden bird feeding affects multiple wild species. This study demonstrated that there are species variations in the use of garden bird feeders. Body mass and ambient temperature interacted to influence the time which a typical bird spent at a feeder, where the larger species spent longer at the feeders as temperature decreased whereas smaller species used the feeders more at higher temperatures. There was also an interaction between dominance score and ambient temperature where more dominant species spent longer at the feeders at higher temperatures but smaller species spent longer feeding as temperature decreased. Body mass and dominance also affected the frequency with which a bird was likely to visit a feeder, with more visits being made by smaller species and more dominant species. Overall, this study suggests that due to the variation in use of a feeder, the extent of the impact of garden bird feeding could differ between species.

2.2 Introduction

In the UK it is estimated that around 48% - 64% of households provide food for garden birds (Davies et al., 2009; Davies et al., 2012), spending an estimated £240-290 million each year on feeding equipment (Jones and Reynolds, 2008), resulting in an estimated one bird feeder for every nine feeder using birds (Davies et al., 2009) and enough bird seed to fully support around 196 million garden birds (Orros and Fellows, 2015). However, despite there being over 40 different species which use bird feeders (Chamberlain et al., 2005), and the considerable effects which can be caused by supplementary feeding (reviewed by Robb et al., 2008a), there is a distinct lack of research comparing the feeding behaviours of a range of species at bird feeders. More commonly, research focuses on one species or a single order of species. By focusing on one species alone, it is possible that we are missing important differences regarding how a range of species use a food source. Additionally, feeding behaviours, such as when and how often a food source is

visited, may be misinterpreted due to interactions between species which are likely to alter the behaviour of birds.

One way to quantify the use of a supplementary food source is to measure the frequency and duration of time a bird spends at a feeder. It has previously been shown that larger birds are able to spend longer at a food patch than smaller conspecifics (Richner, 1989), and a bird is less likely to visit a foraging site if a larger species is already there (Shelley et al., 2004) showing clear inter-specific competition. It has also been shown that larger species tend to be more dominant (Alatalo and Moreno, 1987; Robinson and Terborgh, 1995) and dominant individuals visit feeders more frequently (Ekmaan and Lilliendahl, 1993). Additionally, in a study comprising 18 tropical birds and mammals it was shown that body mass correlated positively with time spent feeding and dominance rank (French and Smith, 2005). Dominance is indicated by the number of pairwise competitive interactions which are won or lost (Cuthill et al., 1997; Kozlovsky et al., 2014) usually at a food source and can be between or within species. Therefore, body mass and dominance can be considered to be important factors in determining how a bird will use a food source and this is likely to affect interspecific dynamics at a feeding station.

Furthermore, abiotic factors have been shown to have an important influence on foraging behaviour (e.g. Bronikowski and Altman, 1996; Weiser et al., 1997; Aublet et al., 2009). However, there is little direct evidence of how foraging behaviour at a supplementary food source is impacted by ambient temperature. As energy requirements increase in colder temperatures (Hilton et al., 1999), it is expected that there will be an increase in the use of feeding stations by all species (Carrascal et al., 2012a), but it is unknown if all species will increase their usage equally. Additionally, as winter progresses and temperature decreases, natural food availability will also decrease (Clark and Dukas, 2000); consequently, it is expected that there will be more inter-specific competitive interactions at feeding stations.

To meet energy requirements, particularly in cold winter conditions, individuals must locate and utilise a food source which will provide sufficient energy while not being energetically costly to locate and consume. Ultimately, it is preferential to choose a high energy resource which requires minimal searching and handling time; this

increases the net energy gained from that food source (Lucas, 1983; Tome, 1988). In a choice experiment American Tree Sparrows (*Spizelloides arborea*) and Harris' Sparrows (*Zonotrichia querula*) were found to both choose the food with lower handling time (Keating et al., 1992). However, access to the optimal food source may be limited; for example, dominant individuals are more likely to have access to a preferred food source (Bautista et al., 1995). This study will assess the use of two different food types; where one has a longer handling time but equal nutritional content to the other; this could give a better understanding of how different food types affect feeding behaviour across a range of species.

It should also be taken into consideration that the feeding ecology of the six study species is likely to impact the feeding behaviour at a supplementary food source. Both the Greenfinch and Chaffinch are primarily granivorous, particularly during the winter months where there is low arthropod availability (MacMillan, 1981; Kalejta-summers, 1997). Additionally, these were the largest of the six species and therefore have larger crops which will allow a greater consumption of food before digestion. This will likely allow a greater time to be spent at a bird feeder. Robins are generally insectivorous (Atkinson et al., 2004) so are less likely to be observed at feeders which are filled with seeds. Great Tits and Blue Tits have a similar ecology and both will feed on insects but rely on seeds during the winter months (Kallander, 1981). This is likely to result in heavier use of the supplementary food at low temperatures when insects are less active. Coal Tits cache food (Brotons, 2000), and therefore may be less reliant on supplementary food in the winter when compared with other species. Differences in feeding ecology as described is likely to affect how often a species will use supplementary food and therefore the impact of garden bird feeding will also vary between species.

Overall, this study aims to understand how a range of species differ in their use of supplementary food by comparing and contrasting species' behaviours in relation to their phenotype. I investigated how body mass and dominance influence food use in winter in six species of garden birds: Greenfinch (27.66g), Chaffinch (21.81g), Robin (18.98g), Great Tit (18.61g), Blue Tit (10.88g) and Coal Tit (9.06g). Dominance was measured as the proportion of competitive interactions which a species won in relation to the total number of interactions in which that species was involved in

(winning an interaction involved one bird successfully supplanting another). It was predicted that larger and more dominant species would spend longer at feeders and that they would also visit more frequently, compared with smaller, less dominant species. Furthermore, I assessed the influence of ambient temperature on food use and inter-specific competition at feeders. At lower temperatures, it was expected that all birds would spend longer at feeders and would visit more frequently, and that lower temperatures would result in more competitive interactions. Finally, I addressed whether different handling times of two food types influenced interspecific differences in supplementary food use. Feeders containing a food type with a lower handling time were predicted to be visited more often, and that larger and more dominant species will have greater access to this food source.

2.3 Methods

2.3.1 Study Site and Experimental Design

From November 2014 to February 2015 on the Penryn Campus of the University of Exeter in Cornwall, UK (N˚50.17, S˚5.13) three feeding stations were set up, each approximately 200 m apart. Three stations only were used due to logistical limitations, primarily limited space at the study site. At each feeding station there were two bird feeders (Premium Plastic Seed Feeder 4 Port, John E Haith Ltd, Grimsby, UK), one on either side of a feeding pole, set 35 cm apart and 1.2 m high. Three of the four feeding ports were sealed off, only allowing access to one feeding port per feeder and therefore increasing the potential for competition at feeders. In pilot studies where ports were not sealed off, very few competitive interactions occurred which may have impacted the reliability of statistical testing, additionally too many feeding events occurred simultaneously for accurate observations to be recorded. The first feeder contained sunflower hearts (*Helianthus* spp) (John E Haith Ltd, Grimsby, UK) (hereafter, 'hearts') and the second feeder contained sunflower seeds (*Helianthus* spp) (John E Haith Ltd, Grimsby, UK) (hereafter, 'seeds'). Sunflower seeds are not husked and therefore require greater handling time compared with sunflower hearts (as described by Woodrey 1990), and were thus hypothesised to be a less favoured food type. The positions of the hearts and seeds feeders on the feeding pole were alternated every four to five days to control for the position of the feeder causing a preference in the number of visits to a particular food type. Feeders were filled as often as required to ensure there was always a plentiful supply of food. In pilot studies it was noted that it took approximately two weeks for the feeding stations to be regularly used. The feeders were put in place with a constant supply of food available from mid-August ready for data collection beginning in the first week of November. However, data regarding predator behaviour was not simultaneously collected, so the impact of predator abundance could not be accounted for. The birds were studied over the winter period as this is when they are in mixed flocks (Grubb, 1987; Szekely et al., 1989). Additionally, more birds are likely to use a supplementary food source during the cold winter months (Chamberlain et al., 2005) and this is when most households provide food (Jones and Reynolds, 2008), which allows better replication the effects of garden bird feeding.

The feeding stations were observed for 87.45 ± 3.45 (mean ± SE) minutes, beginning at 15 ± 4 (mean ± SE) minutes after sunrise for a total of 28 days from November 2014 through February 2015, giving a total of 40.81 hours of observations; the 28 days were chosen at random. Observations were undertaken at a similar time of day (beginning a few minutes after sunrise) to avoid differences in feeding behaviour, which are likely to occur through the day. Variation in observation duration was due to video battery life under varying in colder weather but was not found to have a significant effect on the number of feeder visits recorded ($F_{1, 27}$ = 0.002, P= 0.96). An equal number of observations were made with the two food types in each position (i.e. hearts on the left and seeds on the right, or *vice versa*). For the observations, a video camera (Sony Handycam DCR-SR37, Sony Europe Limited, Surrey, UK) was mounted on a tripod approximately 2 m away from the feeding station with the height adjusted according to the needs of each site to obtain the clearest picture. The video recordings were later analysed using VLC media player (VideoLAN, Paris, France). Only one feeding station was observed each day due to logisitcal limitations and the three feeding stations were observed in rotation until each station was observed 10 times. Data collected from the video analysis included which species was feeding, how long it fed for and which feeder it landed on (hearts or seeds). The duration of time a bird spent at a feeder was accurate to the nearest second and was calculated using the time stamp given in the playback software. Additionally, if there were any competitive interactions at the feeding station these were noted. Competitive interactions were identified as a bird displacing another from a feeder or a clear, but unsuccessful, attempt to displace a bird; the species involved in the interaction and the winner of the interaction was noted; the winner was defined as the bird which either successfully supplanted another or the bird which remained on the feeder. These interactions allowed a 'species dominance score' to be created for each species. Dominance interactions (wins and losses) were tallied for each species; separate tallies were made for each food type. The dominance score was then calculated by dividing the number of interspecific interactions a species won by the total number of interspecific interactions that species was involved in, regardless of who initiated the interaction (using the CAtt method as reviewed by Bayly et al., 2006).

The effects of daily temperature on the duration spent at a feeder, the number of visits made and the number of competitive interactions which occurred were also analysed. The minimum daily temperature for each observation day was taken from the Met Office (Devon, UK) database for the nearest weather station, 13.9 kmaway at Culdrose (N˚50.08, S˚5.26). Weather information was not available for the study site as the records were incomplete.

2.3.2 Statistical Analyses

The full dataset was plotted to check for outliers; from this inspection three points were removed where duration spent on a feeder exceeded 300 seconds (omitted durations were 304, 374 and 554 seconds, all were recorded for Greenfinch); the next longest duration was 253 seconds, the average duration was 5.48 ± 0.27 (mean $\pm$ SE) seconds. The omitted values were considered to be outside the normal foraging behaviour for this species. Secondly, species which were observed considerably fewer times than the remaining focal species and had a sample size which was too small to conduct robust analysis were also excluded, which gave a remainder of six species. The excluded species were Blackcap (*Sylvia atricapilla*, three observations), Bullfinch (*Pyrrhula pyrrhula*, 48 observations), Dunnock (*Prunella modularis*, four observations), Goldfinch (*Carduelis carduelis*, 12 observations) and Great Spotted Woodpecker (*Dendrocopos major*, five observations); the species which were included in the study were observed 668.5 ± 263.37 (mean $\pm$ SE) times. The final dataset comprised a total of 4,011 observations of the six focal species and 467 competitive interactions. However, it was not possible to identify individuals within the species and so the actual number of individuals which visited the feeders was unknown and the number of observations of each species may be inflated by some species individuals using the feeders more frequently than others. This has been statistically controlled for in so far as this is possible by including feeding station as a random effect in all analysis.

There were three response variables: mean daily duration, visit frequency and number of competitive interactions. For duration, the raw data were averaged to create a mean duration per species per food type per feeding station per day. For visit frequency, the raw data were counted to give a total number of visits each day per species per food type per site. The total daily numbers of heterospecific and conspecific competitive interactions were also counted for each species at each food

type. Additionally, I assessed whether the total time spent on a feeder differed between species. To do this, the mean duration each species spent at each food type per feeding station per day was multiplied by the total visits per day a species made to each feeder at each feeding station. All response variables were natural log-transformed to normalise data and model checking plots were used to confirm that this was successful in each case.

Explanatory variables included food type, minimum daily temperature, species, body mass and dominance score. The measurements for body mass were adult values for each species taken from Birds of the Western Palaearctic (Snow et al., 1988).

Statistical analysis was carried out in R (The R Foundation for Statistical Computing, 2015) using the lme4 package and data were analysed using General Linear Mixed Models (GLMMs). All two-way interactions were included in the models and backwards step-wise model simplification was used to remove non-significant terms, with alpha set at P=0.05. The initial models included food type, minimum daily temperature and species as the explanatory variables. Once it was established that there were species differences for the response variables, the term 'species 'was replaced with body mass or dominance score to test if these factors could explain any differences seen. All models in the analysis included food type and minimum daily temperature as explanatory variables. Model check plots were used for all analyses to test for non-normal residuals. Results are presented for all main effects and any significant two-way interactions. Where post-hoc analysis was required GLMMs were conducted. This was done to find differences in behaviour at the two different food types, where data for each species was analysed independently. Additionally, a Chi squared test was used to test for significant differences in the total numbers of inter- and intra- specific competitive interactions.

In all of the above models, feeding station was included as a random effect to account for site effects, and potential pseudo-replication in the likely event that some feeder visits were made by the same individuals. The position of each food type was not included in the analysis because a balanced number of observations were made with each food type on the left and on the right.

2.4 Results
2.4.1 Inter-Specific Variation in Supplementary Food Use

There was a significant interaction between species and food type which influenced how long was spent at a feeder (x^2_5= 23.21, P = <0.001, n=234; figure 2.1). Post-hoc analysis showed that coal tits and great tits spent significantly longer at the seeds feeder (x^2_1= 4.03, P = 0.05, n=6; x^2_1= 4.68, P = 0.03, n=6, respectively), but chaffinches and greenfinches spent significantly longer at the hearts feeder (x^2_1= 3.89, P = 0.05, n=6; x^2_1= 5.41, P = 0.02, n=6, respectively). There was no significant difference in duration spent at each feeder for blue tits (x^2_1= 0.25, P = 0.62, n=6) or robins (x^2_1= 2.87, P = 0.09, n=6). Temperature had no significant effect on the duration a species spent at the feeders (x^2_1= 1.54, P = 0.215, n=234).
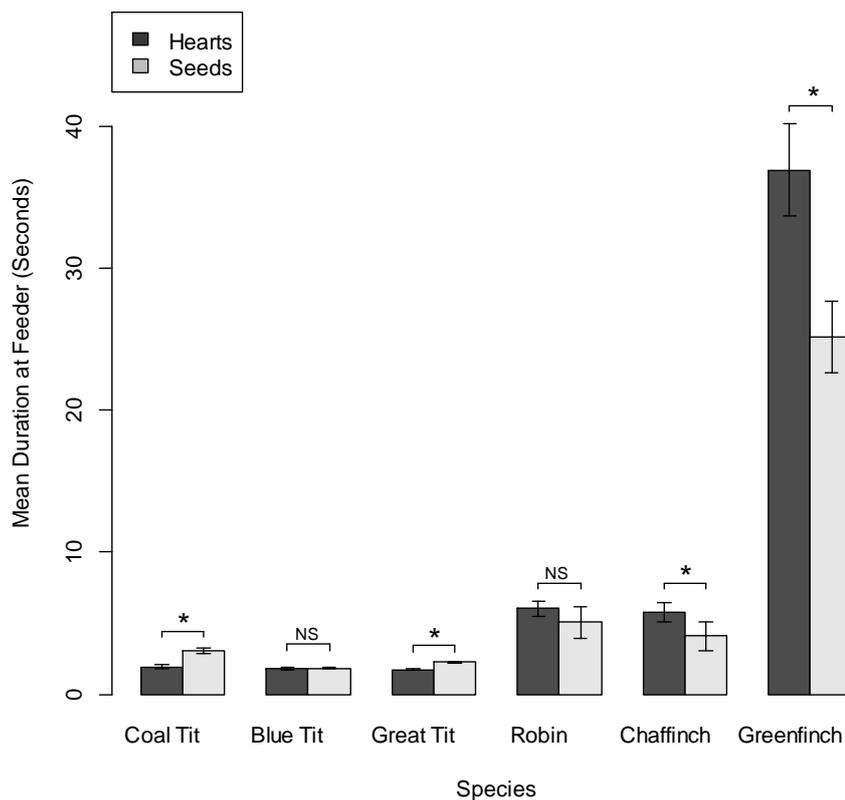
Figure 2.1: Bar graph showing the mean duration each species spent at each food type. Mean Durations were used here for the purposes of illustration; error bars represent the Standard Error of the Mean. The difference was significant at P<0.05, indicated by '*'.

The visit frequency was significantly affected by an interaction between the species and food type (χ^2_5= 18.66, P = 0.002, n=234; figure 2.2) where species varied in how often they visited the hearts and seeds feeders.   Post-hoc GLMMs showed that coal tits visited the seeds feeder a marginally significant number of times more than the hearts feeder (χ^2_1= 3.48, P = 0.06, n=6); blue tits (χ^2_1= 7.60, P = 0.006, n=6), great tits (χ^2_1= 4.99, P = 0.03, n=6), robins (χ^2_1= 9.98, P = 0.002, n=6) and chaffinches (χ^2_1= 5.37, P = 0.02, n=6) all visited the hearts feeder significantly more often than the seeds feeder. However, greenfinches did not visit one food type significantly more often than the other (χ^2_1= 2.70, P = 0.10, n=6). The frequency of visits to a feeding station was not affected by the mean daily temperature (χ^2_1= 2.18, P = 0.140, n=234).
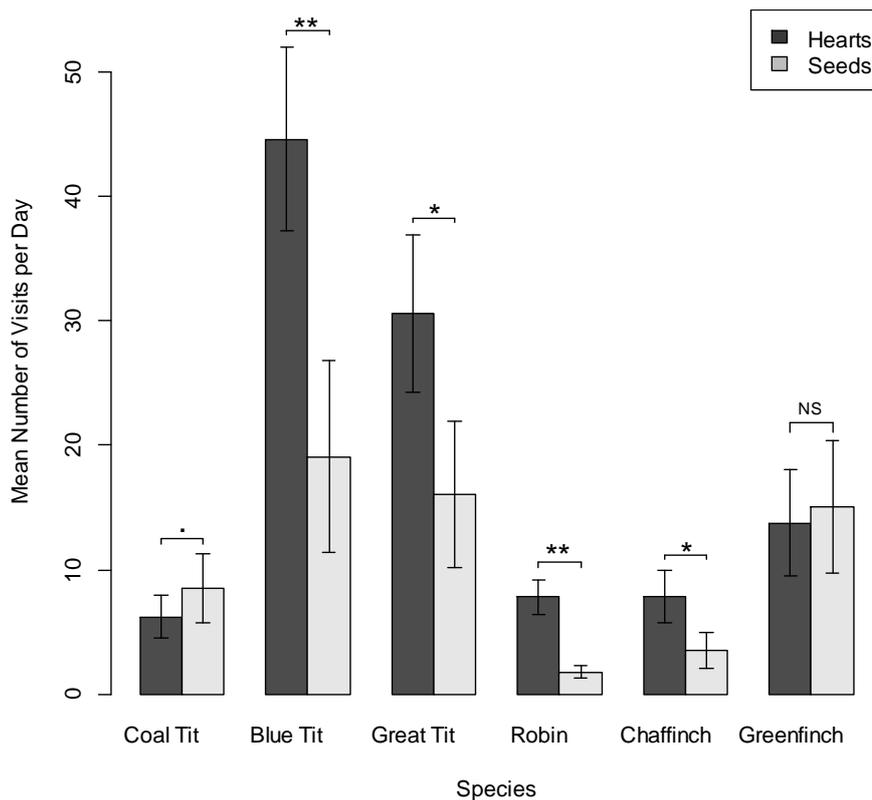
Figure 2.2: Bar graph showing the frequency of visits each species made to each food type. The error bars show the Standard Error of the Mean. The notations above the bars show the level of significance; i.e. '***'=<0.001, '**'=0.001, '*'=0.01, '.'=0.05, NS= not significant.

When the mean daily duration and daily frequency of visits were multiplied together for each species the following results were found for each food type. The total time a species spent on a feeder per observation period was significantly affected by an interaction between species and food type ($\chi^2{}_5 = 23.59$, P = <0.001, n=234; figure 2.3). A series of post-hoc GLMMs showed that blue tits, great tits, robins and chaffinches all spent significantly more total time per observation period on the hearts feeder ($\chi^2{}_1 = 13.22$, P = <0.001, n=6; $\chi^2{}_1 = 6.86$, P = 0.009; $\chi^2{}_1 = 18.26$, P = <0.001; $\chi^2{}_1 = 11.63$, P = <0.001, respectively). However, coal tits and greenfinches did not spend a significantly longer total time at either food type ($\chi^2{}_1 = 2.13$, P = 0.15; $\chi^2{}_1 = 1.31$, P = 0.25, respectively). The mean daily temperature had a marginally non-significant effect on the total time a species spent on a feeder ($\chi^2{}_1 = 3.47$, P = 0.06, n=234).
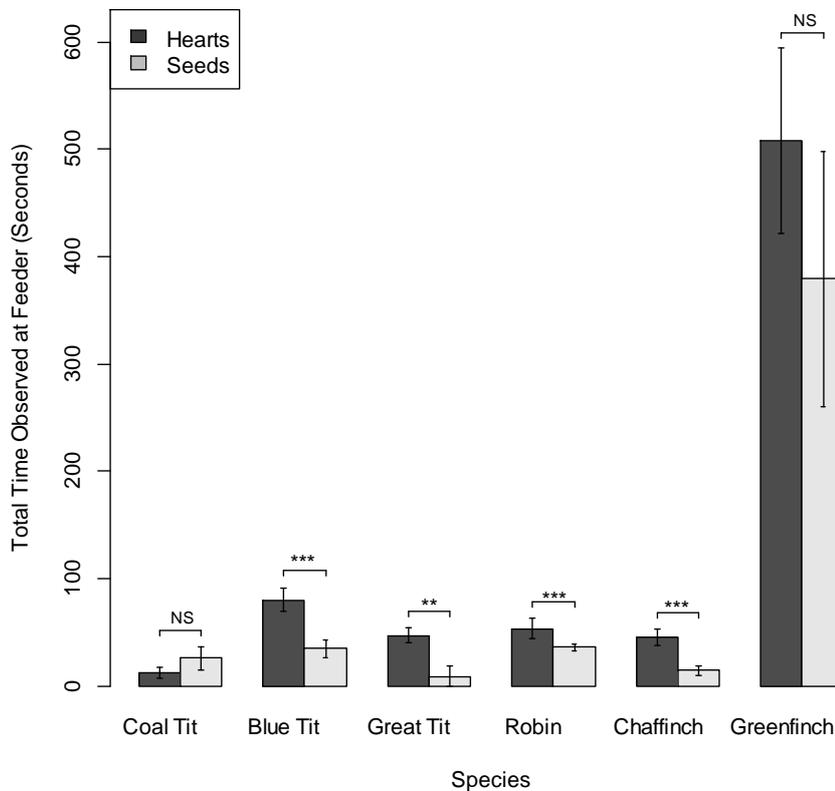
Figure 2.3: Bar graph showing the mean of the total time a species was seen at a feeder each day. The error bars show the Standard Error of the Mean. The notations above the bars show the level of significance; i.e. '***'=<0.001, '**'=0.001, '*'=0.01, '.' =0.05, NS= not significant.

2.4.2 The Effect of Species' Traits on Feeder Use

There was a significant interaction between body mass and food type which affected the duration spent at a feeder (x^2_1 = 13.16, P = <0.001, n=234). Larger species spent more time on feeders, but the slope of this relationship was greater for the higher quality food resource, i.e. hearts. Additionally, there was an interaction between body mass and temperature which affected the duration spent at feeders (x^2_1 = 21.20, P = <0.001, n=234; figure 2.4). Larger species spent less time at the feeders as temperature increased; this effect was similar but not as strong for mid-weight species, and the smallest two species did not use the feeders at all at the lowest temperatures, but increased their time spent at a feeder as temperature increased.
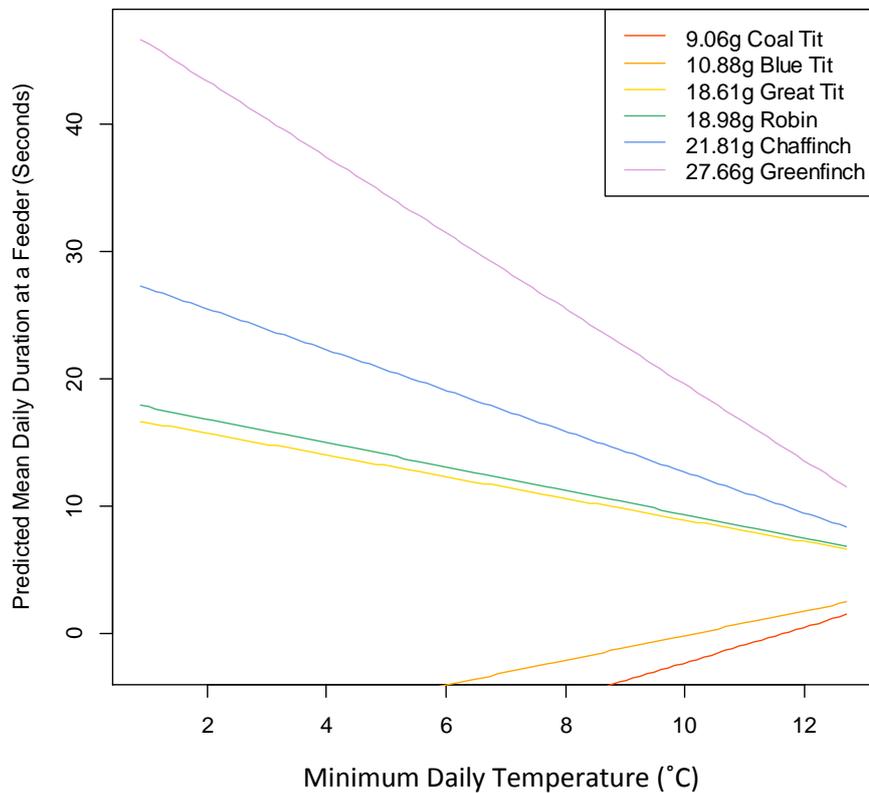
Figure 2.4: The interaction between body mass and the minimum daily temperature which predicts the mean duration a bird is likely to spend at a feeder. This figure uses the statistical model to predict the duration a bird is likely to spend at a feeder according to body mass at a range of daily temperatures.

Body mass had a significant effect on how often a species visited a feeding station (χ^2_1= 11.64, P = <0.001, n=234), where lighter species tended to visit more frequently. In this model food type also significantly impacted how often a feeder was visited (χ^2_1= 16.10, P = <0.001, n=234, figure 2.5) with a greater number of visits being made to the hearts feeder. There was no significant effect of temperature on the frequency of visits made (χ^2_1= 2.75, P = 0.097, n=234).

There was a significant interaction between dominance score and food type which affected the duration spent at a feeder (χ^2_1= 8.16, P = 0.004, n=234, figure 5). A positive association between dominance score and duration at hearts feeders was seen, but no relationship was apparent for the lower quality resource, i.e. seeds.
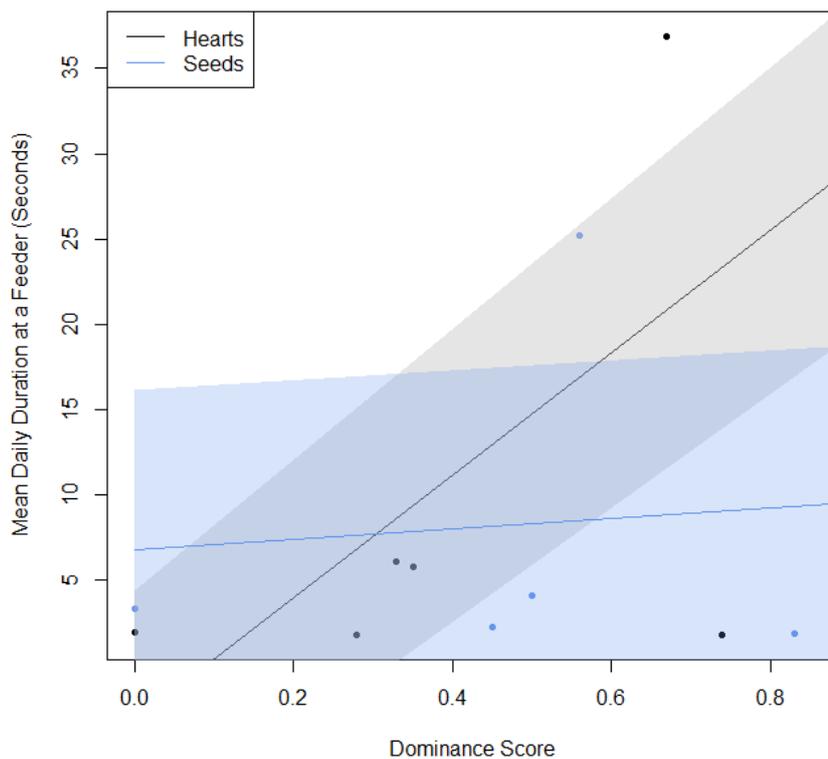
Figure 2.5: The relationship between the duration a bird is able to spend at each feeder according to their calculated dominance scores at each food type. Lines are predicted from the model and the shaded area indicates the 95% confidence intervals. For the purposes of illustration, the points represent mean dominance for each species at each feeder.

There was also a significant interaction between dominance score and temperature which affected the duration spent at a feeder (x^2_1= 8.72, P =0.003, n=234, figure 2.6). The least dominant species spent longer at a feeder as temperature increased. However, the general trend for most species was to spend less time on the feeders as temperature increased; this effect was stronger for more dominant species.
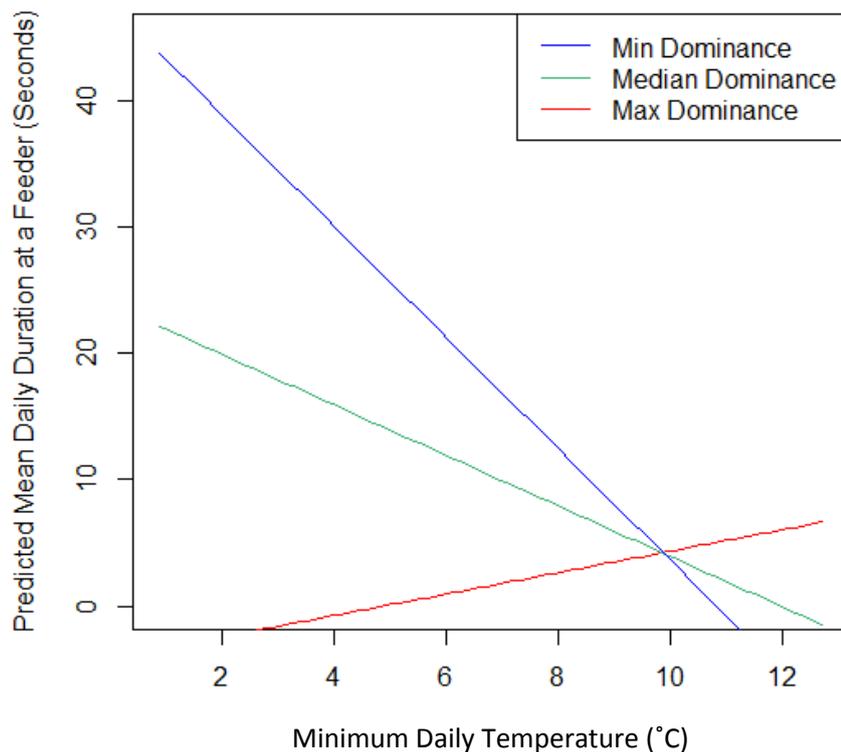
Figure 2.6: Predicted data from the statistical model has been used to illustrate the interaction between dominance score and minimum daily temperature which predicts the duration a bird is likely to spend at a feeder. The maximum dominance score was 0.83 for blue tits at the hearts feeder, the median dominance score was 0.45 and was for great tits at the seeds feeder, the minimum dominance score was 0 which was obtained by coal tits at both feeders as well as robins at the seeds feeder. Only three dominance scores have been used for this graph to simplify the illustration for greater clarity.

Dominance had a significant effect on how often a species visited a feeder (x^2_1 = 11.42, P= <0.001, n=234), where the more dominant species tended to visit more often. Food type also had a significant effect on how often a species visited a feeder (x^2_1 = 12.16, P = <0.001, n=234). However, temperature had no effect on how often a

feeder was visited ($\chi^2{}_1 = 0.01$, P = 0.924, n=234). There were no significant interactions.

2.4.3 The Effect of Temperature and Food Type on the Occurrence of Competitive Interactions

The number of interactions at feeders differed amongst species ($\chi^2{}_1$ = 23.40, P= <0.001, n=233); from most to least likely to be involved in a competitive interaction: greenfinch, blue tit, great tit, chaffinch, robin, coal tit. This pattern was potentially driven by a correlation between the total amount of time species were observed and the number of competitive interactions they were involved in (Pearson's correlation, $t_{(10)}$ = 19.66, P = <0.001; figure 2.7). Intraspecific competition was more likely to occur than interspecific competition ($\chi^2{}_1$ = 28.32, P= <0.001, n=467). There was no significant effect of temperature on the total number of competitive interactions which occurred at feeders ($\chi^2{}_1$ =0.50, P = 0.48, n=233) and food type had no significant effect on the total number of competitive interactions occurring at feeders ($\chi^2{}_1$ = 3.02, P = 0.08, n=233).
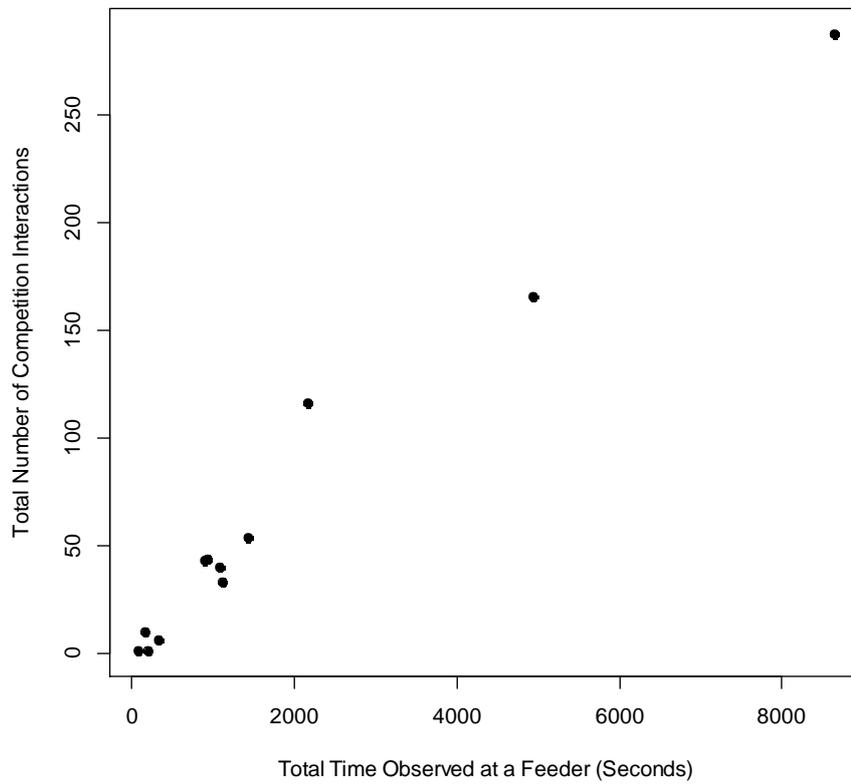
Figure 2.7. The total number of seconds a species was observed for over the whole season plotted against the total number of competition interactions which that species was observed in. Separate points have been created for each species at each food type.

2.5 Discussion

This study has shown that there are interspecific differences in foraging strategies which affected utilisation of supplementary food sources. The six focal species spent different amounts of time on a supplementary food source, but there were also species' differences in the use of the two food types (figure 2.1). Additionally, there were differences in the frequency with which species visited a supplementary food source, which again differed between provisioned food types (figure 2.2). Generally, larger species visited for a longer duration, whereas smaller species visited more frequently, but this did not equate to an equal amount of time being spent on the feeders across species (figure 2.3). This is likely to mean that species are consuming unequal quantities of food at a feeder. Additionally, dominance score affected both the duration and frequency of visits, where more dominant species tended to spend longer on feeders and visited more often. The minimum daily temperature had no significant influence on the number of visits made to a feeder; however, ambient temperature did interact with body mass and dominance score to affect duration spent at feeders significantly (figure 2.4). This could mean that during harsher conditions some birds are more able to monopolise a predictable food source. The total numbers of competitive interactions were also not significantly affected by the minimum daily temperature. However, intraspecific interactions were more likely to occur than interspecific interactions. These results confirm there are clear species' differences in feeding behaviour at garden bird feeders, which should be addressed when considering the impacts of supplementary feeding.

2.5.1 Duration of Visits to Feeding Stations

The duration spent on feeders is potentially part of a starvation-predation trade off (McNamara, 1990), where some birds will spend longer on the feeder at the risk of being predated. It has been shown that feeding birds are more likely to be taken as prey than those not feeding (Roth et al., 2006), so it may be a tactic for birds, such as Blue Tits, to take a seed and eat under cover to reduce the time open to predation, as was often observed during this study.

When considering the differences in duration spent at the feeders it was found that this depended on which species was feeding; this may be explained by bill morphology. For example, a greenfinch may spend longer than other species at the feeders because they are able to consume this food source more efficiently than

other species, whereas a robin is unlikely to spend as much time on a seed feeder because a bill which has evolved for an insectivorous diet is less suited to eating this food source. However, robins did visit the feeders more often than other species which were not included in this study, which possibly suggests a low availability of suitable insects in the area at the time of study. The possibility of bill morphology affecting feeding duration is supported by a previous study in which the husking time of three granivorous birds was affected by bill and seed structures (Hrabar and Perrin, 2002), however this focuses on finch species only. Additionally, smaller birds tended to spend longer at the seeds feeder than the hearts feeder; this could be because the seeds were larger than the hearts and therefore potentially more difficult to manipulate, increasing the time it would take to obtain a seed. Conversely, larger birds spent longer on both feeders overall, which is possibly due to a larger crop allowing for increased food intake before needing to digest, or alternatively this result could also be indicative of the increased food requirements needed to maintain a larger body (Kleiber, 1947; Nagy, 1987). Larger species also spent comparatively more time on the preferred hearts feeder which could indicate competitive exclusion of smaller birds at this resource (Alatalo, 1981). However, additional studies which include control measures with reduced competition would be required to explore this possibility. Furthermore, some species may be more competent at manipulating certain food types (Durell, 2000) which may have allowed species such as the Greenfinch or Chaffinch to utilise the seeds feeder with minimal impact on handling time. Additionally, the natural diet of the focal species is likely to affect how much they utilise supplementary food. Species which are primarily insectivorous, such as the Robin, may use it less than a primarily granivorous species such as the Greenfinch. The natural availability of a species preferred food source may also affect how frequently it visits a garden bird feeder and again this will be differ among species depending on their diet. In terms of garden bird feeding, it would benefit a greater number of species if there were more types of food available which would cater for a wider range of diet specialisations.

There was also an interaction between temperature and body mass which affected the duration spent at feeders. The larger four species spent longer at the feeders at lower temperatures but the smallest two species did not visit at all at low temperatures and increased visit duration at warmer temperatures. This could be

due to larger species excluding the smaller species when food resources are limited (Alatalo and Moreno, 1987). Providing more food could help to reduce this issue; the provision of only one or two feeders may limit access of some species to the supplementary food. By increasing access to food sources there is greater potential for a wider range of species to benefit, particularly if feeders are designed to limit the size of bird which can use it, preventing smaller birds from being dominated.

Within species there are conflicting results on whether dominance affects the duration spent at feeders (Enoksson, 1988; Ficken et al. 1990). However, between species it was found that dominance ranking positively correlated with the duration spent at hearts feeders although there was no effect of dominance at seeds feeders. This suggests that the dominant species may have been able to monopolise the preferred food source. It is also possible that more dominant species were able to remain feeding for longer because they were less likely to be supplanted by other species (Hartzler, 1970). However, dominance hierarchies may have less of an effect at a superabundant food source (Desrochers et al., 1988), and dominance may be affected by the proximity of a feeding station to an individual's home range (Brittingham and Temple, 1992). The feeders in this study were customised to have only one feeding port in order to ensure that all competitive interactions could be observed. In an average garden with standard feeders, it is probable that dominance would have less of an effect.

2.5.2 Frequency of Visits to Feeding Stations
There was a significant interaction between food type and species which affected how frequently individual species visited the feeders. It is possible that the species which were seen more frequently at feeding stations had larger population sizes, but without an intensive capture-mark-recapture scheme in the area this cannot be verified. However, it is likely that there are some species which are more synurbic (Duchamp et al., 2004) and better at adapting to using bird feeders; it has been shown that urban and rural avifauna composition differs, and this has been linked to the provision of food (Tryjanowski et al., 2015). Additionally, the food provided as a supplementary source is not naturally found in this area, but it may be closer to some species' natural diets than others. For example, an insectivorous Robin may be less inclined to incorporate seeds into the diet than a Great Tit. When providing a supplementary food source the natural diet of target species' should be considered

in order to best provide for those populations. Furthermore, unequal information transfer between- and within-species may mean that not all individuals within a population possess the skills required to access this unnaturally presented food source (Aplin et al., 2012). Another potential explanation for the differences seen could be that interspecific dominance forced subordinate species (Coal Tits in this case) to utilise the less favoured food source to a greater degree (Carrascal and Alonso, 2006). Additionally, as previously mentioned, a Greenfinch may find that the husk on the seeds does not increase the handling time significantly enough for it to be disadvantageous and so will not show a preference by visiting one food type more than another.

It was also found that smaller species visited feeders more frequently. This is possibly due to the feeding behaviour of the relatively smaller species (i.e. tits) where a bird would take a seed from the feeder and eat it elsewhere, whereas the larger species (Chaffinch and Greenfinch) tended to eat at the feeder, so required fewer visits to obtain a sufficient number of seeds. Furthermore, the large crop size of the Greenfinch and Chaffinch will allow these species to consume a greater volume of food while sitting at the feeder, in comparison to the smaller tit species. Another possible explanation is that smaller birds have a relatively high metabolic rate (Kendeigh, 1970) and therefore need to eat more frequently to maintain energy balance.

Dominant species were found to visit feeders more often; it is possible that they were able to do this because they had greater access to food sources (Soma and Hasegawa, 2004), particularly if natural food availability was scarce. Alternatively, the dominant species in this study may have also been the species which were more suited to using a seed feeder.

As predicted, the food source with lower handling time (sunflower hearts) was the preferred food source and was visited significantly more frequently. This concurs with Keating et al. (1992) who found the same result with American Tree Sparrows and Harris' Sparrows (*Spizelloides arborea* and *Zonotrichia querula*). The lower handling time allows for an increased intake rate of food, which has been shown to influence food choice to a greater extent than nutritional content (Soobramoney and Perrin, 2007). This could be important to consider when providing supplementary

food in the garden; to deliver a greater benefit to the birds it is recommended to provide a food source with a low handling time suitable for the species' being targeted.

The minimum daily temperature had no significant impact on the frequency of feeder visits in this study; this is inconsistent with a previous study by Bonter et al. (2013). It is possible that no significant effect was found due to particularly mild weather in Cornwall (temperature range for this study was 0.9 to 12.7 ℃), so natural food availability may not be particularly limited and the increased energy expenditure at low temperatures would not be as great. However, the same negative result was found at lower temperatures (-12.2 to 9.4 ℃) (Brittingham and Temple, 1992), and a wider temperature range (-4.2 to -17.4 ℃). Another potential explanation for the lack of effect is that the study area was in a microclimate different from the recorded climate which was measured 13.9 km away.

2.5.3 Occurrence of Competitive Interactions

The occurrence of competitive interactions was not affected by the minimum daily temperature; again this may be explained by the previously mentioned mild conditions and microclimate.   Conversely, in a study focusing on Great Tits, lower temperatures resulted in a higher number of displacements per hour; this result was however strongly linked to reduced arthropod availability (Carrascal et al., 1998) which may have not occurred during the current study.

It was observed that some species were more likely to be involved in competitive interactions than others; however, this was also correlated with the amount of time each species was observed over the study period. Any potential differences in dominance between sex and age group were not accounted for in this study; these two factors have been shown to have an impact on dominance behaviour in several avian species (Wallace and Temple, 1987; Enoksson, 1988; Richner, 1989; Korsten et al., 2007). Also, because there are differences within species, it cannot be said for this study whether the most dominant Blue Tit is more or less dominant than the least dominant Great Tit, for example. These factors potentially confound the results of this study and indicate that much more information is required on how a range of species interact at a food source. This information could be obtained by creating a

large multi-species colour ringing scheme to identify individuals which are involved in competition interactions.

Nonetheless, it was observed that there were more intraspecific than interspecific interactions. This is unexpected because status signalling within a species should reduce the need for competitive interactions at feeders (Grasso et al., 1996). However, the result obtained in this study may be influenced by very high numbers of competition interactions occurring between greenfinches (greenfinches were involved in 453 interactions, whereas all other species were involved in a total of 346 interactions). Further, it has been shown that if individuals were unknown to one another within a species, aggressive interactions were more likely to occur than if individuals were familiar (Lemel and Wallin, 1993). However, in this study it was not possible to note which individuals were acquainted within and between species; a social network analysis across several species could provide more answers, as demonstrated in work by Farne et al., (2012).

2.5.4 Conclusion

Overall, there were differences in foraging behaviour between species, some of which can be explained by body mass and dominance. However, temperature did not affect feeding frequency but did influence feeding duration when interacting with other factors. This study has shown that it is not possible to explain the foraging behaviour of multiple species at a supplementary source by a single variable. When providing food to garden birds, it would appear to be important to consider which species are likely to be supported by the food source being provided. Some species have been shown to use a supplementary food to a greater extent than others. Therefore these species may be impacted to a greater extent by any effects of supplementary food availability.

Future studies which aim to quantify the use of a supplementary food may find that it is important to consider the impacts of ambient temperature and the influence of interactions at a feeder with other species. Both of these factors have been shown to influence behaviour at a garden bird feeder. Further work would be beneficial to repeat this study over several winters and across several different study sites with a larger range of species in order to increase reliability and to confirm repeatability of these findings. Additionally, different food and feeder types could be used to assess

whether these variables impact the composition of species which use the supplementary food. Furthermore, this study does not take into account the individual variation within a species, which could be important to aid understanding of interspecific relationships in terms of foraging behaviour.

Chapter 3

Do Body Mass and Yellow Plumage Chroma Predict the Use of Bird Feeders by Blue Tits?

3.1 Abstract

Supplementary food is often provided to a natural population in order to increase survival or reproductive success. One of the most widespread examples of providing supplementary food to a natural population is garden bird feeding, but the full impact of this is not well known. To gain a better understanding of individual differences in supplementary food use Blue Tits (*Cyanistes caeruleus*) were tagged using Passive Integrated Transponder (PIT) tags. Bird feeders which were fitted with Radio Frequency Identification (RFID) technology were then able to remotely record visits of individuals. Using this I examined whether morning body mass and yellow chroma of the breast feathers influenced the feeding frequency of individuals at two different food types. Additionally, it was considered whether ambient temperature and time of day affected individual foraging behaviour. I demonstrated that morning body mass which was measured at ringing may be a good predictor of how frequently an individual was likely to visit a feeder in the following weeks and months, where lighter birds visited more often. Morning body mass also interacted with the time of day to influence feeding frequency; it was observed that lighter individuals fed more frequently during the early morning and midday than heavier birds. However, the yellow chroma of the breast feathers did not predict feeding frequency. Overall, there was a strong preference for the food type with a lower handling time.

Due to the individual differences found, it is suggested that further phenotypic and environmental factors are explored which may impact an individual's foraging behaviour. Additionally, it may be important to consider how individuals differ in their use of supplementary food when assessing the longer term impacts of bird feeding.

3.2 Introduction

Food limitation has long been considered to have a substantial impact on population ecology (White, 1978; Oro and Furness, 2002). An individual's ability to find enough food can ultimately affect the success of that individual, either by impacting its survival (Korslund and Steen, 2006) or by affecting its reproductive output (Soler and Soler, 1996). If individual reproductive output and survival are limited by food supply, the size of a given population will therefore fluctuate as greater or fewer individuals survive or reproduce.

In many biological systems, supplementary food is provided to a natural population. Food is often provided to increase the reproductive output of a species (Schoech et al., 2008) or to increase survival rates (Castro et al., 2003; Lopez-Bao et al., 2008). Possibly the most widespread example of food provisioning occurs in gardens, where in the UK alone, the general public provide enough food to support 30 million Great Tits (Robb et al., 2008b). Providing a supplementary food source to garden birds is a highly prevalent activity (Jones and Reynolds, 2008), the consequences of which are largely unknown (Robb et al., 2008a). Although it has been shown that there are clear differences among individuals in the extent to which they take advantage of supplementary food (Ficken et al., 1990; Robb et al., 2011), there are still relatively few studies which have considered individual differences in the use of a supplementary food source (Hoodless et al., 1999; Gonzales et al., 2006; Siriwardena et al., 2007, but see Crates et al., 2016). This is often due to logistical difficulties of following large numbers of individuals in the wild (Clutton-Brock and Sheldon, 2010). It has been shown that there are a wide range of factors which might drive individual variation in foraging behaviour, such as age, size, availability of, and access to, natural food sources and individual feeding specialisations such as focusing on a particular prey type or location (Slater, 1974; Stamps, 2007; and reviewed by Bolnick et al., 2003). It may therefore be important to understand how individuals use supplementary food because there may be particular phenotypes which are being differentially supported more than others (Plummer et al., 2013b) which could potentially lead to a perturbation of natural selection. Two examples of phenotypic characteristics which may be hypothesised to predict individual differences in the use of supplementary food are body mass and the carotenoid content of feathers.

Previous studies have indicated that larger members of a population are able to spend longer at a food patch than smaller conspecifics (Richner, 1989). Also, in accordance with the starvation-predation trade-off as described by Lima (1986), individuals with a higher body mass will visit more frequently. This is because it is metabolically more costly to carry more weight and so larger birds must feed more frequently. Alternatively, where a reliable food supply is available, an individual should be able to maintain a lower body mass without the risk of starvation (Rogers, 1987), which optimises its ability to escape predation (Pascual and Senar, 2015). Therefore, individuals which utilise a constant and abundant supplementary food source to the greatest extent may also be the lighter individuals within a population. However, body mass is likely to fluctuate through the day and can change considerably over longer time periods (MacLeod et al., 2005). In a short term study it could be useful to ascertain whether a single morning body mass measurement can account for differences in feeding behaviour between conspecifics.

It is also possible that the colouration of an individual may also impact the usage of supplementary food. There is a correlation between plumage colouration and dominance, even when birds are in winter plumage (Rohwer, 1975) and it has been shown that dominant individuals visit feeders more frequently (Ekman and Lilliendahl, 1993). However, in Blue Tits, which are the focal species for this study, the UV-reflecting crown does not correlate with dominance or likelihood of winning a competition in winter (Korsten et al., 2007; Vedder et al., 2008). It is therefore thought that the yellow breast feathers may signal status in winter and influence the frequency with which an individual is likely to access a food source. This is supported by research on Great Tits where it has been shown that there is a preference for carotenoid rich foods (Senar et al., 2010). Consequently, individuals with greater access to a preferential food source could be considered to be 'more yellow' as they are likely to have more carotenoids available to deposit into feathers (Saks et al., 2003).

There are also several environmental factors which may influence the feeding behaviour of garden birds. Decreasing ambient temperature is likely to result in an increased amount of time spent foraging (Hogstad, 1988) due to increased metabolic costs (Carrascal et al., 2012b). However, the effect of ambient temperature on

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feeding behaviour at a provisioned food source has not been investigated before. Feeding behaviours are also likely to be influenced by the time of day. According to the bimodal foraging theory, activity will be greatest just after dawn and just before dusk as shown in captive Zebra Finches (*Taeniopygia guttata*) (Dall and Witter, 1998). In contrast, it was shown by Bonter et al. (2013) that several species do not follow this pattern of feeding at a supplementary food source, but have a steadier rate of activity through the day with a slight peak a few hours before sunset. When a predictable food source is available, it makes ecological sense for an individual to increase feeding activity just before sunset (Olsson et al., 2000); this reduces the mass of fat reserves an individual must carry through the day (Haftorn, 1992) and reduces risk of predation (Gosler et al., 1995).

In order to understand better the effects of garden bird feeding, this study aims to identify whether there are individual differences in feeding frequency at supplementary food sources which can be explained by phenotypic factors, namely morning body mass and feather colouration. Blue Tit individuals will be recorded at feeding stations using Radio Frequency Identification (RFID) technology to collect data electronically. It was predicted that Blue Tits of a lower mass and less saturated yellow chroma (duller looking) will visit a feeder more frequently. I also examined the influence of temperature and time of day on individual foraging behaviour. At lower temperatures, it was expected that all individuals will visit the feeders more often, but heavier birds will have greater access. Feeding activity was also predicted to be greater just before sunset. Individuals of a lower body mass were predicted to feed earlier in the day than individuals of a higher body mass. This is because by maintaining a lower body mass, individuals that use this strategy are at greater risk of starvation by depletion of fat reserves through the night and therefore should have to feed earlier in the morning. In addition, I examined how food quality influenced foraging behaviour. Two different food types were presented: sunflower seeds and sunflower hearts (i.e. de-husked sunflower seeds). Sunflower hearts have a shorter handling time than sunflower seeds (Woodrey, 1990), and hearts have previously been shown to be the preferred food type for American Tree Sparrows and Harris' Sparrows (Keating et al., 1992). This is probably because a reduced searching and handling time for a food resource increases the net energy gain (Lucas, 1983; Tome, 1988). Therefore, it was predicted that the hearts would be preferred over the

seeds. Food type is also likely to interact with body mass, feather chroma and temperature, where larger individuals and those with greater colour saturation would have greater access to the preferred food source and there would be a greater preference for the preferred food source at lower temperatures.

3.3 Methods

At the University of Exeter Penryn Campus (N˚50.17, S˚5.13), three feeding stations were set up between November 2014 and March 2015, each approximately 200 m apart. At each feeding station there were two bird feeders (Premium Plastic Seed Feeder 4 Port, John E Haith Ltd, Grimsby, UK), each containing a different food type. One contained sunflower hearts (John E Haith Ltd, Grimsby, UK) and the other contained sunflower seeds (John E Haith Ltd, Grimsby, UK). The two feeders were placed on either side of a feeding pole, set 35 cm apart and 1.2 m high. The positions of the feeders on the feeding pole were alternated every four to five days to control for the position of the feeder causing a preference in the number of visits to a particular food type. The feeders were filled as often as required to ensure there was always a plentiful supply of food in all feeders. Access to the food was by one feeding port on each feeder only and the remaining feeding ports were sealed off. In order for the food sources to be discovered and to be used regularly by a range of individuals, the feeding stations were established several months prior to the beginning of data collection. The study took place during the winter period because more birds are likely to use a supplementary food source during this time (Chamberlain et al., 2005) and this is when most households provide food (Jones and Reynolds, 2008), which allows this study to replicate the effects of garden bird feeding.

Mist-netting took place from September 2014 through to March 2015, targeting blue tits. There were 54 Blue Tits caught that were fitted with a metal BTO identification ring, and body mass measurements were taken to the nearest 0.01 g using digital scales. Mist-netting always took place in the morning to reduce the variation in body mass which occurs through the day. Birds were also fitted also with a Passive Integrated Transponder (PIT) tag which was incorporated into a plastic colour ring (IB Technology, Aylesbury, UK); the PIT tags had individual ID codes. Finally, for a subsample of 24 individuals a measurement of colour was taken using a Jaz El-200 spectrophotometer (Ocean Optics, Dunedin, Florida, USA) and a premium grade reflection probe (Ocean Optics, Dunedin, Florida, USA). Colour measurements began to be taken at a later date than mist-netting had started due to unavailability of equipment in the beginning, hence the reduced number of individuals for which a colour measurement was able to be taken. The spectrophotometer was used to take

four readings of the yellow breast feathers. Chroma and hue are good measures of carotenoid content of feathers (Saks et al., 2003). I chose not to use hue due to the UV content of Blue Tits breast feathers making it difficult to obtain an accurate measurement for hue (Hill and McGraw, 2006). Before each set of four readings, the spectrophotometer was calibrated to a white standard (100% reflectance) using a WS-1 SS Diffuse Reflectance Standard (Ocean Optics) and dark (0% reflectance) where the internal light source was switched off. Readings were taken perpendicular to the breast feathers, with a pointer tip being used to standardise the distance the measurement was taken from the feathers and to block out any natural light, (Saks et al., 2003; Quesada and Senar, 2006). The pointer was moved away from the bird between each reading. The four readings were obtained through the software package OOIBase (Ocean Optics, Dunedin, Florida, USA) and averaged to create one mean reading per individual. The mean readings were used to calculate the yellow chroma of the feathers. To calculate chroma, the equation $\sum R_i / \sum R_{\lambda320-\lambda700}$ was used, where R = the percentage reflectance at the ith wavelength and i = wavelengths 550-700 nm for yellow chroma as described in Hill and McGraw (2006).

Data describing blue tit visitations to each bird feeder were collected using RFID readers (Protopic, Kirkcaldy, Scotland, UK) attached to the bird feeders; this method has been reviewed by Bonter and Bridge (2011) and implemented by Aplin et al. (2014). A copper loop fixed onto the feeding perch created an electrical current when a PIT-tagged bird visited the feeder, reading an individual code from the PIT tag. The individual identification code, along with the date and time of visit, was recorded to an SD card. The RFID kit collected data from all three of the feeding stations, in rotation, for 3-5 days at a time, giving a total of 55 days of data collection. Time of day was recorded by the RFID readers accurate to one second. For each feeding event, the time of sunrise for that day was subtracted from the time of feeding as recorded by the RFID readers and rounded to the nearest minute to find the number of minutes after sunrise at which each feeding event occurred. The times of each feeding event were then grouped into three categories'; morning, midday and evening. Each category consisted of a four hour time period from the first feeding events which occurred within one hour before sunrise until the last feeding events which occurred within the 11th hour after sunrise. This was used to analyse differences in feeding activity through the day.

To analyse whether ambient temperature affected the feeding behaviour of blue tits, the mean daily temperature for each observation day was taken from the Met Office (Devon, UK) database for the nearest weather station, 13.9 km away at Culdrose (N˚50.08,S˚5.26).

3.3.1 Statistical Analyses

The raw dataset was first checked to remove any duplicate readings at the RFID readers. Duplicate readings occurred if a bird stayed on a feeder for longer than one second due to the reading interval settings of the RFID reader. Any duplicate readings of the same ID number which occurred within five seconds were omitted; this interval was chosen as observational pilot studies showed that it was unlikely that a Blue Tit would leave the a feeder and make a second visit within this time frame.

General linear mixed models (GLMMs) were carried out in R (The R Foundation for Statistical Computing, 2015) using the statistical package lme4. The complete data set, where N= 24, was used for all analyses apart from the analysis which tested for the effect of yellow chroma on feeding frequency, where a subset was used and N= 6. The response variable used to test for phenotypic differences in feeding behaviour was the total daily number of visits which were made by each individual to each feeder at the three feeding stations. The explanatory variables were body mass and chroma of the yellow breast feathers. These variables were tested in two-way interactions with mean daily temperature and food type ('hearts' or 'seeds'). An interaction between mean daily temperature and food type affecting the frequency of visits made to a feeder was also tested for. Step-wise model simplification was used to remove non-significant terms of two-way interactions, with alpha set at P=0.05. Bird ID, feeding station and date were all used as random factors in these models to avoid pseudoreplication to account for site effects and any season variation. Right skewed data were corrected using a natural log transformation and model checking plots were used on all analyses to check for non-normal residuals.

To test whether time of day affected the frequency of feeding by Blue Tits, the mean daily number of visits made by each individual to each food type at each feeding station was used as the response variable. The time of day, which was grouped by morning, midday and evening, was used as an explanatory variable in two-way

interactions with morning body mass and food type. There were an insufficient number of data points to test whether yellow chroma influenced the time of day which an individual was most likely to visit a feeder. Again, bird ID, feeding station and date were used as random factors. Right skewed data were corrected using a natural log transformation and model checking plots were used on all analyses to check for non-normal residuals.   Results are presented for all main effects, and all biologically relevant two-way interactions that were tested.

3.4 Results

Of 54 blue tits which were tagged, 24 returned to the feeding stations and 5,952 readings were taken from those 24 individuals. The mean number of readings from each individual was 248 ± 60.54 (mean ± SE). Of the birds for which a colour measurement was taken, only six individuals returned to the feeders, giving 1,246 RFID readings.

There was a significant interaction between mean daily temperature and food type which influenced the number of visits made per day (χ^2_1 = 5.61, P =0.02, n=483, figure 3.1). As temperatures increased, the number of feeding events at the hearts feeder increased, whereas at the seeds feeder the feeding events decreased with increasing temperature. Morning body mass which was recorded at initial capture also significantly affected the number of visits an individual made to a feeder (χ^2_1 = 8.64, P =0.003, n=483, figure 2), where lighter birds tended to visit more frequently. However, this does not control for intraspecific competition. There was no significant interaction between the body mass and food type which influenced the number of visits made (χ^2_1 = 2.03, P =0.15, n=483). There was also no significant interaction between the body mass and mean daily temperature which influenced the number of visits (χ^2_1 = 1.92, P =0.17, n=483).
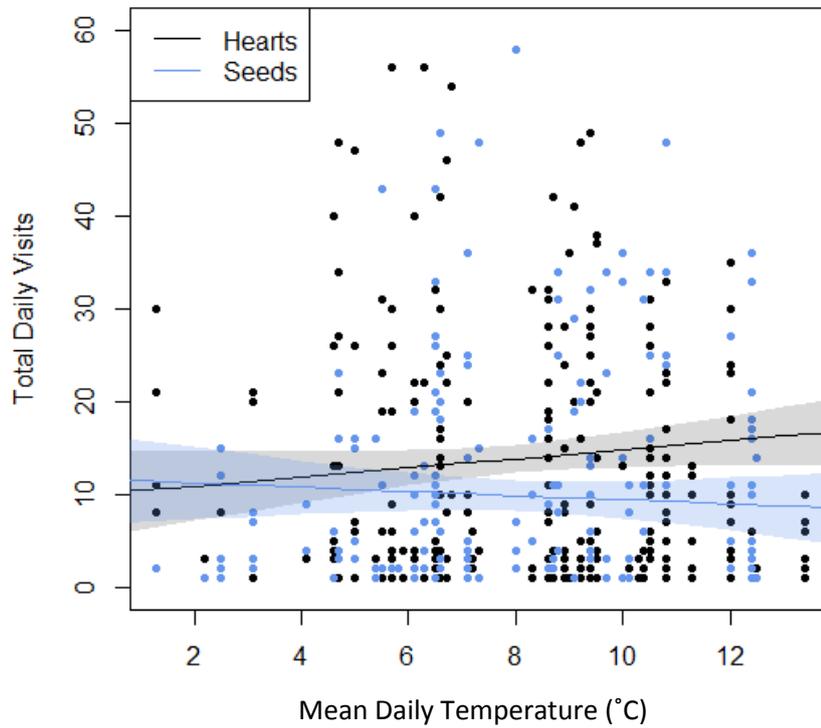
Figure 3.1. The daily number of visits made to each food type plotted against the mean daily temperature. The data points represent the total number of visits which were made each day to each feeder, according to the mean daily temperature of that day. The blue data points and trendline represent the seeds feeder, while the black data points and trend line represent the hearts feeder. The trendline shows model predictions of the number of visits which are made according to food type and the shaded areas represent 95% confidence limits.
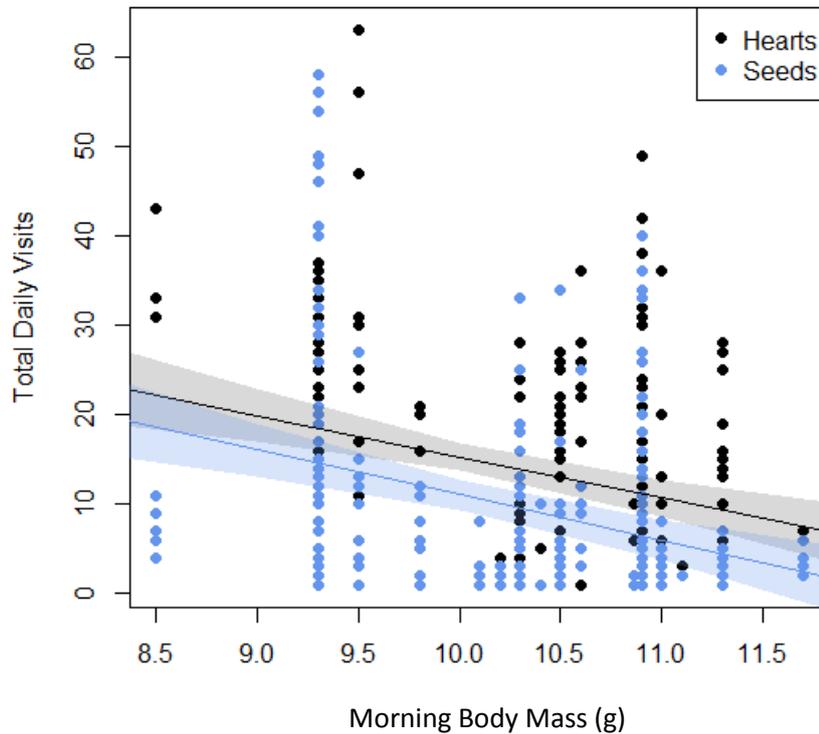
Figure 3.2: The total number of visits made each day to each food type plotted for each recorded body mass. Each data point represents the total number of visits made to a feeder each day according to the morning body mass which was recorded for each individual at initial mist-netting capture. The blue data points and trendline represent the visits which were made to the seeds feeder, while the black data points and trend-line represent the visits to the hearts feeder. The trendline shows model predictions of the number of visits which were made according to body mass. The shaded areas around each trend line indicate the 95% confidence limits.

Yellow chroma did not have a significant effect on the frequency of visits made to a feeder (χ^2_1= 2.12, P = 0.15, n=107). However, food type very highly significantly affected the number of visits made to a feeder (χ^2_1= 25.06, P = <0.001), where more visits were made to the hearts feeder. There was no significant interaction between yellow chroma and food type which influenced the number of visits made to a feeder (χ^2_1= 1.12, P = 0.29).

There was a significant interaction between body mass recorded at the time of ringing and time of day which affected the frequency of feeding ($\chi^2{}_2$= 8.57, P = 0.014, n=947, figure 3). Lighter individuals visited more frequently in the early morning and midday than their heavier counterparts. In the evening, all individuals fed equally. The food type significantly affected the frequency of feeding, where more feeding events occurred at the hearts feeder as predicted, ($\chi^2{}_1$= 33.10, P = <0.001, n=947). There was no significant interaction between time of day and food type ($\chi^2{}_1$= 1.54, P = 0.46 n=947), indicating that there was not a strong preference for one food type at a particular time of day.
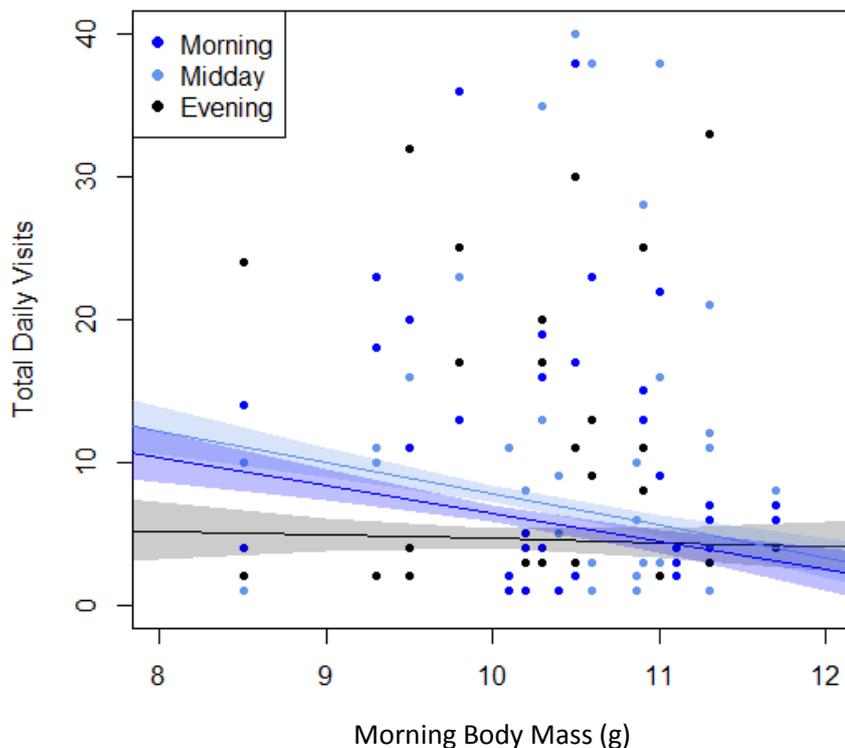
Figure 3.3: The total number of feeding events atthree different times of day on each day of data collection plotted against the morning body mass of the individuals which was recorded during ringing. All feeding events which occurred were grouped into morning (dark blue data points), midday (light blue data points) and evening (black data points) for each day. The trendlines indicate model predictions of the number of visits which are made according to the recorded body mass. The shaded areas around each trendline indicate the 95% confidence limits.

3.5 Discussion

This study exemplifies the use of RFID readers as a method to quantify individual differences in feeding behaviour (in addition to observational studies (Ficken et al., 1990) and stable isotope analysis (Robb et al., 2011)).   It was shown conclusively that the body mass which was recorded at the time of ringing significantly impacts an individual's feeding frequency (figure 3.2) as well as influencing what time of day an individual is likely to be feeding (figure 3.3), despite the body mass measurement being taken weeks or months previously. The yellow chroma of the breast feathers did not predict the feeding behaviour of an individual, indicating that access to a food source was not influenced by greater colour saturation of yellow feathers. The mean daily temperature interacted significantly with food type affecting the number of visits made to a feeder (figure 3.1). However, the result was not as predicted. Additionally, the hearts feeder was visited significantly more frequently than the seeds feeder overall.

It was found that the body mass which was recorded during the initial mist-netting and ringing sessions significantly influenced the number of visits made to a feeder as well as the time of day an individual is likely to feed. This suggests that any fluctuations in body mass which occur diurnally may have a lesser impact on how an individual uses a bird feeder than long-term trends. Previous research has suggested that heavier individuals need to feed more frequently due to increased metabolic costs of carrying fat reserves (Nagy, 1987; McNamara, 1990; Brodin, 2001); however, increased time spent foraging increases an individual's exposure to predation. A heavier individual is also at increased risk of predation due to reduced escape flight performance (Houston and McNamara, 1993; Witter et al., 1994). Therefore, the increased risk of predation must be outweighed by the reduced risk of starvation to make this a viable strategy, according to the starvation-predation trade-off theory (Houston et al., 1993). However, it was observed that it was the lighter individuals which visited a feeder more frequently.   This is likely to be due to the reduced risk of starvation in an area where a predictable and abundant food source is available. This allows for a reduced body mass (Rogers, 2015) and greater flight performance for predation avoidance. However, using structural size, such as bill length or tarsus length, or remotely weighing individuals at each visit is likely to give a better indication of how body size and mass influences feeding behaviour at a bird

feeder. Unfortunately, due to restrictions within the study, I was unable to obtain these measurements. An alternative explanation for the observed result is that the supplementary food which was provided may in fact be a less favoured food choice, and the lighter individuals which were seen to utilise the supplementary food source to a greater extent may have been competitively excluded from preferable natural food sources, such as insects, by larger, more dominant individuals (Krams et al., 2013).

As fat reserves are depleted during the night, to avoid starvation a bird will have to compensate by having an increased foraging rate early in the morning (Bednekoff and Houston, 1994). For individuals with a lower body mass this is likely to be particularly true and I found there was greater feeding activity of lighter individuals in the early morning. Larger individuals may have not had to feed as frequently early in the day due to greater fat reserves, or alternatively they may have had greater access to natural food sources which reduced their need to utilise the supplementary food. Larger individuals appeared to feed more frequently towards the end of the day which is, in fact, the most logical strategy if a predictable and abundant food supply is available due to the reduced starvation risk (Olsson et al,. 2000; Bonter et al., 2013). Therefore this ideal strategy reduces predation risk by being less active through the day. However, for the smaller individuals with greater flight performance there is likely to have been a lower risk of predation which meant that they did not have to wait until later in the day to accumulate fat reserves. Therefore, the lighter birds were seen feeding more often in the morning than evening with feeding activity being greatest in the middle of the day. This is similar to results found in Great Tits, where predation and starvation risk were considered to both be low, allowing a steady daily gain in body mass, rather than peaking later in the day (MacLeod et al., 2005). These results indicate that within a species, individuals are implementing different starvation-predation tradeoff strategies, and it is therefore likely that there are additional factors which influence an individual's foraging behaviour. This is explored further by Houston and McNamara (2014).

According to my findings, morning body mass taken in the weeks or months before observation could still be considered to be a good indicator of an individual's feeding behaviour. The second phenotypic factor which was tested to predict feeding

behaviour was the yellow chroma of the breast feathers. However, it was found that feeding frequency was not influenced by the yellow chroma of the breast feathers. Conversely, in Siskins (*Carduelis spinus*) the length of the yellow wing stripe (and therefore the carotenoid content of the feathers) was found to be an indicator of foraging ability (Senar and Escobar, 2002) and in Hihi it was shown that more colourful individuals, specifically males, tended to forage for carotenoid-rich foods (Walker et al., 2014). Most importantly, the yellow chroma of blue tit breast feathers has been found to be an indicator of foraging ability (Garcia-Navas et al., 2012). So it was unexpected to see no effect of yellow chroma on the use of a carotenoid-rich supplementary food source (Halvorsen et al., 2002). However, a previous study found no significant difference in yellow chroma of blue tit breast feathers when comparing between a high and low quality habitat (Ferns and Hinsley, 2008), which suggests there are factors which potentially influence the carotenoid saturation of yellow feathers, other than the diet of an individual. The null result which was obtained may also be due to a very small sample size resulting in a lack of variation between individuals which visited the feeders. It is possible that of the birds for which a colour measurement was available, there may have been a bias towards certain individuals using the feeders which were similarly coloured, and therefore data could not be collected for a spectrum of differently coloured individuals, allowing for the detection of behaviour differences.. This could be rectified by having a larger sample size, increasing the chances of a range of phenotypes visiting the feeders.

The ambient temperature on a given day is also likely to influence how often a bird visits a supplementary food source. In colder temperatures birds need to feed more to boost energy reserves (Kendeigh, 1949; Seibert, 1949; Ockendon et al., 2009). I therefore expected to see a greater use of supplementary food at lower temperatures (Zuckerberg et al., 2011; Bonter et al., 2013). However, I observed only a slight increase in the use of the seeds feeder and a decreased use of the hearts feeder. It is possible that due to a reduced starvation risk at higher temperatures, greater exploration of the location of two food types was able to occur, resulting in an increased use of the preferred hearts (bearing in mind that the two food types were regularly switched between the left and right side of the feeding station). Furthermore, it was found that there was a considerable overlap in the use of the two food types at lower temperatures. This suggests that there is greater

competition for the preferred food source (i.e. hearts) when natural foods are more limited, resulting in the seeds being utilised to a greater extent by those unable to access the hearts. A further explanation for the decreased use of the hearts feeder at low temperatures is the high chance of inter-specific competition. Grey squirrels (*Sciurus carolinensis*) were highly prevalent at the study site and may have made more use of the feeders at lower temperatures; the squirrels along with larger bird species may have prevented the Blue Tits from feeding. Furthermore, the increased use of the hearts feeder at higher temperatures may have been counteracting the decreased use of the seeds feeder, and overall there would have been little difference in the use of the supplementary food.

As well as phenotypic and environmental factors influencing the feeding behaviour of blue tits, the type of food which is provided is also likely to be important in determining how often an individual visits a supplementary food source.

There was a clear preference for sunflower hearts. This is likely to be due to a lower processing time, which allows for an increased rate of food intake (Soobramoney and Perrin, 2007) as well as reduced energy expenditure required opening the seeds. An increased rate of consumption can increase individual fitness (Lemon, 1991) due to a greater net energy intake. This makes the sunflower hearts the logical preferred choice. However, the seeds feeder was not ignored and there were still a reasonable number of visits made to this food source. It is possible that some individuals were prevented from accessing the preferred food source (hearts) by competitive exclusion (Shelley et al., 2004; Carrascal and Alonso, 2006), either inter- or intra- specifically. However, competitive interactions were not recorded for this study so it cannot be confirmed whether there were a greater number of competitive interactions at the preferred food source. To rectify this, a method such as that used by Farine et al. (2012) could be used to determine whether individuals were interacting at a bird feeder and therefore potentially competing for a food source. Additionally, it has been shown that there is visual discrimination of viable and empty seeds by great tits (Walther and Gosler, 2001). It is therefore possible that there is a similar ability to discriminate food items which have become spoiled in damp weather; this is more likely to happen to the hearts which do not have a protective husk. Furthermore, there may have been niche separation in skills where some

birds were more capable of processing sunflower seeds which required husking. This topic has been well documented in finch species (Fringillidae) (Nuijens and Zweers 1997; Hrabar and Perrin, 2002; Van der Meij et al., 2004), but not in tit species (Paridae).

In summary, this study indicates that we cannot generalise a whole species as acting or reacting in a homogenous way; there are subtle individual differences which are complex to explain thoroughly and are influenced by many factors, both physiological and environmental. This research showed that body mass influenced the frequency with which an individual fed as well as what time of day it fed. This suggests that a body mass measurement taken when a bird is ringed may be a good phenotypic predictor of feeding behaviour, as well as being relatively straightforwardto obtain. However, structural size measurements may be more accurate and daily fluctuations in mass will need to be taken into consideration in future studies (MacLeod et al., 2005). In terms of garden bird feeding, this study suggests that it may be important to ensure supplementary food is available early in the day to support individuals with lower fat reserves that may rely on predictable food availability in the morning. Additionally, it is likely that supplementary food sources are supporting smaller individuals more than their larger counterparts. This has the potential to alter the demography of a population and should be explored further. The yellow chroma of the breast feathers was not shown to influence feeding activity, but this research would benefit from being repeated with a larger number of individuals. Mean daily temperature had an effect on the number of visits made per day but not as expected. However, the result obtained indicates the importance of including data on ambient temperature in supplementary feeding studies, as it could have important implications regarding the feeding behaviour of birds. Additionally, food type influenced the number of visits individuals made to the feeding stations. When providing bird feed in gardens it may be important to understand which foods are preferred in order to ensure that a high quality resource is being provided to support targeted wild populations appropriately.

Longer term studies which follow individuals over several seasons are required to follow the effects of supplementary feeding throughthe year. This could help to identify further the impact of garden bird feeding on natural populations. Additionally,

future reseach could be conducted to follow individuals of several species to compare how phenotype and the environment affect feeding behaviour across species. This could further inform us how garden birds use supplementary food, and give us more evidence to predict how garden bird feeding may impact wild bird populations.

Chapter 4

General Discussion

4.1 Introduction

Supplementary feeding can be used to help buoy natural populations which are in decline, usually by increasing survival and/or reproductive success. Examples include the Florida Scrub Jay (*Aphelocoma coerulescens*) (Schoech et al., 2008), Bearded Vultures (Oro et al., 2008) and Kakapo (Elliot et al., 2001). However, in some cases supplementary feeding has gone beyond the conservation of a species and takes on a more recreational purpose. This can be done to increase populations for hunting (Armenteros et al., 2015) or to bring wildlife in closer proximity for viewing (Davies et al., 2012). Possibly the most widespread example of recreational feeding is the provision of supplementary food to garden birds (Jones and Reynolds, 2008; Davies et al., 2012; Orros and Fellows, 2015). The effects of providing food to garden birds are wide-ranging, but the full impacts are not wholly understood (Robb et al., 2008a). One reason for this is that there are over 40 species of bird which will use garden feeders in the UK (Chamberlain et al, 2005), but many studies tend to focus on a single species. This could be a problem if important interactions or differences in behaviour between species are not examined, leading to information potentially being be misinterpreted. A second reason for our limited understanding of the impacts of feeding garden birds is that when a species is studied in the past, conspecifics have been interpreted as equals (Bolnick et al., 2003; Siriwardena et al., 2007). Although many recent studies have tackled this issue and individual differences in uptake of supplemental food are being explored this still requires further investigation because there are, in fact, many behavioural and physical differences which may cause individuals to use garden feeders differently. In this study I have attempted to address these two issues. First, by conducting a multi-species study to compare and contrast feeding behaviours, and secondly by carrying out a single species study which addressed individual differences.

4.2 The Use of Supplementary Food Sources

My studies showed that there was significant variation in how different species and individuals use bird feeders. This indicates that we cannot project information learned from studying one species onto another due to variations in behaviour, and

for some studies it may also be important to understand the differences that exist between individuals and what cause them.

One of the main results was that lighter individuals, and smaller species, visited a bird feeder more frequently. At the individual level, our results contradict predictions made by the starvation-predation trade-off, where it is expected that larger individuals will have to feed more frequently due to the metabolic costs of carrying increased weight (McNamara and Houston, 1990; Brodin, 2001). However, it was thought that the predictions were not upheld because of relatively warm temperatures given the time of year as well as a high abundance of food, including natural sources, which allowed a lower body mass to be maintained without the risk of starvation. However, the body mass of individual Blue Tits was not recorded throughout the study. This could potentially have important implications due to the body mass of an individual fluctuating diurnally. If a system had been used which remotely records the weight of an individual as it lands at a feeder, the results may have been different. The structural size of an individual could also have been used instead of body mass, where the bill length or tarsus length is measured, giving an unchanging measurement of body size. Unfortunately, due to limitations within the study, this was not possible. Intraspecific competition may have also impacted the frequency which an individual visited a bird feeder, however this was not recorded within this study. It has been shown that subordinate individuals may be excluded from a feeder (Polo and Bautista, 2002) and dominant individuals will have priority access to food (Ficken et al., 1990). Recording competitive interactions to construct a dominance rank may be useful in determining whether dominance influences feeder use in Blue Tits.

In the community-level study, it was found that smaller species used the feeders more frequently. However, due to being unable to identify individuals within the populations, it is unknown whether this was simply because there were larger numbers of the smaller species present within the area. A large multi-species RFID study could help to identify if there are simply larger population numbers of some species or if differences in foraging behaviour cause an increase in the frequency of being observed at a feeder. Additionally, the overall diet of each species was not measured and therefore it was not possible to say whether particular species tended to include a higher percentage of supplemental food within its diet, which could

explain why some species were observed at the feeder more frequently. Stable isotope analysis could help identify whether some species tend to utilise supplemental food to a greater extent, in proportion to its overall diet. If a species is found to genuinely incorporate a higher percentage of supplemental food within its diet that species may also be more likely to be impacted by any effects of supplemental feeding. For example, if the presence of supplemental food allows increased survival or reproduction of a population, and if that food supply were to stop being provided, the population may decline. However, this is subject to dependency on supplementary sources, which has previously been shown to not be of concern in Black-capped Chickadees (Brittingham and Temple, 1992), but this has not been investigated in a wider range of species.

Advancing further on the use of stable isotopes to identify diet composition, several types of bird feed could be used to test whether there are species preferences for a particular type of supplemental food. For example, some species, such as Robins, may prefer meal worms, whereas some finch species may prefer nyger seed. This could help inform the public which bird feed to use according to which species they are targeting. However, this could have adverse effects on the community composition of bird species as it has already been demonstrated that garden bird feeding can influence the structure of avian communities (Galbraith et al., 2015).

At the community level it was also found that larger species spent longer on the feeders despite visiting less frequently. A probable explanation for this result is that larger species of bird were able to spend longer at the feeders because they were less likely to be supplanted by others (Shelley et al., 2004). It is possible that larger species could have competitively excluded smaller species by monopolising a feeder. However, this cannot be confirmed because this study did not include a control where there were multiple feeding ports open and levels of competition were relaxed. Alternatively, the type of food provided and the feeder in which it was presented may have influenced how often or how long a species spent at the feeding station due to differences in foraging ecology. Further investigations exploring how a range of species use a supplementary food source could be insightful, particularly if there are food type preferences or a type of feeding equipment which is preferred by a species. This could enable us to provide better support to species which are in

decline such as the House Sparrow (*Passer domesticus*) (Shaw et al., 2008) and the Blue Tit (British Trust for Ornithology, 2010).

Unfortunately, it was not possible to identify if there was individual variation within a species which influenced the duration spent at a feeder. This could tell us if there were particular individuals who were likely to spend more time at a feeder, and investigate if there were any factors which predisposed that individual to spending more time at a feeder. This information could help inform us of the impact garden bird feeding is having on a population by indicating which individuals are being supported to the greatest extent. However, in this case our study species (i.e. Blue Tit) took food away from a feeder to eat under cover elsewhere, regardless of phenotype, therefore measuring the duration spent at a feeder is unlikely to provide much insight for Blue Tits.

The two studies which I conducted showed that the ambient temperature affected the feeding behaviour of a range of species and individuals within a species in different ways. This could be important to explore further as climate change continues to change environmental conditions. With enough information there is the potential to create predictions on how climate change may impact bird communities. However, within my study, the temperature data was taken from a weather station 13.4km away. For more accurate information on how the climate influences feeding, a temperature reading would ideally be taken at the feeding station itself. An onsite weather station could provide more detailed information, including rainfall and wind-speed which is likely to also influence foraging behaviour (Hilton et al., 1999).

The variation in feeder use may mean that some species or individuals are more likely to be affected by the impacts of supplementary feeding. For example, it was observed that Greenfinches tended to be involved in a higher number of competitive interactions at the feeders and also spent the most time at the feeders overall. The gregarious behaviour of Greenfinches and increased time spent on a feeder could increase the risk of disease transmission. This could potentially explain why finch trichomonosis spread rapidly and impacted Greenfinches more than Chaffinches (Lawson et al., 2012), who were shown to use feeders less. Although the type of food provided and differences in feeding niche is also likely to influence the time a species spends at a feeder.

My study used the frequency and duration spent at a feeder to quantify the use of a supplementary food source. However, the frequency and duration which a bird is observed at a feeder may not be accurate descriptors for the use of a supplementary food source because they do not take into account the mass of food which is consumed per visit. Mass of food consumed, rather than time spent foraging, may better describe how artificial food sources are incorporated into the diet and help to identify more clearly how individuals differ in their use of supplementary food sources. Again, this could be addressed by using stable isotope analysis, where the percentage of supplementary food in an individuals' diet could be quantified. If this was done across several species, this could simultaneously identify individual differences as well as species differences in use of supplementary food.

4.3 Conclusion

Expansion of the urban environment and an increasing human impact on the natural world are continuing to influence wild bird populations (Chace and Walsh, 2006). Further to this, climatic changes and advances in technology as well as the species which are yet to be studied all make it important to continue to review the current literature and advance our current knowledge. As this study has shown, species and individuals employ different foraging strategies in a given situation, and there are a variety of ways to test the differences which exist. Additionally, the differences in behaviour are not simple to explain, but are influenced by a wide range of factors such as the type of food provisioned, the weather, the morphology of a species or individual and the local community composition. These factors can impact individuals and species differently which highlights the importance of studying the effects of supplementary feeding at both the community and individual levels. As garden bird feeding becomes increasingly popular (Chamberlain et al., 2005), it becomes increasingly important to continue to research the impact this is having on wildlife.

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