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What Makes Bird Feeders Attractive to Birds? Implications for Wild Bird Feeder Design

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Contents

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Abstract

With ever increasing levels of habitat destruction and degradation across the globe, many avian populations are being displaced from their historic environments and home ranges towards towns and cities in the search for food and/or shelter. One way to support and sustain the displaced populations would be to use the bird feeding industry with its large global footprint; using supplementary feeders in order to increase the level of food resource readily available in an environment. The use of bird feeders in both urban and semi urban gardens, parks and green spaces is becoming increasingly important in order to provide sufficient nutrients to sustain populations, given the constant increase in environmental stress.

One way to achieve the increased transfer of nutrients to avian populations would be to make supplementary feeders more attractive to birds. This will benefit birds by providing a more attractive reliable food source during winter, benefit people by attracting more birds to parks and gardens and benefit the industry by allowing for the focus marketability of feeders most preferred by specific species.

Currently no work has been done on the colour preference for feeders in temperate granivorous or omnivorous species, with the majority of previous work done on tropical frugivorous or nectivorous species.

This investigation examines two main variables relating to bird feeders: feeder colour and the perch design, in order to investigate if these two factors have any effect on visitation rate both on a population level and within individual species. Birds demonstrated a preference for silver coloured feeders and for feeders with long (80mm) perches. Results examining both avian and human preference suggests a green feeder with a long perch may offer the most marketable combination for industry. There was no recorded effect of UV preference on the selection of bird feeder.

Introduction

In the UK, up to 12.6 million households (75%) put out supplementary food for birds at some point throughout the year, with 7.4 million using bird feeders (BTO, 2014). As a result the UK bird feeding industry is worth an estimated £200m per annum, a figure expected to rise by an estimated 10% year on year (BTO, 2014). Supplementary bird feeders are the source of primary interactions between birds and humans, and this interplay may have a major impact on the structure of avian communities.

Pressure on wild bird populations is increased due to habitat destruction and degradation, and so supplementary feeding is becoming increasingly important as a factor in bird survival and the health of ecosystems (Ewen *et al*, 2015). For the bird food industry, key questions focus on the development and design of feeders that are both effective in attracting birds, and marketable to the public. In this study, the focus is on two factors: feeder colour and perch design.

Colour preferences have been examined in many species of both wild and domestic birds, including the effect of aposematic (warning coloured) prey (Exnerova *et al*, 2007) and an individual's use of colour for sexual selection (e.g. Burley *et al*, 1982), attraction of a mate (Diamond, 1988) and competition (Amundsen, 2000). Although there has been some work investigating colour preference with respect to food choice (e.g. Marples, 1933) and a significant body of work investigating preferred colours of supplementary feeders in hummingbirds (e.g. Grant, 1966, Wheeler, 1980, Handelman & Kohn, 2014), there has been no research conducted into the effect of colour preference on selection of a supplementary bird feeder in temperate passerine birds.

Additionally, there are currently a wide variety of different designs of perch on currently marketed feeders, covering a large range of sizes and shapes, However, other than research into how birds (and other organisms such as bats) perch (or hang) (e.g. Quinn & Baumel, 1990), there is currently no research into the effect of perch design on supplementary feeders on preferences in birds, and whether different designs will experience differing levels of visitation and depletion.

In this study, I examine the effects of feeder colour and perch design on the number of visits to feeders by common garden birds in the UK. The overall aim is to identify the design of feeder that is likely to attract the highest number of birds. Alongside this, I also evaluate the preferences for the different colours of feeders used in the study by likely purchasers of bird feeders, to assess the alignment of avian and human preferences. This study has both ecological conservation benefits in addition to economic implications as it will allow for better marketability of feeders that have an increased benefit to wildlife, specifically by aiming to design a feeder which supports the species and diversity of local avifauna within urban environments.

Urbanisation

Humans have both directly and indirectly had a significant impact on their environment for thousands of years, but this has grown in prominence in the latter half of the 20th century and the beginning of the 21st with increasing global urbanisation and changes in farming practices (Chamberlain *et al*, 2005). At present in the UK, 7% of the land area is urbanised (UK National Ecosystem Assessment, 2011), but in rural and semi urban areas, extensive land clearance for agriculture, housing and infrastructure, together with habitat changes such as the formation of monoculture farming systems have led to extensive habitat fragmentation (Galbraith *et al*, 2015) and alteration of the vegetation structure within habitats (Evans *et al*, 2009). Both of these effects have an impact on overall community structure, and therefore an impact on bird populations (Beebee, 2001).

Globally, this level of habitat destruction and degradation is widely regarded as one of the most important issues facing biodiversity (Brooks *et al*, 2006). Habitat degradation in the UK has led to the displacement of many bird species to less ideal gardens and urban green spaces. This includes species historically associated with woodland or countryside, including DEFRA (2014) indicator species such as Tree Sparrow (*Passer montanus*), Song Thrush (*Turdus philomelus*), Goldfinch (*Carduelis carduelis*) and Great Tit (*Parus major*) (Evans *et al*, 2009 & Goddard *et al*, 2010). In addition, avian species are coming into contact with increased levels of predation, such as that from domestic cats (*Felis catus*) (Beebee, 2001), which cause the deaths of an estimated 25-29 million birds per year (Woods *et al*, 2003). A further challenge is increased completion from other avian species and Grey Squirrels (*Sciurus carolinensis*), which provide significant competition at supplementary feeders (Bonnington *et al*, 2014).

However, the actions of humans such as “gardening with wildlife in mind” (Royal Horticultural Society, 2011, Yorkshire Wildlife Trust, 2013) and providing supplementary feed for birds can go some way to mitigating the negative impacts of increasing urbanisation on bird populations. Parks and gardens make a positive contribution to urban wildlife by providing space for displaced organisms, coupled with the fact that they occupy twice the area of the UK’s national nature reserves (Chamberlain *et al*, 2004). In addition to this, urban green spaces also provide conservation aids such as nest boxes, ponds and supplementary feeders (Goddard *et al*, 2010). Together, this means these sites are of high importance, both as (one of) the main contributors to urban biodiversity (Beebee, 2001) but also to national biodiversity, as shown by the recent inclusion of parks and gardens in the UK's 2014 Biodiversity Action Plan (DEFRA, 2014).

Supplementary Feeding

The act of putting food out for birds (supplementary feeding) is a highly popular activity, especially in more developed or affluent areas such as the United States, Europe, Australia and the UK (Galbraith *et al*, 2015) where between 20-30% of the population provide food for birds at some point throughout the year (Fuller *et al*, 2008). Annually in the UK, 12.6 million households feed garden birds on a regular basis with 60% of these using commercially available bird feeders to provide sustenance (BTO, 2014). As a result, the bird feeding industry has an estimated value of £200 million (per annum) in the UK, which is projected to rise by 10% year on year (BTO, 2014), a figure that is significantly above the global projected growth of 4% in the bird food industry (Lin, 2005). Supplementary feeding has a wide range of documented impacts on birds, both positive and negative, and can influence a wide variety of aspects from individual's behaviour, reproduction, survival and phenology to influencing population sizes and species diversity.

Benefits of supplementary feeding

Survival

Winter is the time of year when natural food resources are at their lowest level of availability (Brittingham & Temple, 1988) but it is also the time when an individual's thermodynamic costs of maintaining body temperature are at the highest (Martin & Karr, 1990); this means that an individual's over winter survival is highly dependent on the characteristics and availability of the food supply (Brittingham & Temple, 1988). During winter, gaining enough food to survive overnight is critical, especially for small passerines. For example, individuals in the Tit family (*Paridae*) can lose up to 10% of their body weight overnight in winter (Olsson *et al*, 2000). As the majority of their energy consumption is used to either maintain body temperature or expelled during the search for food, a site with a bird feeder provides a readily accessible and dependable resource (Cowie & Hinsley, 1988) and may remove the effects of resource depletion (Stephens, 2008). As bird feeders often represent the most abundant and dependable food resource in a habitat (Farine *et al*, 2014), with them often being utilised by many individuals and species, often through the formation of large mixed species flocks through the mutual the search for food (Morse, 1977); this therefore leads to a positive relationship between bird density and available food supply (Berner & Grubb, 1985) within an environment.

Food supplementation however can increase the level of danger from predators who are attracted to the concentrated number of foragers/prey in an area (Stephens, 2008). However, on the other hand, flocking also provides a number of antipredator benefits, with these including increased group vigilance (the many eyes hypothesis; Morse, 1977, 1990) and increasing predator confusion during an attack (Krause & Ruxton, 2002).

The addition or increase of supplementary food into a habitat can have a positive effect on individual survival. In Downy Woodpeckers (*Picoides pubescens*), Carolina Chickadees (*Parus carolinensis*), Tufted Titmice (*P.bicolor*) and White-breasted Nuthatch (*Sitta carolinensis*), supplementary feeding resulted an increase in overall condition and increased rate of injury recovery, resulting in an overall higher level of survivorship within the surveyed populations (Grubb & Cimprich, 1990).

Reproduction

Supplementary feeding is widely regarded as having a positive effect on the reproductive success of birds through a range of mechanisms (Harrison *et al*, 2010); firstly, supplementary feeding concentrates the number of birds in one area prior to mate selection (White *et al*, 2008), while during breeding, it can lead to increased clutch size (e.g. Hen Harriers (*Circus cyaneus*); Redpath *et al* (2001), House Sparrow (*Passer domesticus*); Peach *et al*, 2014), decreased incubation time (Northern mockingbird (*Mimus polyglottos*); Londono *et al*, 2008) and overall higher hatching and fledgling success (e.g. Sparrowhawk (*Accipiter nisus*); Newton & Marquiss, 1981 & White Stork (*Ciconia ciconia*); Hilgartner *et al*, 2014). Supplementary feeding can therefore be a simple yet effective conservation tool for many species and can assist with the enhancement of threatened or endangered populations (Lemon, 1991, Jones, 2011).

Population Distributions and Species Diversity

Supplementary feeding can also have positive effect on population size and species distributions and diversity, for example in the UK, populations of House Sparrow (*Passer domesticus*) (BTO, 2012) and Starling (*Sturnus vulgaris*) (Robinson *et al*, 2006) have increased and Blackcaps (*Sylvia atricapilla*) have colonised new areas of urban and semi-urban habitats (RSPB, 2015). These increases have been indirectly attributed to the broad use and availability of bird feeders, and is thought to have led to the reversing the effects of habitat decline due to hedgerow removal in the 20th century (Arnold, 1983). In addition to this, supplementary feeding may also be responsible for a northern shift in migratory patterns from mainland Europe to the UK in species such as Blackcaps, with this further increasing the size of both domestic and seasonal migratory populations (Rolshausen *et al*, 2009).

Negative effects of supplementary feeding

Survival and Reproduction

Although there are a number of benefits of supplementary feeding at both an individual and population level, in some instances, there may also be negative consequences and implications, despite its common use as a method for combating reductions in populations (Ewen *et al*, 2015). Firstly, one potential drawback is the make-up of the supplementary food as it may not provide the correct nutrients to meet a bird's requirements. For example, populations of Great Tit and Blue Tit declined when fed with fat/suet balls, as although these contain high energy levels, they possess relatively low nutritional value, and led to decreased reproductive success (Harrison et al 2010).

In some species, food availability can influence the sex ratio of subsequent generations. While supplementary feeding of the Kakapo (*Strigopus halroptilus*), introduced to promote breeding (Powlesland & Lloyd, 1994) resulted in an increased population, it also significantly increased the ratio of females to males within the population (Robb *et al*, 2008) and as such resulted in reduced reproductive success due to the lack of availability of a viable mate. This set back conservation efforts from several years to several decades (Clout *et al*, 2002). Supplementary feeding can also lead to dependence on the provided food resource, leading to the loss of foraging skills and potential mortality if the resource is removed. For example, in Bearded Vultures (*Gypaetus barbatus*), supplementary feeding decreases territory quality by reducing territory size due to dependence on the food resource and loss of foraging skills (Oro *et al*, 2008). In small garden species such as Tits, with individuals potentially losing a large proportion of their body mass overnight in extreme conditions (Olsson *et al*, 2000), the removal of a resource therefore could potentially lead to mortality, especially in young and less fit individuals (Brittingham & Temple 1992).

Range Expansion of Non Natives

A further consequence of supplementary feeding is the risk of promoting the range expansion of non-target, non-native or invasive species (Savard *et al*, 2000). One potential reason for this is that invasive species often possess much higher levels of adaptability (due to genetic diversity) to the environment (Cannon, 1999 & Wittmann *et al*, 2013) in addition to often being omnivorous and outcompeting native populations (Davidson *et al,* 2011). While the range expansion of Starlings and House Sparrows in Europe; where they are native, is seen as positive, outside their native range they are considered one of the worst invasive birds globally (Lowe *et al* 2000, GISD 2010). With supplementary food provided in large quantities around the globe, it provides an easily accessible resource for all species, thus increasing the rate of spread of invasive populations. Clavero & Garcia-Berthou (2005) found that the extinction of 54% of species now extinct was caused or severely contributed to by invasive or introduced species, and this supplementary feeding may have negative consequences for native populations.

Health and Disease

Supplementary feeding has also been linked to the spread of disease, which can have a significant impact on both a species diversity and frequency in a habitat. In recent years it is estimated that *Trichomonas gallinae* contracted at birdfeeders has been responsible for the deaths of approximately 1.5 million Greenfinch (*Carduelis chloris*) in the UK: 35% of the national population (Lawson *et al*, 2012). In addition to this, birds that frequent supplementary feeders especially during winter are considerably more likely to be exposed to the pathogen *Mycoplasma gallisepticum* (causing conjunctivitis) than birds who do not use supplementary feeders (Adelman *et al,* 2015). A result of this is that wild birds are therefore potential vectors for a large numbers of diseases (Benskin *et al*, 2009) and bacteria, and this can be exacerbated by the use of birdfeeders. Many of these pathogens also often have a level of transmission potential to humans (zoonotic pathogens) through contact with garden bird feeders, and through those who handle wild birds directly, such as bird ringers (Abulreesh *et al*, 2007). Examples of potential zoonotic pathogens include the bacterium *Salmonella typhimurium,* the protozoan parasite *Trichomonas gallinae* or the viruses associated with Avian Pox (Benskin *et al*, 2009)

Foraging Preferences in Animals

Decisions and the Importance of Decision making in Animals

In nature, decision making affects every aspect of an individual's life and wellbeing, with poor or non-adaptive decisions potentially leading to adverse health or fitness costs (Conradt & Roper, 2005). Each day, and individual will have to make numerous decisions about what, where and when to eat, and balance the costs and benefits of each decision (Krebs & Davis, 1993), with these decisions often being variable on a day by day basis owing to the often significant seasonal and yearly variation in both the location and quality of foraging sites (Hejl and Verner, 1990); thus, animals must choose foraging locations that meet their daily energy requirements (Conradt and Roper, 2005 & Farine *et al*, 2014) while trading off against the potential risk of predation. Animals may forage individually (Ford, Huddy & Bell, 1990) or in groups (Emlen, 1952), however this is often fluid and can change rapidly throughout the year. Foraging in groups carries wide ranging benefits associated with reduced predation (see above) but also the benefit of being able to follow knowledgeable individuals to a food source (Beauchamp & Giraldeau, 1996, Conradt & Roper, 2003). However, there are also costs associated with foraging in groups, such as the increased levels of competition for located resources from others within a group, with aggression particularly apparent towards unrelated (non kin) foragers (Dickinson *et al,* 2009) and winter migrants to the area (Harrington, 1973). Due to this, mean food intake reduces with group size (Beauchamp & Giraldeau, 1996)

Optimal foraging theory (OFT) (MacArthur & Pinanka, 1966) predicts how animals search for food, accounting for factors such as predator avoidance as well as the abundance and quality of food resources, with the assumption that animals will behave optimally, and maximise foraging gains while minimising foraging costs (such as searching for food and risking predation). For example, animals may balance food abundance (Plein, *et al*, 2013) against nutritional value (Hughes, 1993), with decisions made varying seasonally in order to suit environmental conditions (Debussche & Isemann, 1989, Sih, 1982). This has implications for the use of supplementary feeders by birds. In winter low levels of natural food availability can mean supplementary feeders represent areas of the highest levels of resource abundance in the environment (Farine *et al*, 2014), with a result of this being that each feeder can attract large numbers of birds throughout the winter season (Morse, 1977).

Colour preferences in animals

Colour and colour preferences can have a large and significant effect on a wide variety of activities an organism undertakes, from sexual selection of a mate (e.g. Blue Throat (*Luscunua svecica*) and Blue Tit (*Cyanistes caeruleus*) Amundsen, 2000) to food choice (e.g. Steller's jay (*Cyanocitta stelleri*) Slaby & Slaby, 1977). Colour preferences have been documented across a number of different taxa from bumblebees (Genus *Bombus*) (Stephens, 2008) to Hummingbirds (Family: *Trochilidae*) (Handelman & Kohn, 2014) and Guppies (Genus: *Poecilia*) (Godin and McDonough, 2003), with these colour preferences being either innate (e.g. Great Tits (*Parus major*; Lindstrom *et al*, 1999), or reinforced through learning and development (Exnerovena *et al*, 2007). In the context of sexual selection, animals often exhibit preferences for brighter plumages or colouration (e.g. Strawberry Poison Frog (*Dendrobates pumilio*); Maan & Cummings, 2009, Three-spined Sticklebacks (*Gasterosteus aculeatus*); McKinnon, 1995), which give an indication as to the individuals health, level of physical fitness, parasite load or social status within a group or population (e.g. Lawes's Parotia (*Parotia lawesii*; Pruett-Jones *et al*, 1990). In a foraging context, many colour-related factors can interact in order to affect a forager's decisions, with these including the ease of detection or targeting (of prey) and the association of these colours with palatable or unpalatable food items.

Food Selection

Prior to commencing an attack upon a group or flock of prey, predators (specifically birds of prey) will often single out and rarely switch from an individual target before the attack takes place (Cresswell, 1994), with there being several factors which may influence an attackers selection of a target. One of the main deciding factors in this decision is likely to be the level to which an organism stands out in the environment (conspicuousness) or within a group (the oddity effect). The selection of a prey is often variable between species and habitats as although the brightest individuals may be preferentially targeted (e.g. Blue acara cichlid (*Aequidens pulcher*) targeting Guppies (*Poecilia reticulata*) (Godin and McDonough, 2003)) this is not always the case. In sexually dimorphic avian species such as Chaffinch (*Fringilla coelebs*), there is a higher level of documented predation against the more camouflaged females than the brightly coloured males (Götmark & Ahlstrom, 1997). These results are echoed in a wide variety of game birds particularly during the winter and breeding season (e.g. Pheasant (*Phasianus colchinus*) (Kenward *et al*, 1981), Black Grouse (*Lyrurus tetrix*) (Angelstam, 1984) and Capercaillie (*Tetrao urogallus*) (Widén *et al*, 1987)). This can be attributed due to differences in the feeding behaviours of the sexes in addition to the relative abundance of the sex within the environment (Widén *et al*, 1987). This shows that although colour, brightness or conspicousness may be a determining factor in the prey selection, behaviour is also likely to have some effect.

For non-predatory animals, colour also plays a role in prey selection. Many previous studies investigating colour preference in animals often use food as a vector as this allows for an output easily quantifiable (food depletion) in addition to providing experimental repeatability. Several studies, such as that by Marples (1933) used uncoloured (natural) and coloured peanuts in order to test for preference, finding that Great Tit (*Parus major*), Blue Tit (*Cyanistes caeruleus*) and Eurasian Nuthatch (*Sitta europaea*) all have a preference for uncoloured (natural) peanuts then those artificially coloured white. It is worth taking into account that the site had been primed with uncoloured peanuts and thus this preference is may be the avoidance of unrecognised or novel colours, known as neophobia in the short term or dietary conservatism if it persists for a longer time period (Marples *et al,* 1998, Marples & Kelly, 1999, Thomas *et al,* 2010, Richards *et al,* 2014). In the wild, berries, such as those from the Rowan Tree (*Sorbus* sp.) can be a staple part of the diet of some frugivorous species throughout the winter with colour acting as a signal for palatability as berries often undergoing a dramatic colour change once ripe. Eurasian Blackbirds (Diesselhorst, 1972), European Starlings (Feane 1984 in Willson *et al*, 1990) and Sardinian Warblers (Diesselhorst, 1972) all prefer colours of berries that are associated with ripeness, such as red, over colours associated with unripe fruit (such as green or yellow). This shows that with regards food preference, it is likely influenced not only by the colour but also the object coloured.

Table 1 summarises a range of studies on colour preference in birds, focusing primarily on foraging (and the use of supplementary feeders), but also including studies containing data on the collection of coloured objects for nest or bower. Overall, all studies covered include choices by individuals between differently coloured objects (e.g. red or blue). The extensive body of work on sexual selection in relation to colour were omitted from the results, as rather than showing a preference between two morphologically identical objects: with the only variable being colour, studies on sexual selection majorly focus on preferences for more or less intense shades of the same colour, with these often being linked to other factors such as display, dominance, or condition, with colour seen as an honest display of genetic quality (Hadfield *et al,* 2006). In Figure 1, the number of studies reporting a preference for each colour is summarised. Overall, the majority of studies (~60%, 26/45 instances) report a preference for red (Figure 1a) with many focused on coloured food: berries, artificially coloured insects, coloured baits or, nectar dispensing supplementary feeders (10/45 instances); the only type of supplementary feeders used whilst researching colour preferences. These feeders were primarily targeted at hummingbirds, as the colour red is thought to reflect that of the flowers visited (Handelman & Kohn*,* 2014), with very few studies (maximum of 5/45) reporting a preference for any other colour. In addition to preference, few studies reported avoidance of particular colours (Figure 1b), although this was often mentioned offhand in the discussion, rather than as a result. The colour with the highest level or recorded avoidance was yellow (10/36 instances) with red identified as being avoided in the second greatest number of studies (6/36).

Colour Preference relating to Supplementary Feeders

Table 1: Studies on avian colour preference in the literature. The studies examine food selection; usually coloured berries in the case of passerines or coloured flowers for nectivorous species, unless otherwise stated: nest building/decorating (^). In the majority of cases, studies were conducted using adult birds (unmarked), with studies using visually naïve hatchlings marked as (*). Colours preferred and avoided are listed in order of preference/avoidance

Family	Common Name	Scientific Name	Diet	Study Type	Colours Preferred	Colours Avoided	Reference
Anatidae							
	White Pekin Duck*	*Anas platyrhynchos domesticus*	Granivorous/Insectivorous	Lab	Green & Yellow	-	Hess, 1956
Corvidae							
	Steller's Jay	*Cyanocitta stelleri*	Omnivorous	Field Exp	Red	-	Slaby & Slaby, 1977
Icteridae							
	Baltimore Oriole^	*Icterus galbula*	Omnivorous	Field Obs	N/A	Red	Smith, 1928 (in McCabe, 1961)
Mimidae							
	Grey Catbirds	*Dumetella carolinensis*	Insectivorous	Field Obs	Red	Yellow	Willson et al, 1990
Paridae							
	Blue Tit	*Cyanistes caeruleus*	Insectivorous	Field Obs	Natural (Uncoloured), White	Red, Purple	Marples, 1933
	Great Tit	*Parus major*	Insectivorous	Field Obs	Natural (Uncoloured), White	Red, Purple	Marples, 1933

Pellorneidae							
	Brown-Cheeked Fulvetta	*Alcippe poioicephala*	Insectivorous/Nectivorous	Lab	Blue	Black, Red, Yellow	Duan & Quan, 2013
Petroicidae							
	North Island Robin	*Petroica longipes*	Insectivorous/Frugivorous	Field Exp	Yellow	Blue, Brown	Hartley et al, 1999
Phasianinae							
	White Rock Chicken*	*Gallus gallus domesticus*	Omnivorous	Lab	Orange & Blue	-	Hess, 1956
Ptilonorhynchidae							
	Satin Bower Bird^	*Ptilonorhynchus violaceus*	Frugivorous	Field Obs	Blue	-	Edwards, 1920
Pycnonotidae							
	Black-Crested Bulbul	*Pycnonotus flaviventris*	Frugivorous/Insectivorous	Lab	Red	-	Duan & Quan, 2013
	Grey-Eyed Bulbul	*Iole propinqua*	Frugivorous/Insectivorous	Lab	Red	Black, Blue, Green	Duan & Quan, 2013
	Red-Whiskered Bulbul	*Pycnonotus jocosus*	Frugivorous/Insectivorous	Lab	Red	-	Duan & Quan, 2013
	Sooty-Headed Bulbul	*Pycnonotus aurigaster*	Frugivorous/Insectivorous	Lab	Red	Black	Duan & Quan, 2013
Sittidae							
	Eurasian Nuthatch	*Sitta europaea*	Insectivorous	Field Obs	Natural (Uncoloured), White	Red, Purple	Marples, 1933
Sturnidae	European Starling	*Sturnus vulgaris*	Omnivorous	Field Obs	Red	White	Feare, 1984 (In Willson, 1990)
				Field Obs	Blue	White	Feare, 1984 (In Willson, 1990)

Sylviidae							
	Sardinian Warbler	*Sylvia melanocephala*	Insectivorous/Frugivorous	Field Obs	Black	Red	Diesselhorst, 1972
Trochilidae							
	Amazilia Hummingbird*	*Amazilia amazilia*	Nectivorous	Lab	Red, White (+UV), Red, White (-UV)	-	Lunau et al, 2011
	Anna Hummingbird	*Calypte anna*	Nectivorous	Field Obs	Green	-	Grant, 1966
				Field Obs	Red	Green, Blue, Yellow	Wheeler, 1980
				Lab	Red,	-	Stiles, 1976
	Black Chinned Hummingbird	*Archilochus alexandri*	Nectivorous	Field Obs	Yellow	-	Lyerly et al, 1950
				Field Obs	Red	Green, Yellow	Goldsmith & Goldsmith, 1979
				Lab	(Colourless) Yellow	-	Bené, 1941
	Broad Tailed Hummingbird	*Selasphorus platycercus*	Nectivorous	Field Obs	Red	-	Meléndez-Ackerman *et al*, 1997
				Field Obs	Red	Yellow	Vickery & Vickery, 1992
	Giant Hummingbird	*Patagona gigas*	Nectivorous	Field Obs	Red	Not Tested	Grant, 1966
	Green Violetear	*Colibri thalassinus*	Nectivorous	Lab	Red	Yellow	Lyerly et al, 1950
				Field Obs	Red	-	Wagner, 1946
	Magnificent Hummingbird*	*Eugenes fulgens*	Nectivorous	Lab	Red, White (+UV), Red, White (-UV)	-	Lunau et al, 2011

	Peruvian Sheartail*	*Thaumastura cora*	Nectivorous	Lab	Red, White (+UV), Red, White (-UV)	-	Lunau et al, 2011
	Ruby Throated Hummingbird	*Archilochus colubris*	Nectivorous	Field Obs	Red	-	Grant, 1966
				Lab	Red	-	Béné, 1941
				Field Obs	(Colourless) Yellow	-	Miller & Miller, 1971
				Field Obs	Red	-	Miller & Miller, 1971
	Rufous Hummingbird	*Selasphorus rufus*	Nectivorous	Field Obs	Red	-	Meléndez-Ackerman et al, 1997
				Field Obs	White	-	Meléndez-Ackerman et al, 1997
				Lab	Red	-	Stiles, 1976
	White Chinned Sapphire*	*Hylocharis cyanus*	Nectivorous	Lab	Red, White (+UV), Red, White (-UV)	-	Lunau et al, 2011
	White Eared Hummingbird	*Basilinna leucotis*	Nectivorous	Field Obs	Blue	-	Wagner, 1946
Troglodytidae							
	House Wren^	*Troglodytes aedon*	Insectivorous	Field Obs	Red	Yellow, Blue, White	McCabe, 1961
Turdidae							
	American Robin	*Turdus migratorius*	Insectivorous/Frugivorous	Field Obs	Black & Red	Yellow	Brown, 1974 (In Willson, 1990)

Eurasian Blackbird	*Turdus merula*	Omnivorous	Field Obs	Red	White	Diesselhorst, 1972
Hermit Thrush	*Catharus guttatus*	Insectivorous/Frugivorous	Field Obs	Red	Yellow, Black, Blue	Willson et al, 1990
Swainson's Thrush	*Catharus ustulatus*	Insectivorous/Frugivorous	Field Obs	Red	Yellow	Willson et al, 1990
Zosteropidae						
Japanese White-Eye	*Zosterops japonicus*	Omnivorous	Lab	Red	-	Duan & Quan, 2013
UK Seed feeding Birds		Granivorous	Field	Blue (Summer)	-	Thomas, 2007
UK Seed feeding Birds		Granivorous	Field	Silver (Winter)	-	Thomas, 2007

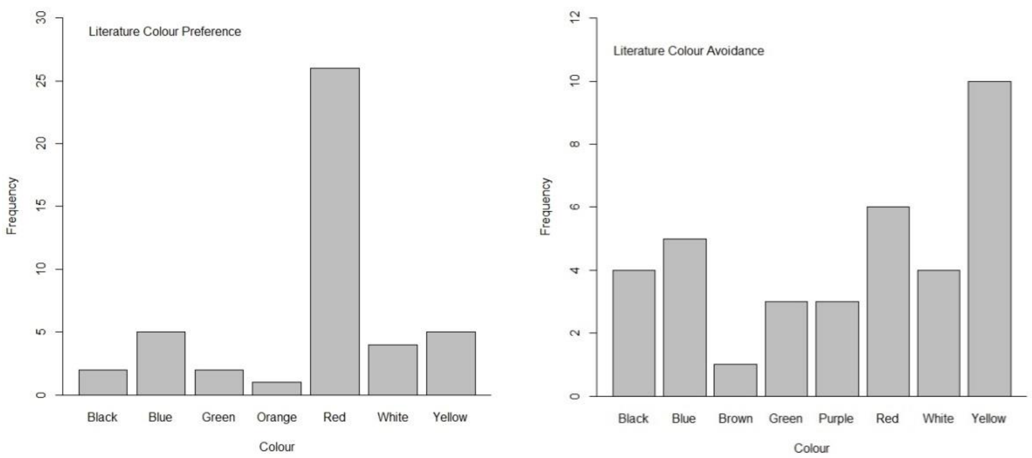


Figure 1: Number of studies demonstrating (a) a first choice preference and (b) avoidance for each colour. Data are taken from table 1.

The finding that yellow objects experience a greater level of avoidance in studies in the literature is perhaps unsurprising. Yellow and green are often colours associated with unripe berries, which become darker (red or black) once ripe and palatable (Takagi *et al*, 2012). Thus, we would predict that yellow might be avoided by frugivorous species. In Table 1, 3/10 records showing avoidance by frugivorous members of the *Turdidae* family. For insectivores, yellow is likely avoided due to its aposematic effect (Johnston & Burne, 2008, Svadova *et al,* 2009); 3/10 instances of avoidance occurred in insectivorous species. In all recorded instances where yellow was the avoided colour, red was the most preferred colour.

Although red was often preferred (Table 1, figure 1a), it was also the second most avoided colour (figure 1b) (6/36 records). When this is further examined, three instances (*Parus major, Cyanistes caeruleus* and *Sitta europaea*) come from the same paper: Marples (1933). In this paper, dyed peanuts are used (versus un-coloured) in order to examine preference, with the unsurprising result that unaltered, undyed peanuts were preferentially selected over dyed peanuts, suggesting an element of neophobia or dietary conservatism and the avoidance of an unknown resource (Thomas *et al,* 2004). This illustrates the importance of the type of controls used in assessing colour preference. Excluding this paper, there are only three documented cases of red avoidance in the literature: Baltimore oriole (*Icterus galbula*) (Smith, 1928 (in McCabe, 1961), Brown Cheeked Fulvetta (*Alcippe poioicephala*) (Duan & Quan, 2013) and Sardinian Warbler (*Sylvia melanocephala*) (Diesselhorst, 1972) all of which are omnivorous, with a diet mostly consistent of insects and fruit.

Together, the data on colour preferences and avoidances suggests that diet may be an important determinant of colour preferences in relation to food. However, there is currently a high level of taxonomic bias in the literature, with the majority of colour preference research (23/46 records) have been undertaken on hummingbirds (family: *Trochilidae*). In addition there is a high level of locational bias towards tropical regions (31/46 studies). Very little is known about the preferences of species found in the temperate regions (but see Marples (1933), particularly preferences relating to supplementary feeders. Throughout the literature, only a single report on colour preference for supplementary feeders in temperate regions was found, with this from non-peer reviewed literature. Thomas (2007), did not distinguish between species, but found that more food was consumed from blue seed feeders during summer and silver feeders during winter.

As colour preference is likely to be context specific and dependant on the activity undertaken (e.g. nest building as compared to sexual selection (Muth *et al,* 2013)), there may be a broad range of factors which may influence or impact on an individual's colour preference such as plumage colour and in the case of supplementary feeders, how plumage relates to background colour (camouflage and crypsis; Mc Pherson, 1988, Gomez & Thery, 2007), fruit and/or flower colouration (Bennett *et al*, 1994), and innate or learned preferences (Ham & Osorio, 2007). As supplementary feeders provide a source of food (rather than being the resource itself), it is likely that these factors will have a considerable role on choice. This project will be the first to examine both general and species level colour preferences in relation to supplementary seed feeders in temperate seed-feeding birds.

Perch Design

A second factor which may be important in feeder design is the size and shape of the perch. The majority of species which feed from supplementary feeders are perching birds belonging to the order Passeriformes. These species have a toe arrangement of 3 forward facing toes and 1 rear facing toe which have evolved to facilitate perching on branches (Quinn & Baumel, 1990). Although there is currently some debate, the general consensus is the feet of Passeriformes contain a network of tendons within the leg known as an Automatic Perching Mechanism (APM) or Tendon Locking Mechanism (TLM). This mechanism passively increases the length of tendons within the leg and foot, causing the toes to grip onto a perch (Galton & Shepard, 2012, Simmons & Quinn, 1994). This means that the toes naturally form an inverted U around the branch, as illustrated in figure 2. This mechanism means that any passerine species is able to land on any type of perch, providing it is strong enough to hold an individual's weight, as it is the body weight of the bird which increases the contraction of the tendon (Watson, 1869) allowing the feet to passively conform to the structure of the perch (Doyle, 2013).

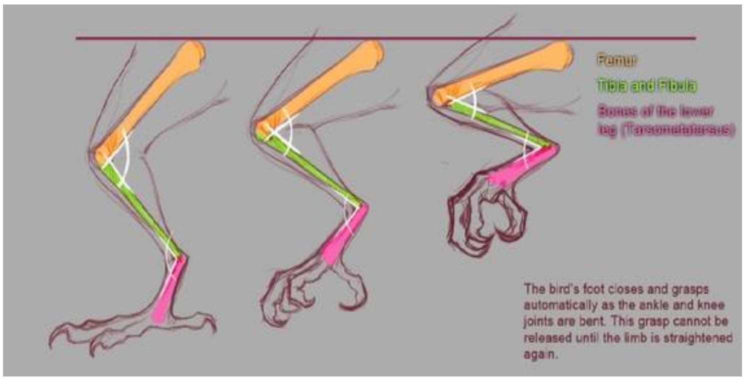


Figure 2: The mechanism by which Passerines perch (from Madrigal, 2013)

The majority of supplementary feeders available on the market are designed so birds are able to perch on branch like structures, but the size and shape of these perches is based on aesthetics rather than avian biology. In addition, there is currently no published research investigating whether the design or shape of perches affects the number of birds or species feeding at supplementary feeders. It may be possible to design a feeder that encourages desired (passerine) species such as Bullfinch (*Pyrrhula pyrrhula*) or Long Tailed Tit (*Aegithalos caudatus*) to feed unhindered, but deters other common garden species such as

Feral Pigeons (*Columba livia*); often considered pests at feeders. The act of designing a supplementary feeder to attract preferred species but deter others has been used with some success in the context of “squirrel-proof” feeders or “sparrow-proof” feeders in order to increase numbers of less dominant but more desirable species such as the Goldfinch (Shochat *et al*, 2010).

The Importance of UV in bird vision

Birds are primarily visual predators of wide variety of prey types, ranging from raptors spotting their prey from long distance to a Blue Tit seeing an aphid on the underside of a leaf (Endler & Mielke, 2005). Birds have very different visual capabilities to humans (Figure 3), the most important of which in the context of this thesis is that the avian visual spectrum extends from 300-700 nm, whereas humans only extends from 400-700 nm. This means that birds can see in the UV range, whereas humans cannot, due to different retinal morphology with (for diurnal species), each bundle of pigments containing 1 Rod (for night vision), 4 spectrally distinct cones (by comparison, humans only have 3: Red, Green, Blue) and 1 Double core photo receptor (for movement), in addition to birds having the SWS1 pigment, allowing for ultraviolet vision (Hart and Hurt, 2007). Coupled with this, species that occupy similar niches are more likely to share a higher percentage of their ocular capabilities (Hart 2001), for example Eurasian Blackbird and European Starling, both primarily ground foragers, share upwards of 95% of their visual capabilities whereas Blackbird and Blue Tit (a species which feeds mostly arboreally) only have a 70% similarity (Hart, 2001).

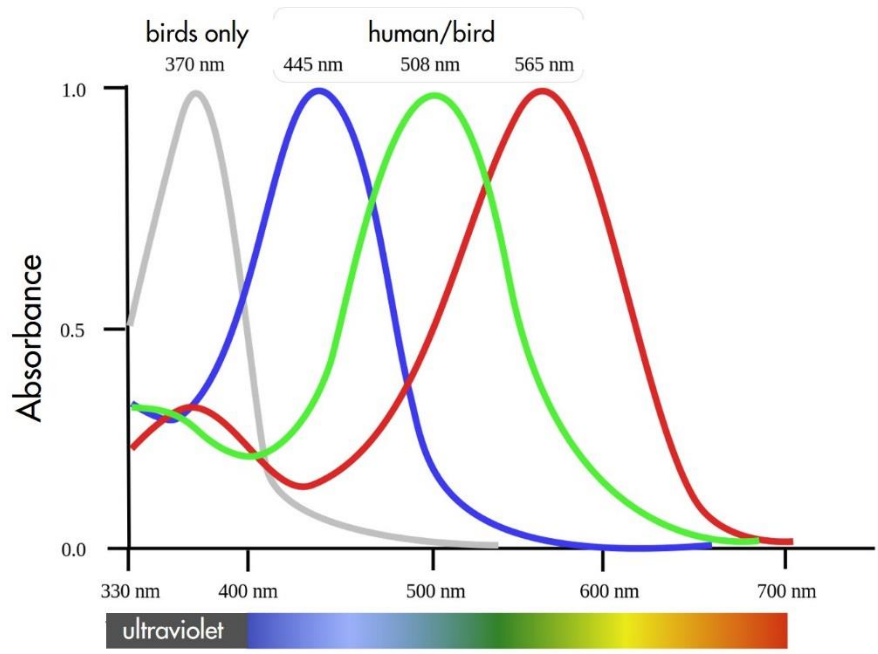


Figure 3: Comparison of Human and Avian cone sensitivity (from Smith, 2015)

As UV is used extensively by foraging birds in the search for food (Hart, 2001), and as Passeriformes have the largest ocular range of any avian order (Hart, 2001a), it is likely that UV may have an impact on an individual's preference for a certain food source over another, yet there is no consideration of the importance of UV in the context of supplementary feeding.

Aims and Objectives

The overall aim of this research is to examine the preferences of birds at different supplementary feeders, specifically focusing on colour (experiment 1) and perch design (experiment 3). This is accompanied by an investigation into human preference for the same colours offered to birds in experiment 1 (experiment 2), where data from experiments 1 and 2 will be collated in order to rank preferences across both groups and overall suggest the best feeder both from an avian perspective and a human/market research perspective. Finally the effect of a UV coating will also be investigated on coloured feeders from both the blue and red ends of the visual spectrum (experiment 4). The aims and hypotheses for each experiment are set out below.

Experiment 1: Feeder colour

The first aim is to investigate the effect of feeder colour on the feeding preferences of wild birds, both overall and at the species level. Based on previous work (table 1) showing that many species exhibit colour preferences and that these preferences differ between species, I hypothesise that:

1) There will be differences between feeder colours in the number of individual visits to feeders, and that some colours will have significantly higher visit rates than others. However, given the paucity of information regarding the feeding preference of temperate seed feeders at supplementary feeders, I cannot predict which colours will be preferred.
2) There will be differences between colours in the rate of depletion of seed within the feeders
3) Different species will have preferences (as measured by visitation rates, hypothesis 1) for different colours (table 1)

Experiment 2: Human preference for feeder colour

The second aim is to investigate the preferences for colours in humans and to compare this to avian preference. Therefore I hypothesise that:

1) There will be differences between colours in the number of individuals who prefer each coloured feeders, also that some colours will have significantly higher visitation rates than others.

2) Different demographics (Adults, Children) will have preferences (as measured by visitation rates) for different colours

Experiment 3: Perch design

The third aim is to investigate the effect of the design of the feeder perch on the feeding preferences of wild birds, both overall and at the species level. I therefore hypothesise that:

1) There will be differences between perch designs in the number of individual visits to feeders and that some perch designs will have significantly higher visit rates than others. However, once again, given the paucity of information regarding the feeding preference of temperate seed feeders at supplementary feeders, I cannot predict which colours will be preferred.
2) There will be differences between perch designs in the rate of depletion of seed within the feeders
3) Different species will have preferences (as measured by visitation rates) for different designs of perch

Experiment 4: UV Preference

The fourth aim is to investigate the effect of applying a UV coating to a bird feeder on the feeding preferences of wild birds, both overall and at the species level. Previous work has shown that birds have UV vision and it can play a crucial role in sexual selection in some species, therefore, I hypothesise that:

1) There will be differences between colours/UV coating in the number of individual visits to feeder
2) Different species will have preferences (as measured by visitation rates) for different colours

Methodology

Field Experiments (avian preference)

Study sites

Data was collected at several field sites in November 2014 to June 2015 for the three avian preference experiments. Experiment 1 (colour) was carried out in January 2015 to May 2015, experiment 3 (perch design) was carried out in March 2015-April 2015 and experiment 4 (UV) in July 2015. The sites used were chosen as they fulfilled three criteria:

1) Must contain a good number of birds and possess a good species diversity
2) Must be easily accessible for regular and frequent fieldwork
3) Must be large enough in order to accommodate the feeder frame; 2.9m long x 1.8m (1.5m above ground) tall.

Originally two field sites, compromising of 4 sample areas overall were chosen, and these sites were used for data collection between January-March 2015

1) Tophill Low Nature Reserve, nr Driffield, East Yorkshire (1 sample location; figure 4)
2) University of Hull Botanical Gardens, Thwaite Hall, Cottingham, East Yorkshire (3 sample locations; figure 5)

A further site was added in order to increase species diversity recorded, and used after March 2015.

3) Suburban gardens, Otley, West Yorkshire (1 sample location; Figure 6)

Tophill Low (TA 075,492) is located 17.5km north of the University of Hull and forms part of an active water treatment plant on the flanks of the River Hull. The site is designated a SSSI for waterfowl but contains a range of habitats including marshes, woodland and grassland (Tophill Low Nature Reserve, 2015). The location used within the Tophill Low field site is consistently used for the supplementary feeding of birds, and had an existing "feeder frame" (Figure 4). The Tophill Low site was used for all field experiments (colour, perch and UV).

The University Botanical Gardens (TA 050,329) is located 2.4km north west of the University and contains semi natural grassland, lake and broadleaf woodland (University of Hull, 2014). The site is surrounded by residential houses and so represents a more urban site than Tophill Low. Three sampling locations within the Botanical Gardens were used (figure 5). This site was used only for the colour preference experiments.

The Otley site (SE 195,472) is 88km WNW from the University of Hull, at the tip of the Leeds metropolitan district, in close proximity to open countryside, dense, unmanaged woodland and moorland (Figure 6). It was selected as it contains species that were absent from the Tophill Low and Botanical Gardens sites, and thus allowed for an increase in the species represented in the data set. These additional species included Eurasian Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*), both of which are red listed species of conservation concern (Eaton *et al,* 2013). The site is also within a suburban garden setting (similar to the Botanical Gardens) and therefore represents the type of habitat at which supplementary feeders are primarily targeted. This site was only used during the colour preference experiment.

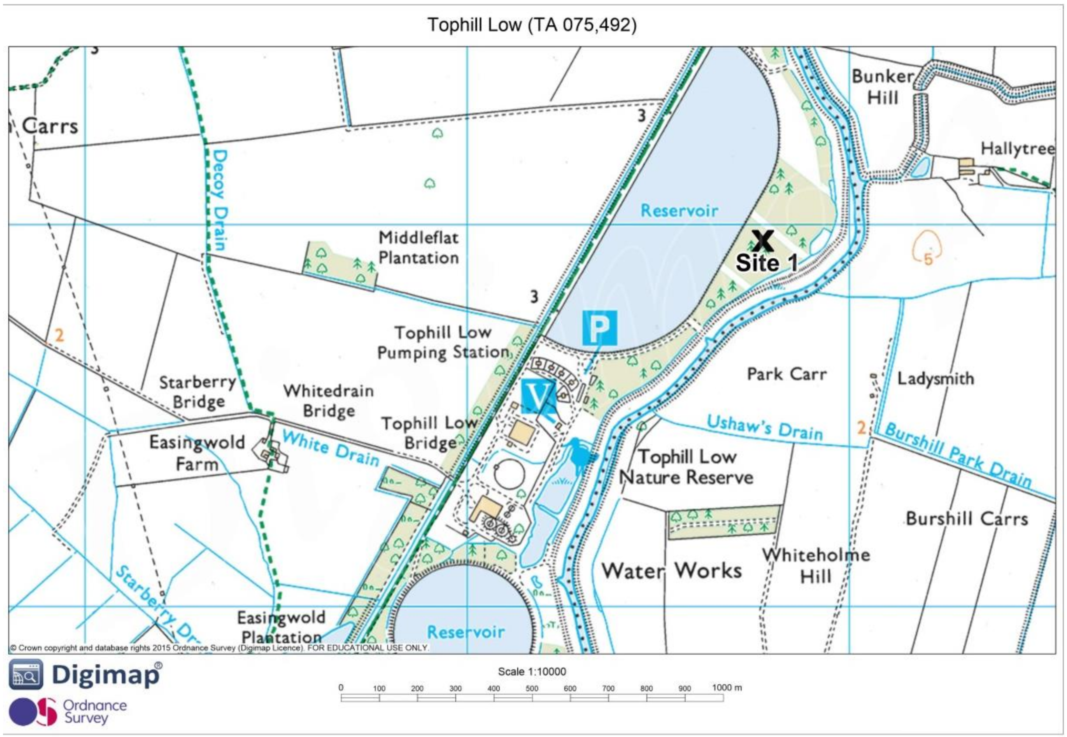


Figure 4: Sampling locations at Tophill Low Nature Reserve

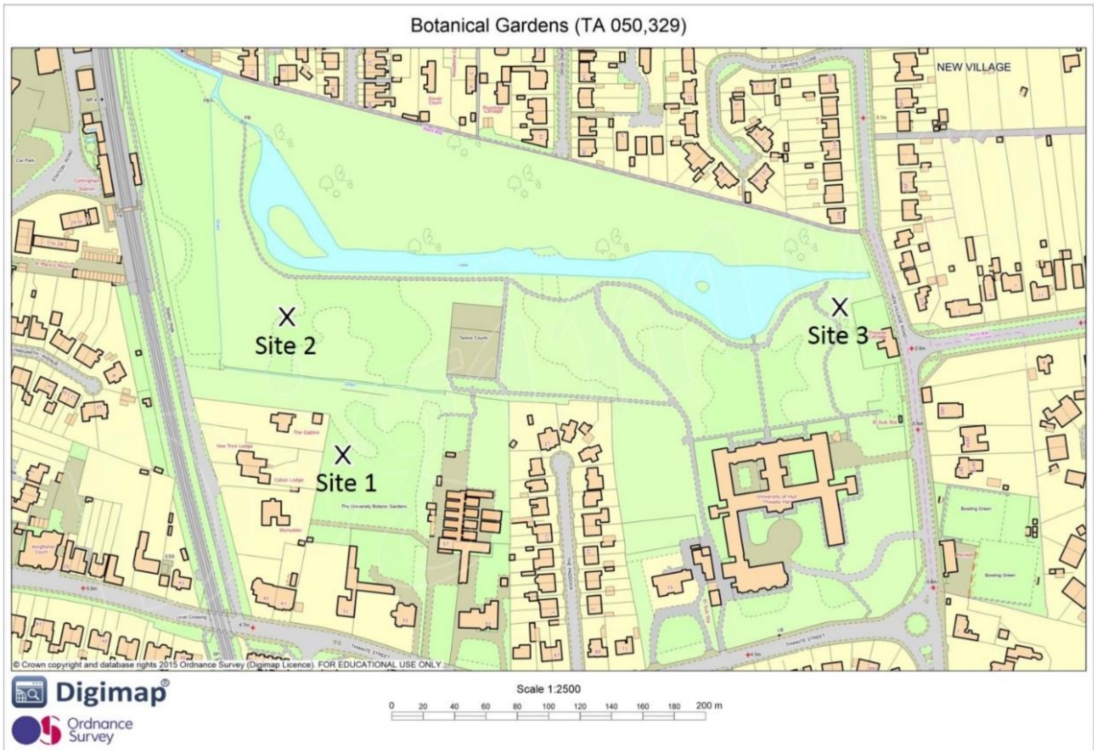


Figure 5: Sampling locations at University of Hull Botanical Gardens

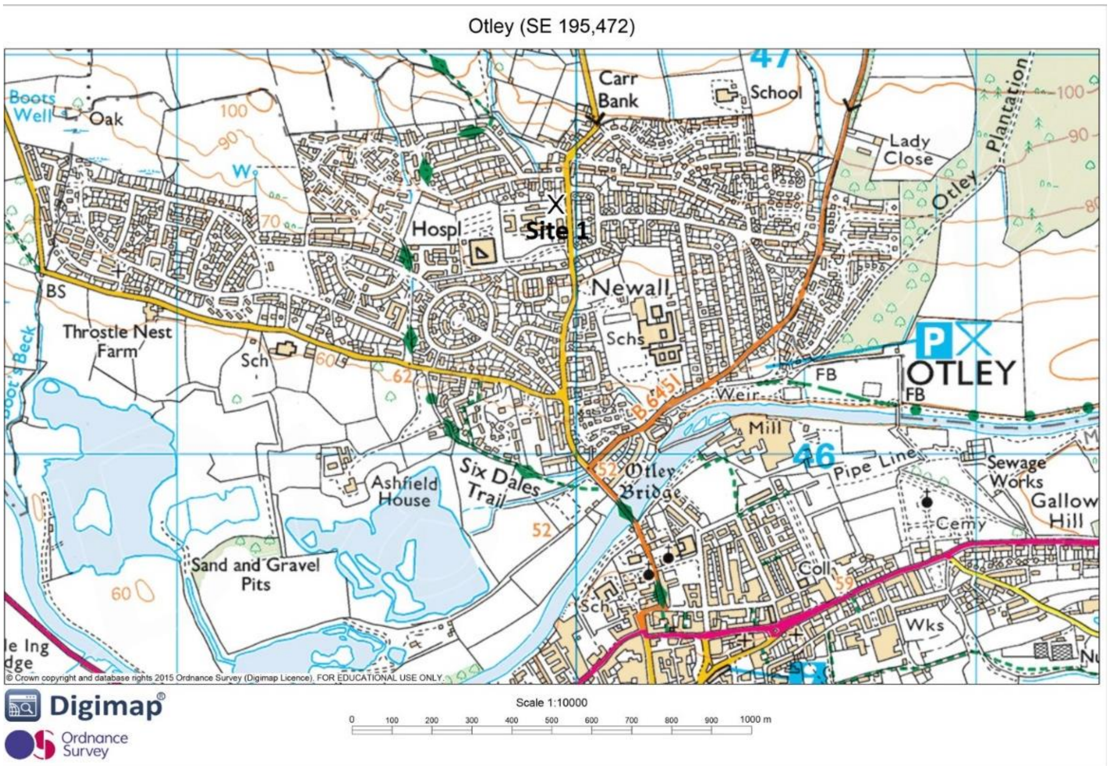


Figure 6: Sampling location at Otley Sample Site

Study Materials (Field)

Prior to data collection, a feeder frame (hereafter "frame") was erected at each sample site (figure 7 & 8), with the same frames being used for the colour, perch and UV preference experiments. The frames measured 2.9 meters long x 1.8 meters tall, and were anchored 0.3m (30cm) into the ground. The distance from the ground to the top bar was ~1.5m, considered to be the optimum height for feeders as it provides protection from most ground predators Lee et al (2005).

The frame was constructed from galvanised electrical conduit with rounded corner joints at each edge of the horizontal bar. Using galvanised metal prevented rusting or corrosion of the frame and thus meant that they could be left in position throughout the winter. A further benefit was that the frames did not provide sufficient friction to allow grey squirrels to climb to the feeders. Grey squirrels occurred in high densities at both the Tophill Low and Botanical Gardens study locations due to their utilisation of the wide ranging supplementary feeding in the area, with the species being known to damage bird feeders in addition to causing interference competition to feeding birds (Bonnington *et al,* 2014).

The frames were erected at the Botanical Gardens and Otley sites, but were not used at Tophill Low due to the existence of a very similarly sized structure already used to feed birds. At all sites, the frames were erected in areas clear of vegetation (including overhanging vegetation) to allow for a clear line of sight for the observer, but close to cover (approx. 3.0 meters) from bushes/understory vegetation in order to provide protection from predation. The Tophill Low frame was positioned marginally closer to vegetation (approx. 2.0 meters) but still allowed for a clear view by observers.

Prior to data collection, a 4-port metal feeder (Nature's Feast All Season Seed Feeder-Large) was hung from all of the frames to ensure that the birds were familiar with the sample location as a source of supplementary food. The feeder remained in place for at least 18 hours before data collection began, and was replaced and refilled each day after data collection was complete. At the Tophill Low site, existing feeders were removed prior to the positioning of experimental feeders and replaced after data collection for the day was complete.

Figure 7: Site and recording equipment at Tophill Low (during perch design experiment)

Figure 8: Site 1 at the Botanical Gardens (during colour preference experiment)

Experiment 1: Avian Colour Preference

To assess colour preference, 8 x Natures Feast Royal Seed Feeders (selected due to their durability and having metal perches and lids) were painted using Hammerite Metal Paint. The colours chosen were: Smooth Black, Smooth Blue, Smooth Dark Green, Smooth Red, Smooth White, Smooth Yellow, Hammered Silver and Purple **(**figure 9a**).** Colours were chosen on the basis of availability, and to encompass a large proportion of the avian colour spectrum (300-700) (Endler & Mielke 2005). Purple was created by mixing blue, red and white Hammerite paints at a ratio of 3:2:1.

The perches and lids of the feeders were removed and painted by hand, including the seed dispensing port. The seed inside was visible to the birds through the transparent plastic cylinder of the feeder, which remained unaltered (Figure 9b), however the seed itself was unlikely to come into contact with a painted surface at any time, in order to further reduce the risk, once painted and dry, the feeder ports and lids were checked for any discrepancies in the paintwork such as scratches or overhangs of paint, with any problems rectified before field use. In addition to this, following every day of field experiments, the feeders were checked for any scrapes/scratches or areas where the paint had been removed. This was again rectified before reuse.

In order to accurately compare the colours of each supplementary feeder (Figure 9c), photos of each lid were taken in a controlled environment with a white standard. From this, their spectral output; using their red/green versus blue/yellow ratio was calculated using ImageJ (Schneider *et al,* 2012). This allows for the visual comparability between each coloured feeder using the same scale, thereby providing both a standardised measurement for each colour and allowing for the repeatability of the colour experiment.

9a)


RED
YELLOW
BLUE
SILVER
GREEN
PURPLE
WHITE
BLACK

9b)

9c)

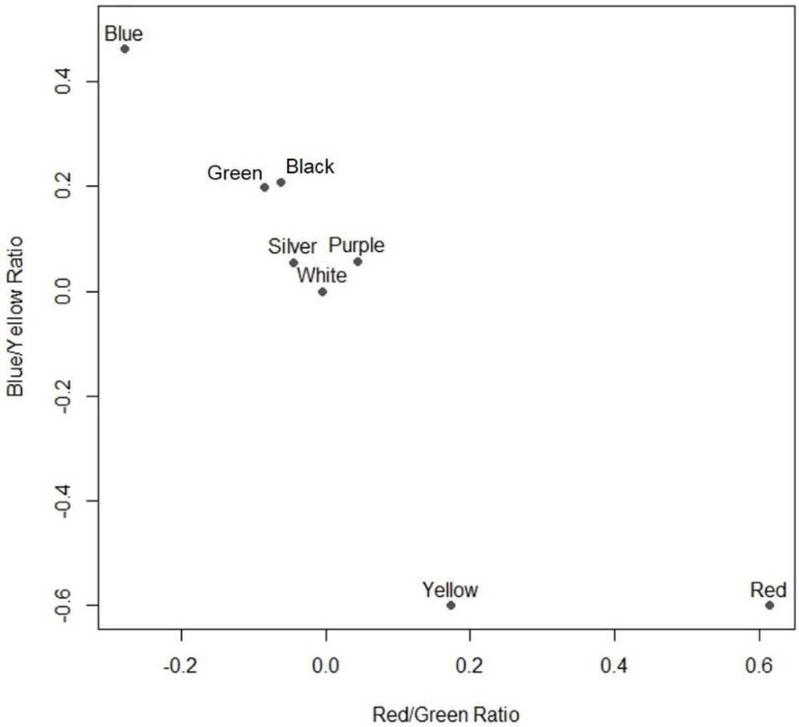

Blue
Green
Black
Silver
Purple
White
Yellow
Red
0.4
0.2
0.0
-0.2
-0.4
-0.6
Blue/Yellow Ratio
-0.2
0.0
0.2
0.4
0.6
Red/Green Ratio

Figure 9: Focused (unedited) photos of each feeder colour (a), Painted feeders in situ (b) and the comparative spectral outcomes for each coloured bird feeder (Red/Green: Blue/Yellow ratio) (c)

Figure 9b show the feeders in situ, focused unedited photos and the plotted spectral output for each coloured feeder, using the R/G/B(/Y) output (a full output can be seen in the Appendix, Table A1). As seen in figure 9c, as is expected, feeders coloured at apposing ends of the visual spectrum (e.g. blue and red) are also found at the extremes of this graph, showing their high level of spectral variability, however, there are several groups of colours which are spectrally very similar, for example Green and Black or Silver, Purple and White. This shows that although visually these colours may look distinct, spectrally they are very similar.

Experiment 3: Avian Preference of Perch Design

To assess preferences for different perch design, 8x Nature's Feast Value Seed Feeder (4 Port) were used as these had removable perches, allowing their replacement with different perch designs, the designs for which were selected in conjunction with Westland Horticulture and designed and created using a 3D Printer and associated software (SketchUp, 2015). Eight different perch designs were used, which are shown in figure 10. Perch lengths (where appropriate) are measured from the end of the perch to the juncture with the bird feeder. The 4 ports on each feeder were positioned at 90° angles to each other around the feeder, meaning that the port facing away from the observer was obstructed from view. To prevent birds feeding unobserved, the rear facing port on each feeder was covered using duct tape; meaning that per feeder there were 3 food ports available for feeding birds.

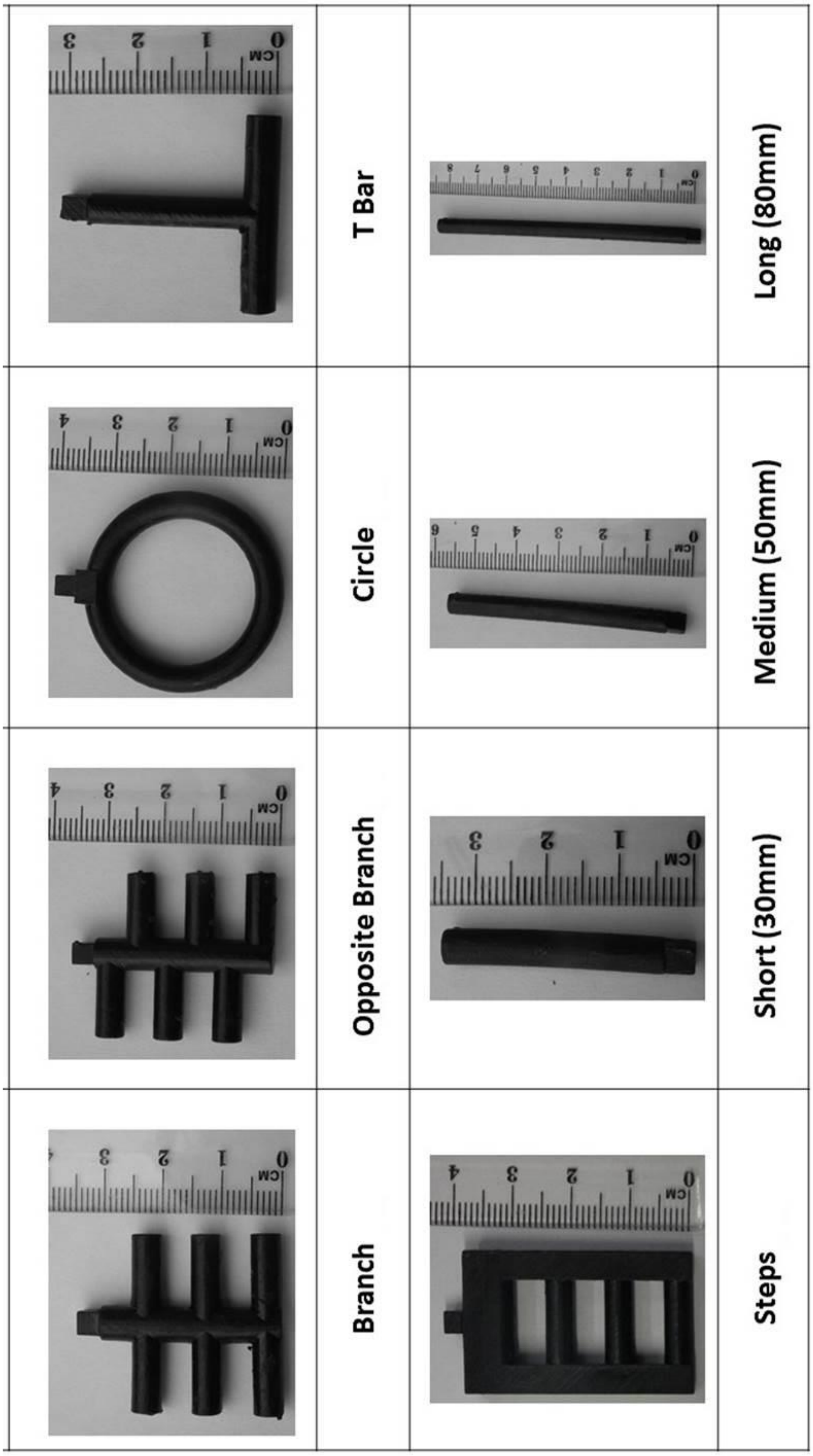


Figure 10: The 8 perch designs used in the preference experiments.

Experiment 4: Avian Preference of UV Coating

As is well documented in the literature, avian vision encompasses the UV end of the spectrum (Endler & Mielke, 2005), therefore, two sets of two coloured feeders were used; at each end of the (human) visible spectrum (red and blue), with these chosen to see if the addition of UV coating to the feeder had an effect on bird preference. For each set, the two feeders were painted with the same base colour (blue or red) with one of the two given an additional UV coating to both the lid and perch area of the feeder. The UV coating was applied using a UV reflective pen designed for security marking of equipment. Visual inspection of the feeders under UV light revealed a noticeable difference (figure 11)

Natural Light	Under UV Lamp
	
	

Figure 11: The Differences in appearances of the blue and red feeders with and without an ultraviolet coating in natural light (full spectrum) (left) versus under natural light plus an ultraviolet torch (right)

Experimental Design and Protocol

Prior to the suspension of the feeders and continuing throughout the data collection, in order to reduce the level of anthropogenic disturbance at and around the study sites; due to all the sites were in publically accessible areas, signs for the general public were erected in all of the sample locations (see appendix A2), with the aim of the signs being to inform members of the public of the research taking place, and encourage them to minimise any disturbance they may cause (such as moving close to the feeders to “have a look”).

During the data collection, the experimental protocol was the same for the Colour, Perch and UV field investigations. Firstly, the food source used to fill all of the feeders including the overnight (sustenance feeders) throughout was “Nature’s Feast, High energy, No Mess, 12 Seed Blend” (Westland Horticulture). This was to ensure continuity throughout all of the data collection, and to remove food preference influencing feeder selection as a confounding variable. In order to remove the (perceived) amount of resource available at the individual feeders, each feeder was filled with seed to visually the same level, as measured using a bar found at the top of the feeder (in order to support the lid). This bar was present at the same position in all feeders and as such was a suitable level to fill up with seed. Feeders (+seed) were then weighed in order to allow for depletion to be calculated over the course of the observation period.

In order to control for the effect of position as a selection pressure within the feeder array (either relative to other feeders or to the surrounding habitat), the feeders were displayed in a predefined random order, decided using a random number generator (Random.org, 2014), this also had the added benefit of removing any human bias in the positioning of the feeders.

During each data collection period, all eight feeders (colour and perch experiments) were displayed simultaneously, suspended at equal distances along the horizontal pole of the frame at 0.3m intervals using clear cable ties. An example of this layout can be seen in Figure 12.

For UV preference only two feeders were displayed at any one time, with each feeder being positioned 0.25m from the centre of the frame (0.5m from the other feeder; Figure 13).

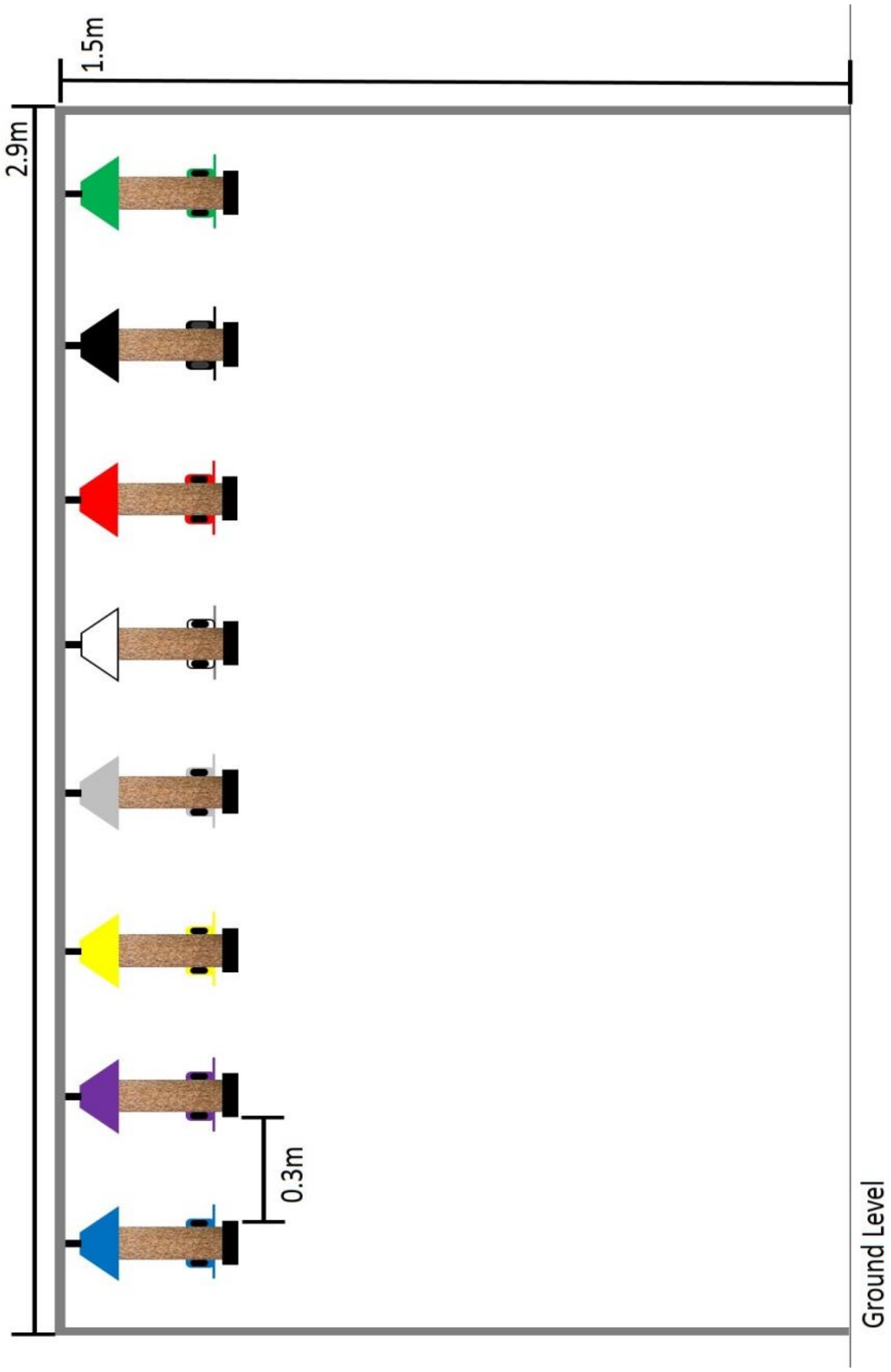


Figure 12: Experimental Field set up for both colour and perch preference.

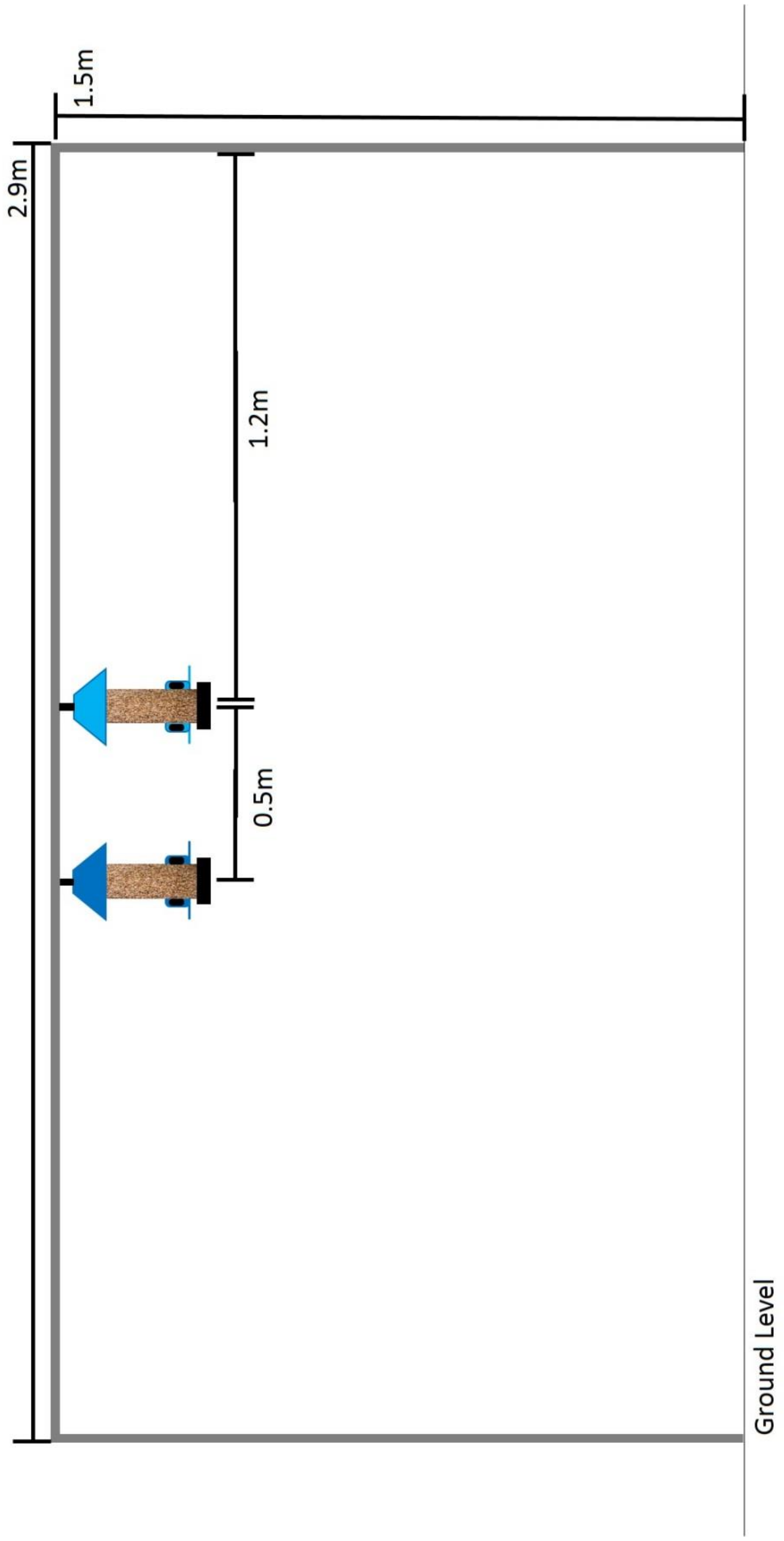


Figure 13: The feeder layout for UV feeder preferences (UV feeder on the Right)

A video camera controlled by in situ recorders (who were encouraged to remain quiet during data collection) was also used and was positioned approximately 10 meters from the frame to record each trial, with this allowing for subsequent analysis of bird visits (see below) if visit rates were too high to allow for in-situ recording (this occurred commonly at Tophill Low). As each recording did not start until the arrival of the first bird to one of the feeders, there was often a (brief) acclimatisation period before each recording period was undertaken. In total, each sample period lasted for 30 minutes (colour and perch) or 15 minutes (for UV), wherein each individual's species and preference was recorded. Due to there being no way to differentiate between individuals of the same species, each visit was counted as an independent data point. This contrasts with the approach taken during the garden birdwatch surveys run by the British Trust for Ornithology; (BTO, 2014) and Royal Society for the Protection of Birds; (RSPB, 2014) where the maximum number of birds of each species observed at any one time is recorded. This approach was not suitable for this project as only a maximum of two birds could feed simultaneously at any one feeder at any one time.

Following the 15/30 minute observation period, the video and in situ recordings were stopped and the feeders repositioned in accordance with the predetermined random order. At the end of each day of observation each feeder was weighed with the total amount of seed consumed being recorded by subtracting the end weight from the start weight. From this, depletion was adjusted to reflect the total time spent in the field (depletion per hour) to standardise the measure across all observation periods and sites. Following a 14 day period of data collection, each feeder was emptied and washed using soap and water, in addition to this each feeder was deconstructed and "deep cleaned" once a month in order to reduce potential disease transmission through the build-up of pathogens. This is in line with the recommendations of the RSPB (2008) who suggest the cleaning of feeders once visibly unclean, however due to the high numbers of birds encountered during each sample period, an increased cleaning routine was put in place as good practice (BTO,2015).

Human colour preference

Human preferences were recorded at two locations over 4 days. Data was collected at the Hull Science Festival (University of Hull, Cottingham Road, Hull, HU6 7RX) on 21st March 2015, and at Spring Garden Centre (Main Street, Sigglesthorne, Hornsea HU11 5QL) on the 19, 20 & 27th June 2015. These two locations provided a cross section of the general public likely to purchase and use of bird feeders.

The same coloured bird feeders as used in Avian colour preference experiments were positioned in a line on the table, with containers corresponding to those colours situated directly behind. An example of the experimental layout can be seen in figure 14. As with the bird colour preference experiments, the order in which the colours were positioned was randomised and feeders were repositioned every 30 minutes throughout each data collection day.

Figure 14: Example of experimental layout for Human colour preference

At each site, willing participants (members of the public) were invited to place a single plastic token in the bucket of their most preferred feeder colour - the one that they considered themselves most likely to buy. This was used as an indicator for preference. Marked counters were used to distinguish between the preferences of adults (those who appeared to be over 18) and children (apparently under 18). Adults and children were differentiated due to the large number of children present at the Science Festival, to allow them to participate in the activity, and the same approach was continued at the garden centre. The number of tokens in each container was counted at the end of the day (Science Festival) and every 2 hours (Garden Centre).

Data Analysis

For the colour, perch and UV preference data, the number of visits to the feeder per observation period was analysed using a generalised linear mixed effects model (*lmer*) using the package *lme4* (Bates *et al,* 2015) in R v3.2.1 (R Core Team, 2015). A Poisson error distribution, as appropriate for count data, was used for the analysis, and observation period was added as a random effect to account for the fact that only one colour (or perch design) could be chosen at any one time. An observation level random effect was added to account for over dispersion in the data (Benjamini & Hochberg, 1995). For the data on colour preference (experiment 1), site was added as an additional random effect, but as all data were collected from the same site for experiments 3 and 4 (perch and UV) this was not needed. To test whether there were significant differences in visit rates between colours, data were relevelled such that each colour was set as the intercept for the model, allowing pairwise comparisons between colours to be made. To assess whether there was an overall effect of colour, the *anova*() function in the package *lmerTest* was used (Schaalje *et al,* 2002). Data were firstly analysed for all species combined, before being analysed separately for each of the species with over 100 independent visits to the feeder array during data collection for colour, perch and UV data collection experiment. To analyse seed depletion rate for both colour and perch experiments, a linear mixed effects model (*lme*) using the package *nlme* (Pinheiro & Bates, 2000) was used with site and observation period as random effects with the assumptions of the model being checked by the visual inspection of plots of the residuals in addition to the quantile-quantile plots. In order analyse whether human's had a preference for feeder colour, a linear mixed effect model (*lme* in the package *nlme* (Pinheiro & Bates, 2000) with site and sample number as random effects.

To evaluate whether there is an overall "best" colour or perch design, two figures were plotted; firstly, the mean number of counters from the human data (mean human preference) was combined with the mean number of visits from the avian data (mean avian preference) for each colour at varying ratios (figure 22) in order to allow recommendations to be made as to the most preferred feeder for birds or the most marketable coloured feeder. In addition, we plotted the mean human and avian preferences for each colour (figure 21). These figures will form the basis of our recommendation to Westland Horticulture, the sponsors of the research.

Results

Experiment 1: Colour Preference

Overall, 7535 individual visits to the feeders were recorded, representing 11 different species, although not all species were recorded at all sites. The numbers of individual visits for each species, at each site, are presented in Table 2. The data from all sites were combined prior to analysis to determine overall colour preferences. For those species for which more than 100 observations were recorded, species level colour preference analyses were also carried out (Greenfinch, Robin, Coal Tit, Great Tit, Blue Tit, House Sparrow and Starling; table 2). Other species occurred only rarely at the feeders.

Table 2. A summary of the frequency of species occurrence and total number of visits to the feeders recorded at the Botanical Gardens, Tophill Low and Otley sample site. This was under the assumption that every visit to a feeder is a unique decision as the actual numbers of individual birds involved within each data collection experiments is unknown.

Species	**Scientific Name**	**Botanical Gardens**	**Tophill**	**Otley**	**Total**
Long Tailed Tit	*Aegithalos caudatus*	2	3	-	5
Bullfinch	*Pyrrhula pyrrhula*	5	-	-	5
Goldfinch	*Carduelis carduelis*	-	3	-	3
Greenfinch	*Chloris chloris*	-	1	135	136
Robin	*Erithacus rubecula*	171	12	105	288
Coal Tit	*Periparus ater*	311	116	109	536
Great Tit	*Parus major*	833	1564	13	2410
Blue Tit	*Cyanistes caeruleus*	810	1824	629	3263
Marsh Tit	*Poecile palustris*	-	16	-	16
House Sparrow	*Passer domesticus*	-	-	701	701
Starling	*Sturnus vulgaris*	-	-	172	172
Site Total		2132	3539	1864	7535

Overall Avian Colour Preference.

There was a significant effect of colour on the number of visits birds made to the bird feeders, (LME, $F_{7, 875}$=6.120, P < 0.001; Figure 15). Pairwise comparisons of the number of visits to each colour revealed that there are significantly more visits to the silver feeder than to any other colour, and significantly more visits to the green feeder than to any of the remaining colours. In addition, birds make significantly fewer visits to the yellow and red feeders than they do to the other colours (P < 0.001; table 3), although there is no difference between the number of visits to red and yellow feeders. Black, blue, purple and white feeders received significantly more visits than red and yellow feeders, and significantly fewer than silver and green, but there was no difference between these 4 colours in the number of visits (table 3, Figure 15).

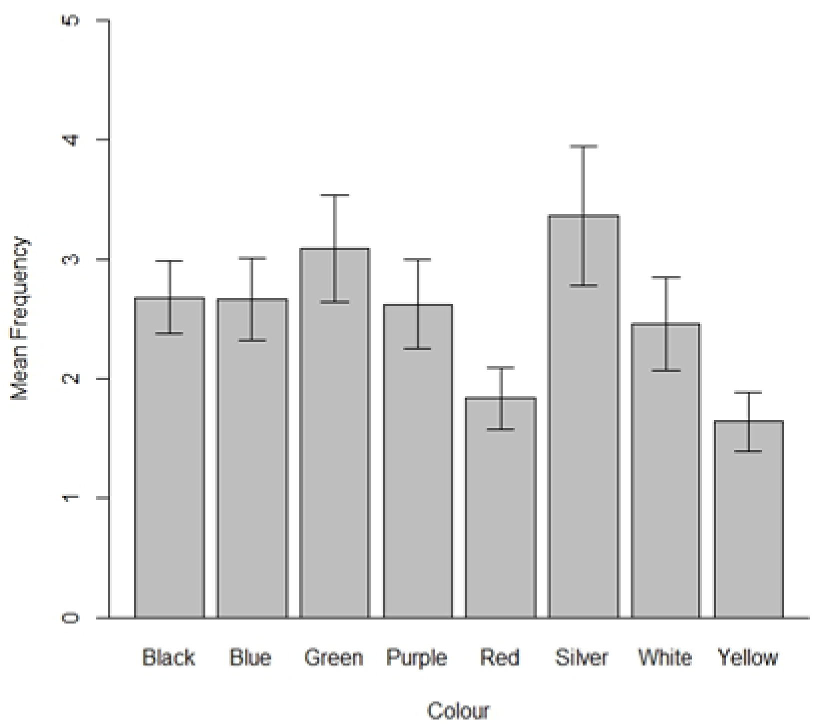


Figure 15: Mean frequency of visits to each colour feeder per 30 minute observation period, pooled across all sites. Error bars represent ±1 S.E.

Table 2**:** GLM output for pairwise comparison of visits to coloured feeders (all sites and all species combined). The cells above the diagonal show the z value, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the estimate (effect size) and associated standard error.

Colour Totals	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	z= -0.135 p=0.892 Adj p=0.892	**z= 3.278** **p=0.001** **Adj p=0.001**	z= -0.499 p=0.618 Adj p=0.666	**z= -7.614** **p <0.001** **Adj p <0.001**	**z= 5.378** **p <0.001** **Adj p <0.001**	z= -1.863 p=0.062 Adj p=0.076	**z=-9.569** **p <0.001** **Adj p <0.001**
Blue	Est=-0.006 SE= 0.045	**x**	**z= 3.413** **p <0.001** **Adj p 0.001**	z= -0.363 p=0.716 Adj p=0.743	**z= -7.483** **p <0.001** **Adj p <0.001**	**z= 5.512** **p <0.001** **Adj p <0.001**	z= -1.728 p=0.084 Adj p=0.098	**z= -9.44** **p <0.001** **Adj p <0.001**
Green	Est=0.142 SE=0.043	Est=0.148 SE=0.043	**x**	**z=-3.774** **p <0.001** **Adj p <0.001**	**z= -10.765** **p <0.001** **Adj p <0.001**	**z= 2.115** **p=0.034** **Adj p=0.046**	**z= -5.128** **p <0.001** **Adj p <0.001**	**z= -12.65** **p <0.001** **Adj p <0.001**
Purple	Est=-0.022 SE=0.045	Est=-0.016 SE=0.045	Est=-0.164 SE=0.043	**x**	**z= -7.129** **p <0.001** **Adj p <0.001**	**z= 5.870** **p <0.001** **Adj p <0.001**	z= -1.365 p=0.172 Adj p=0.193	**z= -9.093** **p <0.001** **Adj p <0.001**
Red	Est=-0.378 SE=0.050	Est=-0.372 SE=0.050	Est=-0.519 SE=0.048	Est=-0.355 SE=0.050	**x**	**z= 12.751** **p <0.001** **Adj p <0.001**	**z= 5.793** **p <0.001** **Adj p <0.001**	z= -2.042 p=0.041 Adj p=0.052
Silver	Est=0.228 SE=0.042	Est=0.234 SE=0.042	Est=0.086 SE=0.041	Est=0.250 SE=0.043	Est=0.606 SE=0.047	**x**	**z= -7.212** **p <0.001** **Adj p <0.001**	**z= -14.586** **p <0.001** **Adj p <0.001**
White	Est=-0.085 SE=0.046	Est=-0.079 SE=0.046	Est=-0.227 SE=0.044	Est=-0.063 SE=0.046	Est=0.292 SE=0.050	Est=-0.313 SE=0.043	**x**	**z= -7.779** **p <0.001** **Adj p <0.001**
Yellow	Est=-0.491 SE=0.051	Est=-0.485 SE=0.051	Est=-0.633 SE=0.050	Est=-0.469 SE=0.052	Est=-0.114 SE=0.056	Est=-0.719 SE=0.049	Est=-0.406 SE=0.052	**x**

Species Specific Colour Preference

Blue Tit

There was a significant effect of colour on the number of visits that Blue Tits made to the different coloured feeders (LME, $F_{7,\ 749.73}$=4.3575, P <0.001; Figure 16a). Pairwise comparison of the number of visits to each colour feeder revealed that Blue Tits made significantly fewer visits to the yellow feeder than to all other colours (P<0.05), with the exception of red. In addition, significantly fewer visits were made to the red feeder than to all other colours (P <0.05) except green, white and yellow. There was no significant difference in the number of visits to the silver, green, blue, purple, black and white feeders (Table 4).

Great Tit

There was a significant effect of colour on the number of visits Great Tits made to bird feeders (LME, $F_{7,\ 259}$=2.6709, P=0.01099; Figure 16b). Pairwise comparisons of the number of visits to each colour feeder reveal that Great Tits made significantly more visits to the green feeder than to the red feeder (P <0.001) . In addition to this, birds visit the yellow feeder significantly less than every other coloured feeder, except red (P <0.05). Great Tits do not appear to have a preference between the black, blue, green, purple, silver or white coloured feeders (Table 5).

Coal Tit

Although there is an significant effect of colour on the number of visits Coal Tits made to bird feeders ($F_{7, 329}$=3.7962, P=0.0005588; Figure 16c) in the overall model, Pairwise comparison shows no significant differences between the birds preference for any colour over others (P>0.05); (Table 6).

House Sparrow

There was a significant effect of colour on the number of visits made to the bird feeders by House Sparrows ($F_{7, 399}$=11.139, P < 0.001; Figure 16d). Pairwise comparisons of the number of visits to each coloured feeder revealed that birds make significantly fewer visits to the yellow feeder than every other coloured feeder (P <0.01), in addition to visiting the green feeder significantly more than the purple (P <0.01), white (P <0.001), red (P <0.001) or yellow (P <0.001) feeders. In addition to this, the purple and red feeders were visited significantly less than the black (purple P=0.009, red <0.0014), blue (purple P=0.008, red P <0.001) and green (purple P=0.003), red P <0.001) coloured feeders. There was no difference in the number of visits to the green, black, blue and silver feeders. (Table 7).

European Robin

There was a significant effect of colour on the number of visits Robins made to the bird feeders (LME, $F_{7, 518}$=3.1033, P = 0.003243; Figure 16e). Pairwise comparisons of the number of visits to each colour revealed that birds make significantly more visits to the black feeder than to the purple (P <0.001) and white (P=0.001) coloured feeders. Robins do not seem to have a preference between the blue, green, red, silver or yellow feeders. (Table 8).

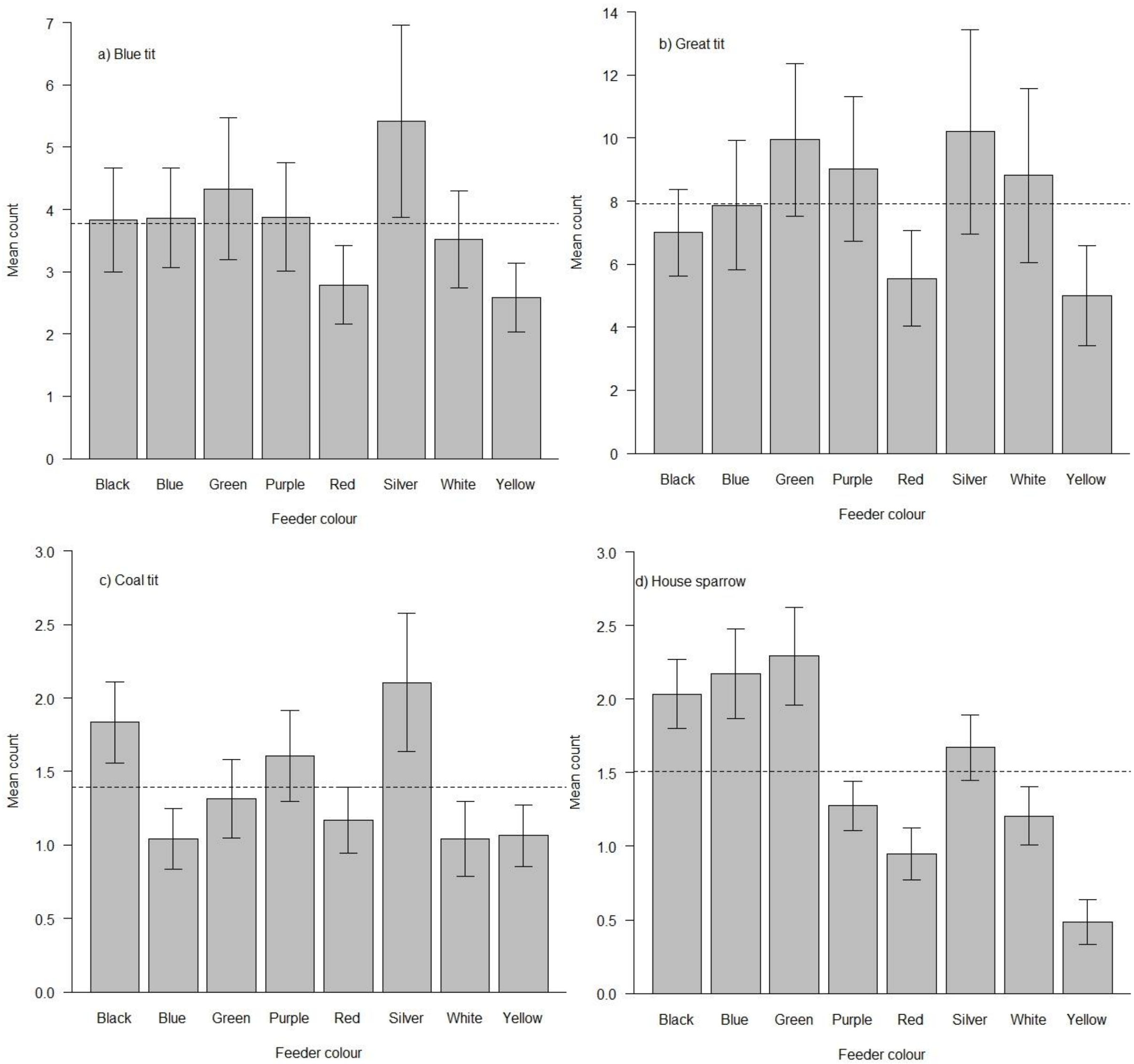
Greenfinch

There was no significant effect of colour on the number of visits Greenfinch made to the bird feeders ($F_{7, 140}$=1.3.3827, P = 0.2172; Figure 16f). Pairwise comparison of the number of visits to each colour revealed that Greenfinch do not seem do have a preference between any different colour of bird feeder (Table 9).

Starling

There was no significant effect of colour on the number of visits birds made to the bird feeders ($F_{7, 84}$=1.2325, P =0.2944; Figure 16g). Pairwise comparison of the number of visits to each colour revealed that Starlings to don’t seem to have a preference between any different colour of bird feeder (Table 10).

Species Specific Preference Graphs



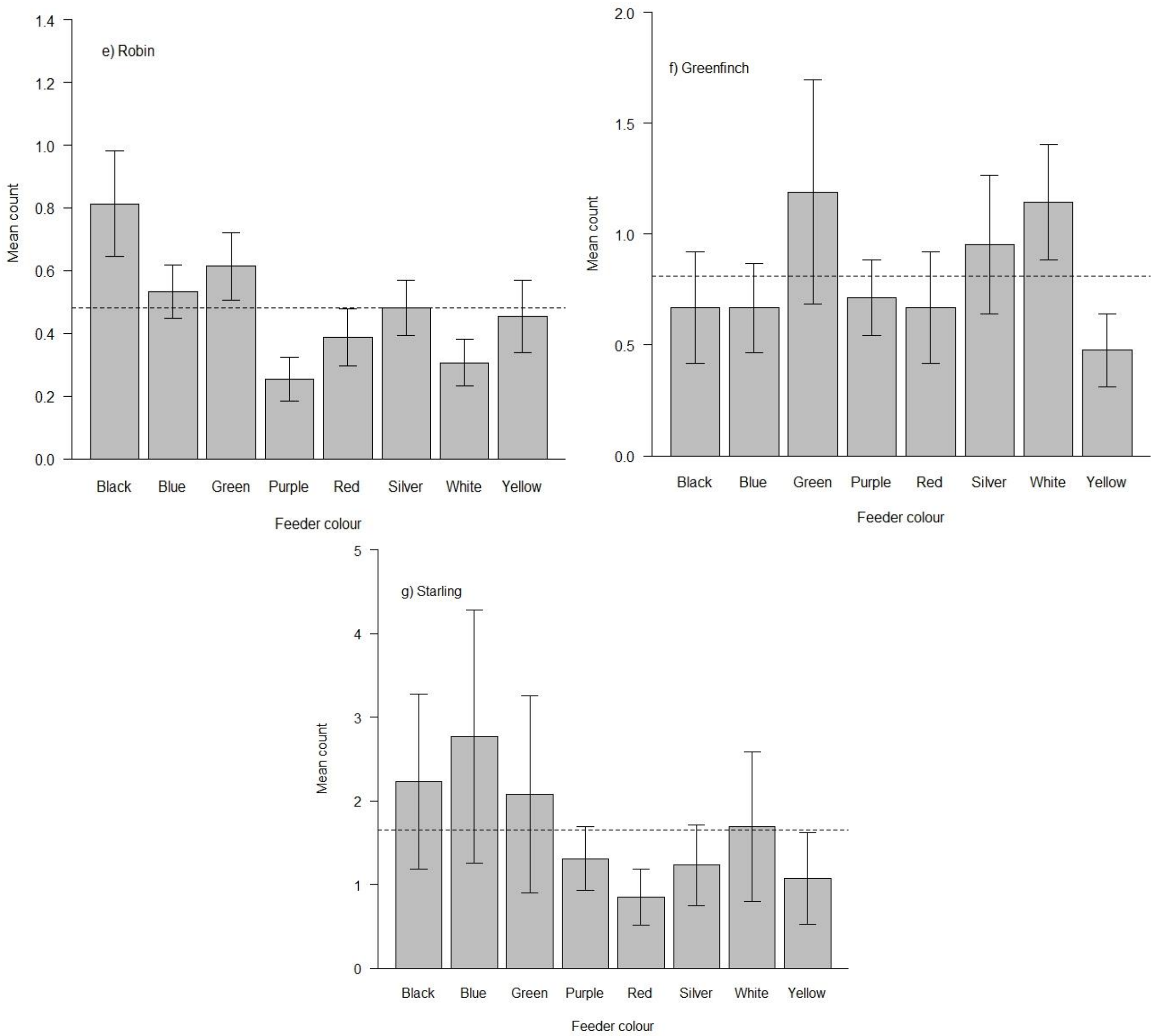


Figure 16: The average number of visits to feeders of all colours per observation period, pooled across all sites, for the 7 most frequently recorded species (with over 100 individual visitations). Blue Tit (*Cyanistes caeruleus*) (a), Great Tit (*Parus major*) (b), Coal Tit (*Periparus ater*) (c) and House Sparrow (*Passer domesticus*) (d), European Robin (*Erithacus rubecula*) (e), European Greenfinch (*Carduelis carduelis*) (f) and European Starling (*Sturnus vulgaris*) (g). Due to differences in frequency of occurrence between species, note the difference in Y axis. The dashed line indicates the expected values for mean visitation to each colour of feeder if the level of visitation was equal for each coloured feeder.

Species Specific Colour Preference: GLM output

Tables 4-10: The GLM output for pairwise comparison of visits to coloured feeders for individually analysed species: Blue Tit (Table 4), Great Tit (Table 5), Coal Tit (Table 6), House Sparrow (Table 7), Robin (Table 8), Greenfinch (Table 9) and Starling (Table 10) from all sites and all data collection periods. For each GLM output, the cells above the diagonal show the z value, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the estimate (effect size) and associated standard error.

Table 4: GLM output of pairwise colour comparison for Blue Tit (*Cyanistes caeruleus*)

Blue Tit	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	z= -0.147 p=0.883 Adj p=0.951	z=-0.535 p=0.592 Adj p=0.829	z=-0.078 p=0.938 Adj p=0.972	**z=-2.668 p=0.008 Adj p=0.035**	z=0.495 p=0.621 Adj p=0.827	z=-0.864 p=0.388 Adj p=0.724	**z=-3.001 p=0.003 Adj p=0.025**
Blue	Est=-0.019 SE= 0.129	**x**	z=-0.389 p=0.698 Adj p=0.849	z=0.069 p=0.945 Adj p=0.945	**z=-2.521 p=0.012 Adj p=0.041**	z=0.642 p=0.521 Adj p=0.810	z=-0.716 p=0.474 Adj p=0.780	**z=-2.855 p=0.004 Adj p=0.024**
Green	Est=-0.069 SE=0.129	Est=-0.050 SE=0.130	**x**	z=0.457 p=0.647 Adj p=0.824	z=-2.132 p=0.033 Adj p=0.084	z=1.028 p=0.304 Adj p=0.608	z=-0.326 p=0.744 Adj p=0.833	**z=-2.466 p=0.014 Adj p=0.042**
Purple	Est=-0.010 SE=0.128	Est=0.009 SE=0.129	Est=0.059 SE=0.130	**x**	**z=-2.589 p=0.010 Adj p=0.039**	z=0.5573 p=0.566 Adj p=0.835	z=-0.785 p=0.432 Adj p=0.757	**z=-2.922 p=0.003 Adj p=0.024**
Red	Est=-0.358 SE=0.134	Est=-0.340 SE=0.135	Est=-0.289 SE=0.136	Est=0.348 SE=0.135	**x**	**z=3.153 p=0.002 Adj p=0.023**	z=1.810 p=0.070 Adj p=0.164	z=-0.334 p=0.739 Adj p=0.862
Silver	Est=0.063 SE=0.127	Est=0.082 SE=0.128	Est=0.133 SE=0.130	Est=0.073 SE=0.128	Est=0.422 SE=0.134	**x**	z=-1.356 p=0.175 Adj p=0.377	**z=-3.485 p <0.001 Adj p=0.013**
White	Est=-0.112 SE=0.130	Est=-0.093 SE=0.130	Est=-0.043 SE=0.131	Est=-0.102 SE=0.130	Est=0.246 SE=0.136	Est=-0.176 SE=0.129	**x**	z=-2.145 p=0.032 Adj p=0.090
Yellow	Est=-0.405 SE=0.135	Est=-0.387 SE=0.135	Est=-0.336 SE=0.136	Est=-0.396 SE=0.135	Est=-0.047 SE=0.141	Est=-0.469 SE=0.135	Est=-0.293 SE=0.137	**x**

Table 5: GLM output of pairwise colour comparison for Great Tit (*Parus major*).

Great Tit	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	z= -0.582 p=0.560 Adj p=0.824	z= 0.747 p=0.455 Adj p=0.739	z=-0.108 p=0.914 Adj p=0.931	z= -2.744 p=0.006 Adj p=0.068	z= -0.061 p=0.951 Adj p=0.949	z= -0.818 p=0.414 Adj p=0.759	**z= -3.961** **p <0.001** **Adj p=0.008**
Blue	Est=-0.106 SE= 0.183	**x**	z= 1.328 p=0.184 Adj p=0.552	z= 0.472 p=0.637 Adj p=0.902	z= -2.169 p=0.030 Adj p=0.157	z= 0.519 p=0.604 Adj p=0.849	z= -0.238 p=0.812 Adj p=0.872	**z= -3.411** **p <0.001** **Adj p=0.015**
Green	Est=0.134 SE=0.180	Est=0.240 SE=0.181	**x**	z= -0.852 p=0.394 Adj p=0.739	**z=-3.474** **p <0.001** **Adj p=0.017**	z= -0.806 p=0.420 Adj p=0.760	z=-1.559 p=0.119 Adj p=0.371	**z=-4.688** **p <0.001** **Adj p=0.002**
Purple	Est=-0.020 SE=0.181	Est=0.087 SE=0.183	Est=-0.154 SE=0.180	**x**	z= -2.636 p=0.008 Adj p=0.088	z=0.047 p=0.962 Adj p=0.981	z= -0.709 p=0.478 Adj p=0.758	**z= -3.870** **p <0.001** **Adj p=0.008**
Red	Est=-0.524 SE=0.191	Est=-0.418 SE=0.192	Est=-0.658 SE=0.189	Est=-0.504 SE=0.191	**x**	z= 2.676 p=0.007 Adj p=0.084	z=1.930 p=0.054 Adj p=0.285	z= -1.265 p=0.206 Adj p=0.501
Silver	Est=-0.011 SE=0.181	Est=0.095 SE=0.184	Est=-0.145 SE=0.180	Est=0.009 SE=0.182	Est=0.513 SE=0.192	**x**	z= -0.755 p=0.450 Adj p=0.745	**z= -3.905** **p <0.001** **Adj p=0.007**
White	Est=-0.151 SE=0.184	Est=-0.044 SE=0.186	Est=-0.285 SE=0.183	Est=-0.131 SE=0.185	Est=0.374 SE=0.194	Est=-0.139 SE=0.185	**x**	**z= -3.176** **p=0.002** **Adj p=0.030**
Yellow	Est=-0.785 SE=0.198	Est=-0.678 SE=0.199	Est=0.919 SE=0.195	Est=-0.765 SE=0.198	Est=-0.260 SE=0.206	Est=-0.773 SE=0.198	Est=-0.634 SE=0.200	**x**

Table 6: GLM output of pairwise colour comparison for Coal Tit (*Periparus ater*).

Coal Tit	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	z=-3.178 p=0.002 Adj p=0.088	z=-2.162 p=0.031 Adj p=0.153	z=-1.040 p=0.299 Adj p=0.679	z=-2.663 p=0.008 Adj p=0.150	z=0.258 p=0.796 Adj p=0.925	z=-3.277 p=0.001 Adj p=0.151	z=-2.996 p=0.003 Adj p=0.112
Blue	Est=-0.616 SE= 0.194	**x**	z=1.063 p=0.288 Adj p=0.743	z=2.188 p=0.029 Adj p=0.194	z=0.546 p=0.585 Adj p=0.814	z=3.445 p=<0.001 Adj p=0.085	z=-0.116 p=0.908 Adj p=0.892	z=0.191 p=0.848 Adj p=0.988
Green	Est=-0.398 SE=0.184	Est=0.218 SE=0.205	**x**	z=1.144 p=0.253 Adj p=0.496	z=-0.518 p=0.605 Adj p=0.941	z=2.439 p=0.015 Adj p=0.188	z=-1.179 p=0.239 Adj p=0.657	z=-0.869 p=0.385 Adj p=0.766
Purple	Est=-0.183 SE=0.176	Est=0.433 SE=0.198	Est=0.215 SE=0.188	**x**	z=-1.652 p=0.099 Adj p=0.408	z=1.307 p=0.191 Adj p=0.731	z=-2.297 p=0.022 Adj p=0.165	z=-1.993 p=0.046 Adj p=0.203
Red	Est=-0.501 SE=0.188	Est=0.114 SE=0.209	Est=-0.104 SE=0.200	Est=-0.318 SE=0.193	**x**	z=2.929 p=0.003 Adj p=0.162	z=-0.661 p=0.509 Adj p=0.728	z=-0.354 p=0.723 Adj p=0.837
Silver	Est=0.044 SE=0.169	Est=0.659 SE=0.191	Est=0.442 SE=0.181	Est=0.227 SE=0.174	Est=0.545 SE=0.186	**x**	z=-3.559 p=<0.001 Adj p=0.112	z=-3.248 p=0.001 Adj p=0.097
White	Est=-0.640 SE=0.195	Est=-0.225 SE=0.215	Est=-0.243 SE=0.206	Est=-0.457 SE=0.199	Est=-0.139 SE=0.210	Est=-0.684 SE=0.192	**x**	z=0.305 p=0.760 Adj p=0.870
Yellow	Est=-0.575 SE=0.192	Est=0.041 SE=0.213	Est=-0.177 SE=0.204	Est=-0.392 SE=0.197	Est=-0.074 SE=0.208	Est=-0.619 SE=0.190	Est=0.065 SE=0.214	**x**

Table 7: GLM output of pairwise colour comparison for House Sparrow (*Passer domesticus*).

House Sparrow	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	z=0.048 p=0.961 Adj p=0.961	z= 0.470 p=0.639 Adj p=0.688	**z= -2.785** **p=0.005** **Adj p=0.009**	**z= -4.383** **p <0.001** **Adj p <0.001**	z= -1.354 p=0.176 Adj p=0.214	**z= -3.263** **p=0.001** **Adj p=0.003**	**z= -6.600** **p <0.001** **Adj p <0.001**
Blue	Est=0.008 SE= 0.157	**x**	z= 0.422 p=0.673 Adj p=0.698	**z= -2.838** **p=0.005** **Adj p=0.008**	**z= -4.440** **p <0.001** **Adj p <0.001**	z= -1.406 p=0.160 Adj p=0.203	**z= -3.319** **p <0.001** **Adj p=0.002**	**z= -6.649** **p <0.001** **Adj p <0.001**
Green	Est=0.072 SE=0.155	Est=0.065 SE=0.155	**x**	**z= -3.243** **p=0.001** **Adj p=0.003**	**z= -4.822** **p <0.001** **Adj p <0.001**	z= -1.823 p=0.068 Adj p=0.101	**z= -3.72** **p <0.001** **Adj p=0.001**	**z= 6.959** **p <0.001** **Adj p <0.001**
Purple	Est=-0.484 SE=0.174	Est=-0.492 SE=0.173	Est=-0.557 SE=0.172	**x**	z= -1.691 p=0.090 Adj p=0.127	z=1.459 p=0.145 Adj p=0.193	z=-0.488 p=0.625 Adj p=0.701	**z= -4.324** **p <0.001** **Adj p <0.001**
Red	Est=-0.825 SE=0.188	Est=-0.833 SE=0.188	Est=-0.899 SE=0.186	Est=-0.342 SE=0.202	**x**	**z= 3.117** **p=0.002** **Adj p=0.004**	z= 1.212 p=0.225 Adj p=0.263	**z= -2.811** **p=0.005** **Adj p=0.009**
Silver	Est=-0.222 SE=0.164	Est=-0.230 SE=0.163	Est=-0.295 SE=0.162	Est=0.262 SE=0.180	Est=0.604 SE=0.194	**x**	z= -1.947 p=0.051 Adj p=0.080	**z= -5.55** **p <0.001** **Adj p <0.001**
White	Est=-0.578 SE=0.177	Est=-0.585 SE=0.176	Est=-0.650 SE=0.175	Est=-0.094 SE=0.192	Est=0.248 SE=0.205	Est=-0.356 SE=0.183	**x**	**z= -3.909** **p <0.001** **Adj p <0.001**
Yellow	Est=-1.544 SE=0.234	Est=-1.552 SE=0.233	Est=-0.162 SE=0.232	Est=-1.060 SE=0.245	Est=-0.718 SE=0.256	Est=-1.322 SE=0.238	Est=-0.966 SE=0.247	**x**

Table 8: GLM output of pairwise colour comparison for European Robin (*Erithacus rubecula*).

Robin	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	z=-1.415 p=0.157 Adj p=0.426	z=-1.053 p=0.292 Adj p=0.631	**z=-3.693** **p <0.001** **Adj p=0.018**	z=-2.725 p=0.006 Adj p=0.121	z=-1.745 p=0.081 Adj p=0.277	**z=-3.251** **p=0.001** **Adj p=0.049**	z=-2.387 p=0.017 Adj p=0.161
Blue	Est=-0.377 SE= 0.266	**x**	z=0.784 p=0.433 Adj p=0.600	z=-2.077 p=0.038 Adj p=0.153	z=-0.969 p=0.333 Adj p=0.489	z=-0.117 p=0.907 Adj p=0.832	z=-1.561 p=0.119 Adj p=0.288	z=-0.562 p=0.574 Adj p=0.611
Green	Est=-0.275 SE=0.261	Est=0.218 SE=0.278	**x**	z=-2.597 p=0.009 Adj p=0.059	z=-1.502 p=0.133 Adj p=0.266	z=-0.557 p=0.577 Adj p=0.580	z=-1.946 p=0.052 Adj p=0.128	z=-1.116 p=0.264 Adj p=0.385
Purple	Est=-1.169 SE=0.317	Est=-0.684 SE=0.329	Est=-0.845 SE=0.325	**x**	z=1.279 p=0.201 Adj p=0.436	z=2.141 p=0.032 Adj p=0.152	z=0.679 p=0.497 Adj p=0.581	z=1.584 p=0.113 Adj p=0.312
Red	Est=-0.784 SE=0.288	Est=-0.293 SE=0.302	Est=-0.446 SE=0.297	Est=0.447 SE=0.349	**x**	z=0.891 p=0.373 Adj p=0.578	z=-0.610 p=0.542 Adj p=0.592	z=0.432 p=0.666 Adj p=0.741
Silver	Est=-0.473 SE=0.271	Est=-0.034 SE=0.289	Est=-0.157 SE=0.282	Est=0.723 SE=0.338	Est=0.272 SE=0.306	**x**	z=-1.205 p=0.228 Adj p=0.355	z=-0.138 p=0.890 Adj p=0.753
White	Est=-0.980 SE=0.302	Est=-0.492 SE=0.315	Est=-0.599 SE=0.308	Est=0.245 SE=0.361	Est=-0.202 SE=0.331	Est=-0.385 SE=0.320	**x**	z=1.127 p=0.260 Adj p=0.517
Yellow	Est=-0.671 SE=0.281	Est=-0.166 SE=0.295	Est=-0.324 SE=0.290	Est=0.545 SE=0.344	Est=0.135 SE=0.311	Est=-0.041 SE=0.299	Est=0.369 SE=0.328	**x**

Table 9: GLM output of pairwise colour comparison for Greenfinch (*Carduelis carduelis*).

Greenfinch	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	z=0.029 p=0.977 Adj p=1.00	z=1.615 p=0.106 Adj p=0.742	z=0.210 p=0.834 Adj p=1.00	z=0.001 p=0.999 Adj p=0.999	z=1.036 p=0.300 Adj p=0.700	z=1.589 p=0.112 Adj p=0.523	z=-0.781 p=0.435 Adj p=0.641
Blue	Est=0.011 SE= 0.391	**x**	z=1.584 p=0.113 Adj p=0.396	z=0.181 p=0.857 Adj p=0.999	z=-0.027 p=0.978 Adj p=1.00	z=1.006 p=0.315 Adj p=0.629	z=1.558 p=0.120 Adj p=0.371	z=-0.807 p=0.420 Adj p=0.691
Green	Est=0.562 SE=0.348	Est=0.550 SE=0.378	**x**	z=-1.413 p=0.158 Adj p=0.441	z=-1.615 p=0.106 Adj p=0.596	z=-0.595 p=0.552 Adj p=0.773	z=-0.020 p=0.984 Adj p=1.00	z=-2.310 p=0.021 Adj p=0.585
Purple	Est=0.081 SE=0.384	Est=0.069 SE=0.384	Est=-0.481 SE=0.340	**x**	z=-0.208 p=0.835 Adj p=1.00	z=0.829 p=0.407 Adj p=0.712	z=1.388 p=0.165 Adj p=0.421	z=-0.983 p=0.325 Adj p=0.607
Red	Est=0.001 SE=0.391	Est=-0.011 SE=0.391	Est=-0.561 SE=0.348	Est=-0.080 SE=0.384	**x**	z=1.035 p=0.301 Adj p=0.647	z=1.589 p=0.112 Adj p=0.448	z=-0.782 p=0.434 Adj p=0.675
Silver	Est=0.375 SE=0.362	Est=0.363 SE=0.361	Est=-0.187 SE=0.314	Est=0.294 SE=0.355	Est=0.374 SE=0.361	**x**	z=0.572 p=0.567 Adj p=0.757	z=-1.770 p=0.077 Adj p=0.717
White	Est=0.555 SE=0.350	Est=0.544 SE=0.349	Est=-0.006 SE=0.300	Est=0.475 SE=0.342	Est=0.555 SE=0.349	Est=0.181 SE=0.316	**x**	z=-2.284 p=0.022 Adj p=0.314
Yellow	Est=-0.333 SE=0.427	Est=-0.344 SE=0.426	Est=-0.895 SE=0.387	Est=-0.414 SE=0.421	Est=-0.334 SE=0.426	Est=-0.708 SE=0.400	Est=-0.889 SE=0.389	**x**

Table 10: GLM output of pairwise colour comparison for Eurasian Starling (*Sturnus vulgaris*).

Starling	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	z=0.325 p=0.745 Adj p=0.803	z=-0.392 p=0.695 Adj p=0.846	z=-0.916 p=0.360 Adj p=0.719	z=-1.986 p=0.047 Adj p=0.439	z=-1.140 p=0.254 Adj p=0.712	z=-0.754 p=0.451 Adj p=0.702	z=-1.695 p=0.090 Adj p=0.631
Blue	Est=0.114 SE= 0.352	**x**	z=-0.716 p=0.474 Adj p=0.698	z=-1.232 p=0.218 Adj p=0.678	z=-2.281 p=0.023 Adj p=0.630	z=-1.453 p=0.146 Adj p=0.683	z=-1.074 p=0.283 Adj p=0.660	z=-2.001 p=0.045 Adj p=0.636
Green	Est=-0.144 SE=0.367	Est=-0.258 SE=0.361	**x**	z=-0.532 p=0.595 Adj p=0.793	z=-1.624 p=0.104 Adj p=0.582	z=-0.757 p=0.449 Adj p=0.740	z=-0.366 p=0.715 Adj p=0.834	z=-1.323 p=0.186 Adj p=0.744
Purple	Est=-0.354 SE=0.386	Est=0.468 SE=0.380	Est=-0.210 SE=0.395	**x**	z=-1.106 p=0.269 Adj p=0.685	z=-0.224 p=0.823 Adj p=0.853	z=0.169 p=0.866 Adj p=0.866	z=-0.791 p=0.429 Adj p=0.751
Red	Est=-0.856 SE=0.431	Est=-0.971 SE=0.426	Est=-0.712 SE=0.439	Est=-0.502 SE=0.454	**x**	z=0.890 p=0.374 Adj p=0.697	z=1.274 p=0.203 Adj p=0.709	z=0.329 p=0.742 Adj p=0.831
Silver	Est=-0.447 SE=0.392	Est=-0.562 SE=0.387	Est=-0.303 SE=0.401	Est=-0.093 SE=0.418	Est=0.409 SE=0.460	**x**	z=0.393 p=0.694 Adj p=0.883	z=-0.570 p=0.569 Adj p=0.797
White	Est=-0.285 SE=0.379	Est=-0.400 SE=0.372	Est=-0.141 SE=0.387	Est=0.068 SE=0.405	Est=0.571 SE=0.448	Est=0.162 SE=0.411	**x**	z=-0.963 p=0.335 Adj p=0.722
Yellow	Est=-0.699 SE=0.413	Est=-0.814 SE=0.407	Est=-0.555 SE=0.420	Est=-0.346 SE=0.437	Est=0.157 SE=0.477	Est=-0.252 SE=0.442	Est=-0.414 SE=0.430	**x**

Feeder Depletion (Colour)

There was a significant effect of colour on the log depletion per hour made to the bird feeders, (ANOVA, $F_{1,7}$=26.939, P <0.001; Figure 17). Pairwise comparison of the log depletion per hour to each coloured feeder revealed that depletion from the red feeder was significantly lower than all colours with the exception of white and yellow (P <0.01) in addition to depletion from the yellow feeder significantly lower than from all other colours except red (P <0.001, except white, P=0.031). There was no difference in depletion rate between black, blue, green, purple and silver (Table 11).

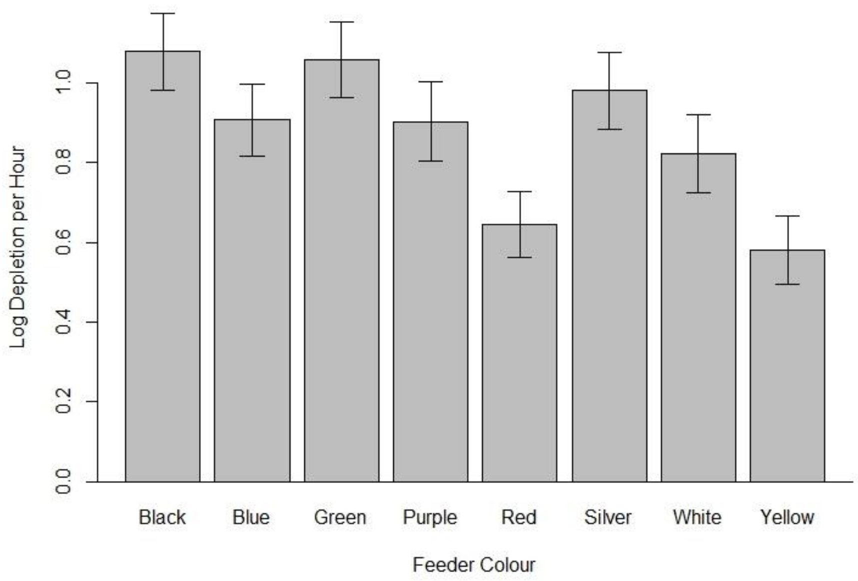


Figure 17: The Log Depletion per hour to feeders of all colours, containing pooled data from all sites and is a summary of all species encountered (Table 2 includes all species encountered and the rates of visitation to all feeders).

Table 11: LME output for pairwise comparison of depletion to coloured feeders for all birds and all sites. For each LME output, the cells above the diagonal show the test statistic; t value, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the test values (effect size) and associated standard error.

Colour Depletion	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	t= -2.083 p=0.038 Adj p=0.070	t= -0.368 p=0.713 Adj p=0.740	t= -2.068 p=0.039 Adj p=0.069	**t= -5.054** **p=<0.001** **Adj p=<0.001**	t= -1.030 p=0.303 Adj p=0.354	**t= -3.307** **p=0.001** **Adj p=0.003**	**t= -5.763** **p=<0.001** **Adj p=<0.001**
Blue	Value=-0.180 SE= 0.086	**x**	t= 1.710 p=0.088 Adj p=0.137	t= 0.015 p=0.988 Adj p=0.988	**t= -2.962** **p=0.003** **Adj p=0.008**	t= 1.050 p=0.295 Adj p=0.375	t=-1.220 p=0.223 Adj p=0.297	**t= -3.669** **p=<0.001** **Adj p=0.001**
Green	Value=0.032 SE= 0.086	Value=0.148 SE= 0.087	**x**	t= -1.694 p=0.091 Adj p=0.1338	**t= -4.671** **p=<0.001** **Adj p=<0.001**	t= -0.661 p=0.509 Adj p=0.548	**t= -2.929** **p=0.004** **Adj p=0.008**	**t= -5.379** **p=<0.001** **Adj p=<0.001**
Purple	Value=-0.179 SE= 0.0864	Value=0.001 SE= 0.867	Value=-0.147 SE= 0.087	**x**	**t= -2.977** **p=0.003** **Adj p=0.008**	t= 1.034 p=0.302 Adj p=0.367	t= -1.235 p=0.217 Adj p=0.304	**t= -3.684** **p=<0.001** **Adj p=0.001**
Red	Value=-0.437 SE= 0.086	Value=-0.257 SE= 0.087	Value=-0.405 SE= 0.087	Value=-0.258 SE= 0.087	**x**	**t= 4.011** **p=<0.001** **Adj p=<0.001**	t= 1.742 p=0.082 Adj p=0.135	t= -0.707 p=0.480 Adj p=0.537
Silver	Value=-0.0891 SE= 0.086	Value=0.091 SE= 0.087	Value=-0.057 SE= 0.087	Value=0.090 SE= 0.087	Value=0.348 SE= 0.087	**x**	**t= -2.269** **p=0.024** **Adj p=0.047**	**t= -4.718** **p=<0.001** **Adj p=<0.001**
White	Value=-0.286 SE= 0.086	Value=-0.106 SE= 0.087	Value=-0.254 SE= 0.087	Value=-0.107 SE= 0.087	Value=0.151 SE= 0.087	Value=-0.197 SE= 0.087	**x**	**t= -2.449** **p=0.014** **Adj p=0.031**
Yellow	Value=-0.498 SE= 0.086	Value=-0.318 SE= 0.087	Value=-0.466 SE= 0.087	Value=-0.319 SE= 0.087	Value=-0.061 SE= 0.087	Value=-0.409 SE= 0.087	Value=-0.212 SE= 0.087	**x**

Experiment 2: Human Preference

Overall, 732 (1037) individual counters were placed in the preference containers, 587 from adults, 145 from children and 305 from unknown demographics (omitted from the results). There was a significant effect of colour on the number of counters placed in the container for each colour (ANOVA, $F_{1, 7}$=7.651, P=<0.001; Figure 18). Pairwise comparison of the displayed preference for each coloured feeder revealed that there are two clear colour categories; those colours which were found attractive: comprising of blue, green, red and yellow and those found less attractive: black, purple, silver and white. Colours in the attractive group were consistently and significantly preferred over those colours in the less attractive group (P <0.05), however there were no significant differences in the preference towards colours in the same block (Table 12)

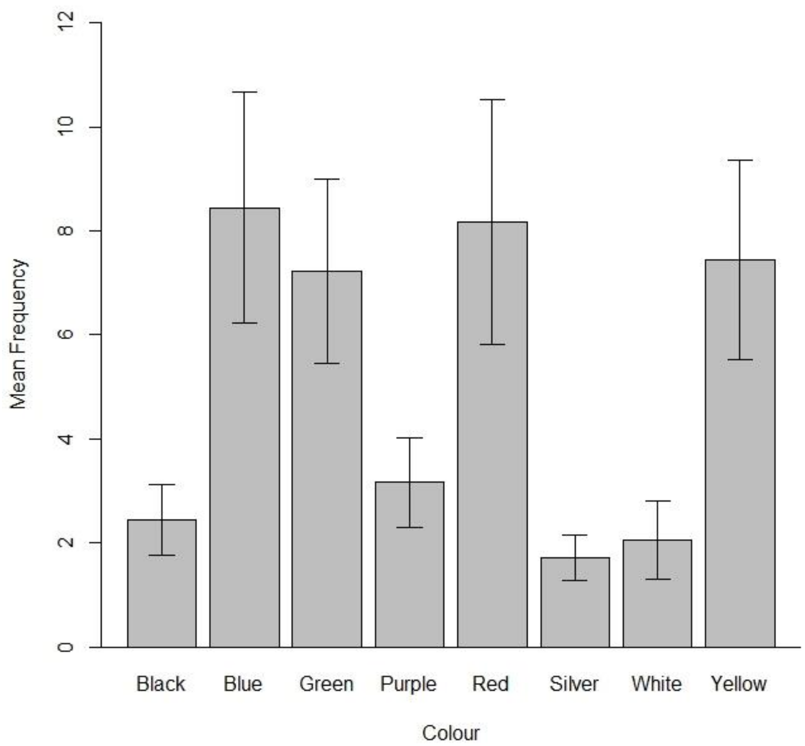


Figure 18: The mean frequency of preference for each coloured feeder in humans, data is pooled from all sites, both demographics and across all sample periods. The error bars illustrate the variation in frequency between sample periods.

Table 12: LME output for pairwise comparison of frequency of selection of all coloured feeders by humans at all sample sites, encompassing both the adult and children demographics. The cells above the diagonal show the test statistic; t value, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the test values (effect size) and associated standard error.

Human Colour Totals	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	**t= 3.693 p=<0.001 Adj p=0.001**	**t= 4.577 p=<0.001 Adj p=<0.001**	t= 0.624 p=0.535 Adj p=0.713	**t= 4.473 p=<0.001 Adj p=<0.001**	t= -0.312 p=0.756 Adj p=0.882	t= 0.052 p=0.959 Adj p=1.000	**t= 4.525 p=<0.001 Adj p=<0.001**
Blue	Value=7.889 SE=2.136	**x**	t= 0.884 p=0.380 Adj p=0.591	**t=-3.069 p=0.003 Adj p=0.005**	t= 0.781 p=0.439 Adj p=0.614	**t= -4.005 p=<0.001 Adj p=<0.001**	**t= -3.641 p=<0.001 Adj p=0.001**	t= 0.832 p=0.409 Adj p=0.602
Green	Value=9.778 SE=2.136	Value=1.889 SE=2.136	**x**	**t= -3.953 p=<0.001 Adj p=<0.001**	t= -0.104 p=0.918 Adj p=1.000	**t= -4.889 p=<0.001 Adj p=<0.001**	**t= -4.525 p=<0.001 Adj p=<0.001**	t= -0.052 p=0.959 Adj p=1.000
Purple	Value=1.333 SE=2.136	Value=-6.556 SE=2.136	Value=-8.444 SE=2.136	**x**	**t= 3.849 p=<0.001 Adj p=<0.001**	t= -0.936 p=0.353 Adj p=0.582	t= -0.572 p=0.570 Adj p=0.725	**t= 3.901 p=<0.001 Adj p=<0.001**
Red	Value=9.556 SE=2.136	Value=1.667 SE=2.136	Value=-0.222 SE=2.136	Value=8.222 SE=2.136	**x**	**t= -4.785 p=<0.001 Adj p=<0.001**	**t= -4.421 p=<0.001 Adj p=<0.001**	t= 0.052 p=0.959 Adj p=1.000
Silver	Value=-0.667 SE=2.136	Value=-8.556 SE=2.136	Value=-10.444 SE=2.136	Value=-2.000 SE=2.136	Value=-10.222 SE=2.136	**x**	t= 0.364 p=0.717 Adj p=0.873	**t= 4.837 p=<0.001 Adj p=<0.001**
White	Value=0.111 SE=2.136	Value=-7.778 SE=2.136	Value=-9.667 SE=2.136	Value=-1.222 SE=2.136	Value=-9.444 SE=2.136	Value=0.778 SE=2.136	**x**	**t= 4.473 p=<0.001 Adj p=<0.001**
Yellow	Value=9.667 SE=2.136	Value=1.778 SE=2.136	Value=-0.111 SE=2.136	Value=8.333 SE=2.136	Value=0.111 SE=2.136	Value=10.333 SE=2.136	Value=9.556 SE=2.136	**x**

Age specific Preference

Adults

For adults, there was a significant effect of colour on preference for coloured bird feeders (ANOVA, $F_{1,7}$=10.485, P=<0.001; Figure 19). As with the overall preference, due to the large proportion of adults contributing to the total preference, there is very little variation between overall and overall preference. Pairwise comparison of the displayed preference for each coloured feeder revealed that the level of preference is split into two distinct groups; the attractive group, including blue, green, red and yellow, and a less attractive group including black, purple, silver and white. There is a significant difference between coloured feeders in the two groups (P <0.05), however there was no significant difference between any colours in the same group (Table 13).

Children

For children there was not a significant effect of colour on preference for coloured bird feeders (ANOVA $_{1,7}$= 2.033, P=0.67; Figure 20). Pairwise comparison of the displayed preference for each coloured feeder revealed that there was no significant difference between the preference for any of the colours (P=>0.05) (Table 13).

Age Specific Preference Graphs

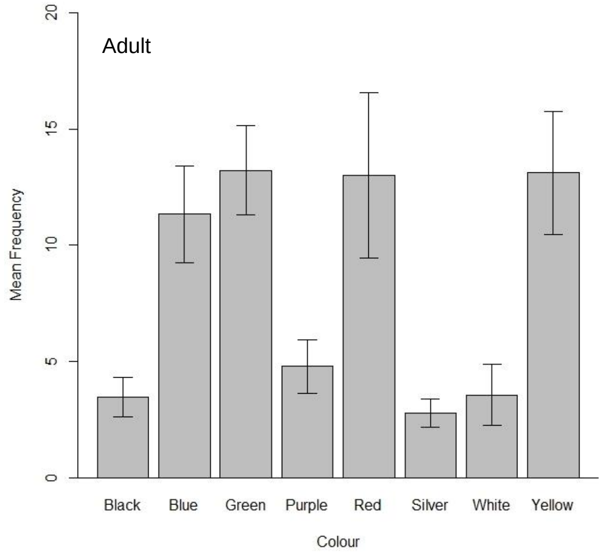


Figure 19: The mean frequency of the level of preference to feeders of all colours by the Adult Demographic, data from all sites and all sample periods (error bars illustrate the standard error).

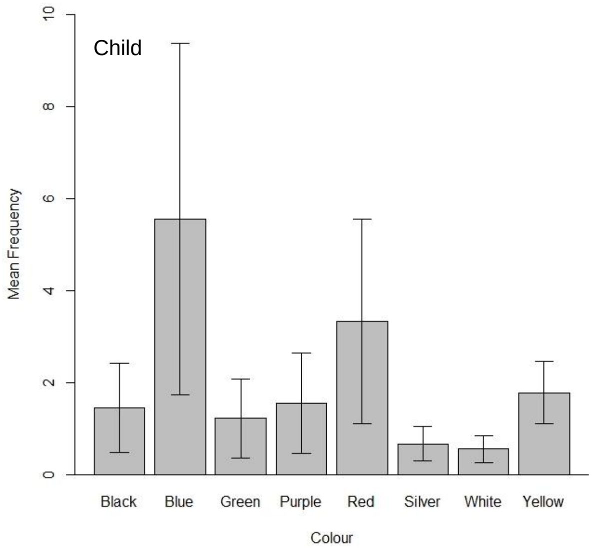


Figure 20: The mean frequency of the level of preference to feeders of all colours by the Child Demographic, data from all sites and all sample periods (error bars illustrate the standard error). Though comparable, these two demographics contained a variable sample size, as illustrated by the difference in y axis. The adult demographic was much more numerous than that of the child group.

Age Specific Preference, GLM output

Tables 19 & 20: The LME output for pairwise comparison of frequency of selection of all coloured feeders for both the adult (Table 19) and child (Table 20) demographics from all sample sites across all data collection periods. For each LME output, the cells above the diagonal show the test statistic; t, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the test value and associated standard error.

Table 19: LME output of pairwise colour comparison for the Adult Demographic

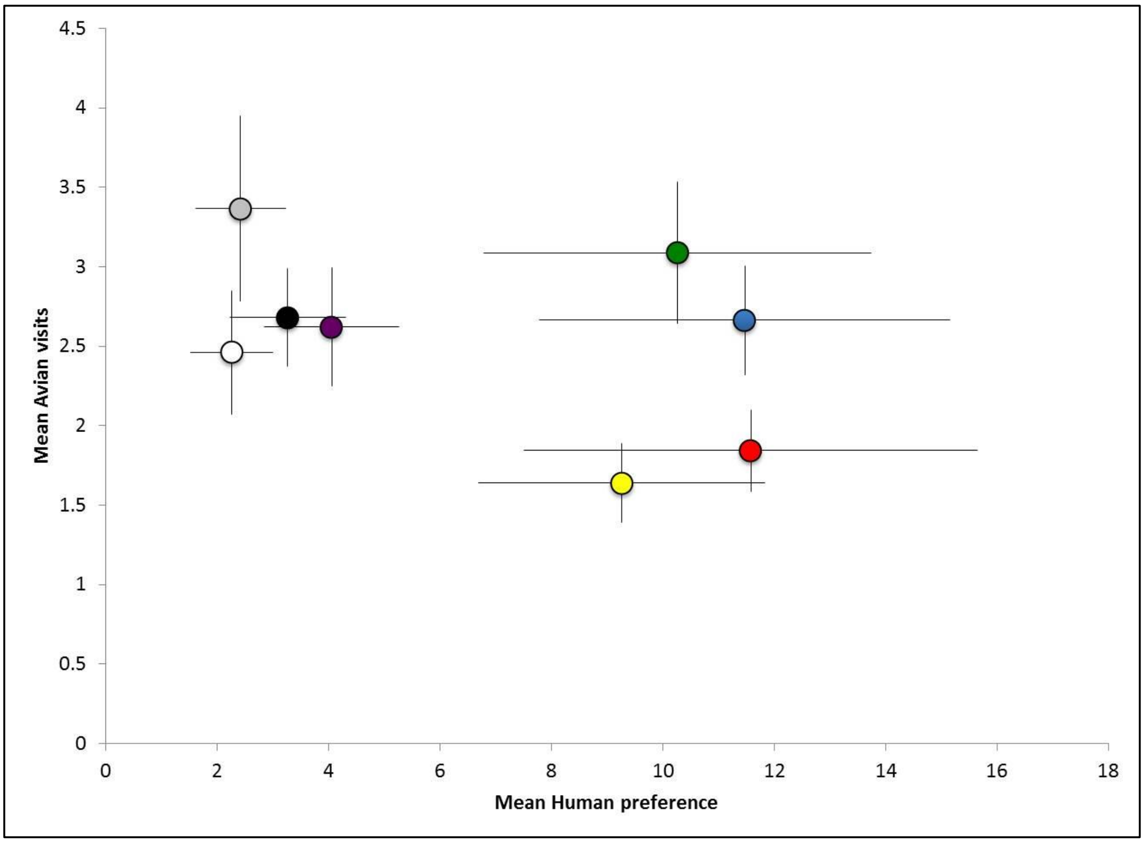
Adult Colour Totals	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	**x**	**t= 3.942 p=<0.001 Adj p=<0.001**	**t= 3.139 p=0.002 Adj p=0.004**	t= 0.474 p=0.636 Adj p=0.810	**t= 3.759 p=<0.001 Adj p=0.001**	t= -0.474 p=0.636 Adj p=0.810	t= -0.255 p=0.799 Adj p=0.895	**t= 3.285 p=0.001 Adj p=0.003**
Blue	Value=6.000 SE=1.522	**x**	t= -0.803 p=0.424 Adj p=0.659	**t= -3.467 p=<0.001 Adj p=0.002**	t= -0.182 p=0.856 Adj p=0.887	**t= -4.416 p=<0.001 Adj p=<0.001**	**t= -4.197 p=<0.001 Adj p=<0.001**	t= -0.657 p=0.513 Adj p=0.718
Green	Value=4.778 SE=1.522	Value=-1.222 SE=1.522	**x**	**t= -2.664 p=0.009 Adj p=0.015**	t= 0.620 p=0.536 Adj p=0.715	**t= -3.613 p=<0.001 Adj p=0.001**	**t= -3.394 p=<0.001 Adj p=0.002**	t= 0.146 p=0.884 Adj p=0.884
Purple	Value=0.722 SE=1.522	Value=-5.278 SE=1.522	Value=-4.056 SE=1.522	**x**	**t= 3.285 p=0.001 Adj p=0.003**	t= -0.949 p=0.345 Adj p=0.568	t= -0.730 p=0.467 Adj p=0.688	**t= 2.810 p=0.006 Adj p=0.011**
Red	Value=5.722 SE=1.522	Value=-0.278 SE=1.522	Value=0.944 SE=1.522	Value=5.000 SE=1.522	**x**	**t= -4.234 p=<0.001 Adj p=<0.001**	**t= -4.015 p=<0.001 Adj p=<0.001**	t= -0.474 p=0.636 Adj p=0.810
Silver	Value=-0.722 SE=1.522	Value=-6.722 SE=1.522	Value=-5.500 SE=1.522	Value=-1.444 SE=1.522	Value=-6.444 SE=1.522	**x**	t= 0.219 p=0.827 Adj p=0.891	**t= 3.759 p=<0.001 Adj p=0.001**
White	Value=-0.389 SE=1.522	Value=-6.389 SE=1.522	Value=-5.167 SE=1.522	Value=-1.111 SE=1.522	Value=-6.111 SE=1.522	Value=0.333 SE=1.522	**x**	**t= 3.540 p=<0.001 Adj p=0.002**
Yellow	Value=5.000 SE=1.522	Value=-1.000 SE=1.522	Value=0.222 SE=1.522	Value=4.278 SE=1.522	Value=-0.722 SE=1.522	Value=5.722 SE=1.522	Value=5.389 SE=1.522	**x**

Table 20: LME output of pairwise colour comparison for Child Demographic

Child Colour Totals	Black	Blue	Green	Purple	Red	Silver	White	Yellow
Black	x	t= 2.487 p=0.016 Adj p=0.111	t= -0.134 p=0.894 Adj p=1.000	t=0.067 p=0.947 Adj p=0.982	t=1.143 p=0.258 Adj p=0.657	t=-0.471 p=0.639 Adj p=0.943	t= -0.538 p=0.593 Adj p=0.977	t= 0.202 p=0.841 Adj p=1.000
Blue	Value=4.111 SE=1.653	x	t= -2.622 p=0.011 Adj p=0.105	t= -2.420 p=0.019 Adj p=0.105	t= -1.344 p=0.184 Adj p=0.573	t= -2.958 p=0.005 Adj p=0.063	t= -3.025 p=0.004 Adj p=0.104	t= -2.286 p=0.026 Adj p=0.122
Green	Value=-0.222 SE=1.653	Value=-4.333 SE=1.653	x	t= 0.202 p=0.841 Adj p=1.000	t=1.277 p=0.207 Adj p=0.579	t= -0.336 p=0.738 Adj p=0.984	t= -0.403 p=0.688 Adj p=0.963	t= 0.336 p=0.738 Adj p=0.984
Purple	Value=0.111 SE=1.653	Value=-4.000 SE=1.653	Value=0.333 SE=1.653	x	t= 1.076 p=0.287 Adj p=0.669	t= -0.538 p=0.593 Adj p=0.977	t= -0.605 p=0.548 Adj p=0.958	t= 0.134 p=0.894 Adj p=1.000
Red	Value=1.889 SE=1.653	Value=-2.222 SE=1.653	Value=2.111 SE=1.653	Value=1.778 SE=1.653	x	t= -1.613 p=0.112 Adj p=0.393	t= -1.681 p=0.098 Adj p=0.394	t= -0.941 p=0.351 Adj p=0.755
Silver	Value=-0.778 SE=1.653	Value=-4.889 SE=1.653	Value=-0.556 SE=1.653	Value=-0.889 SE=1.653	Value=-2.667 SE=1.653	x	t= -0.067 p=0.947 Adj p=0.982	t= 0.672 p=0.504 Adj p=0.941
White	Value=-0.889 SE=1.653	Value=-5.000 SE=1.653	Value=-0.667 SE=1.653	Value=-1.000 SE=1.653	Value=-2.778 SE=1.653	Value=-0.111 SE=1.653	x	t= 0.739 p=0.463 Adj p=0.925
Yellow	Value=0.333 SE=1.653	Value=-3.778 SE=1.653	Value=0.556 SE=1.653	Value=0.222 SE=1.653	Value=-1.556 SE=1.653	Value=1.111 SE=1.653	Value=1.222 SE=1.653	x

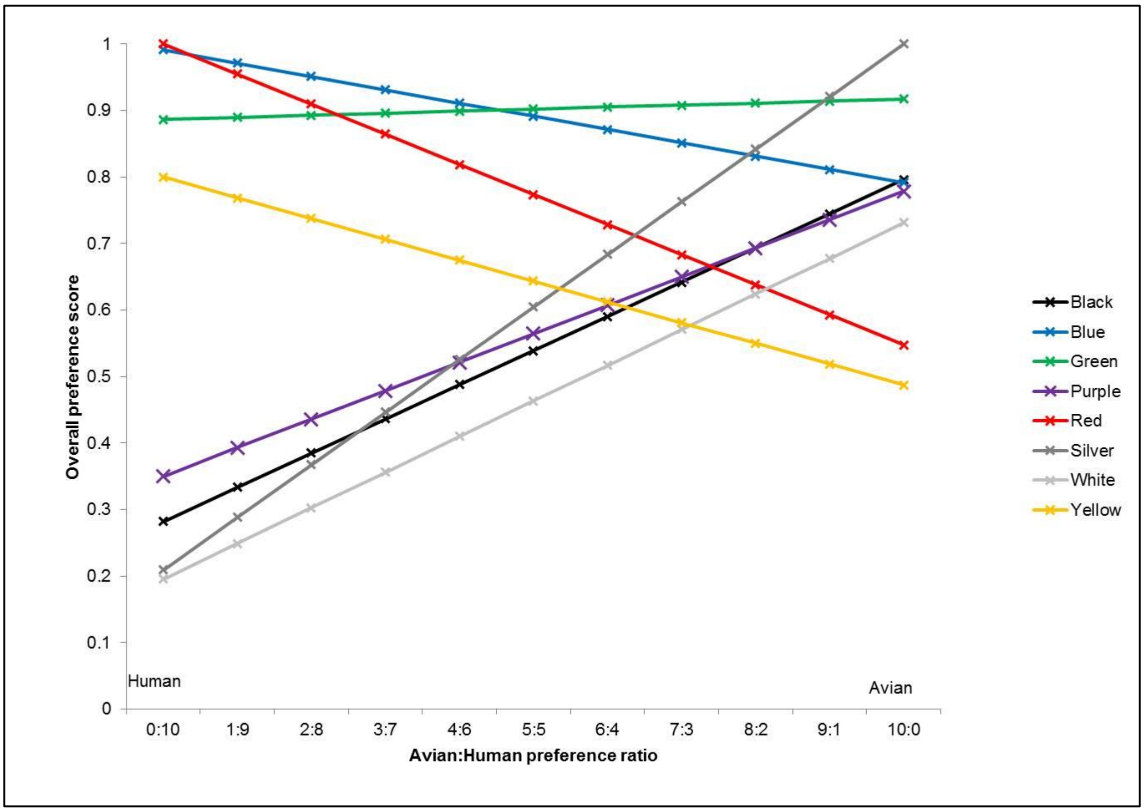
Avian and Human Combined Colour Preference

By combining avian and human colour preference, we can evaluate the relative preferences of humans and birds, to assess whether both prefer similar feeders (which would then be easily marketable) or whether there are contrasts in the preferences. As figure 21 shows, the overall most visited coloured feeders by avian species (y axis) were silver and green; due to a strong preference by the most common species: Blue Tit and Great Tit, whereas the colours with the highest level of visitation by humans (x axis) are blue and red. Although red is the most preferred colour in the literature (Table 1) and with humans, it has a low level of visitation in the field investigation. The two colours which are therefore most visited by both avian species and humans are green and blue, due to their occurrence at the top right corner of the figure, illustrating a high preference. This suggests that overall and giving equal weighting to the preferences of avian species and humans, a green feeder would be most preferred option



The mean avian and mean human coloured feeder preference (with standard error). Data used is from all sites, all species (and demographics for humans) and across all sample periods. (Figure 21)

Further examining the colour preferences of both avian species and humans at variable levels allow for the comparison of coloured feeders given variable importance of a species opinion. As figure 22 shows if preference is weighted entirely towards human preference (0:10 avian: human), the most preferred coloured feeders are red and blue, whereas if preference is weighted towards birds (10:0 avian to humans), the colours with the highest level of visitation are silver and green. The colour with the highest preference for the largest proportion of the figure is green; which consistently has a high level of preference for both humans and avian species. Blue is also consistently high.



The mean avian and mean human coloured feeder preference (with standard error). Data used is from all sites, all species (and demographics for humans) and across all sample periods. (Figure 22)

Experiment 3: Perch Design Preference

Overall, 13,143 individual visits to the feeders were recorded, representing 9 different species. During this field investigation, all 28 observation periods were conducted at a single field site: Tophill Low Nature Reserve. The number of individual visits for each species is presented in Table 14 for illustrative purposes, however all data was combined from all observation periods prior to analysis to determine overall perch design preference. For those species for which more than 100 observations were recorded, species level perch preference analyses were also carried out (Blue Tit, Great Tit, Coal Tit and Goldfinch; table 14). Other species occurred only rarely at feeders.

Table 14: A summary of the frequency of species occurrence to the feeders at the Tophill Low Sample site. As discussed previously, this was under assumption that every visit to a feeder is a unique decision as the actual number of individual birds involved within each data collection experiment is unknown.

Species	Scientific Name	Occurrence
Chaffinch	*Fringilla coelebs*	27
Goldfinch	*Carduelis carduelis*	1304
Greenfinch	*Chloris chloris*	32
Robin	*Erithacus rubecula*	3
Coal Tit	*Periparus ater*	322
Great Tit	*Parus major*	5154
Blue Tit	*Cyanistes caeruleus*	6220
Marsh Tit	*Poecile palustris*	69
Greater Spotted Woodpecker	*Dendrocopos major*	12

Overall Avian Perch Design Preference.

There was a significant effect of perch design on the number of visits that birds made to the bird feeders (LME, $F_{7,182}$=5.827, P=<0.05; Figure 39). Pairwise comparisons of the number of visits to each perch design revealed that there are significantly more visits to the long and the medium perch than are made to any of the remaining perch design (Table 15; figure 23).

In addition, birds make significantly fewer visits to both the opposite and short perch designs than to the long, medium and branched perches (P <0.05), although there is no difference in the number of visits to the short or opposite perch. Birds do not appear to have any preference between the circle, opposite, short or steps perch designs (figure 23)

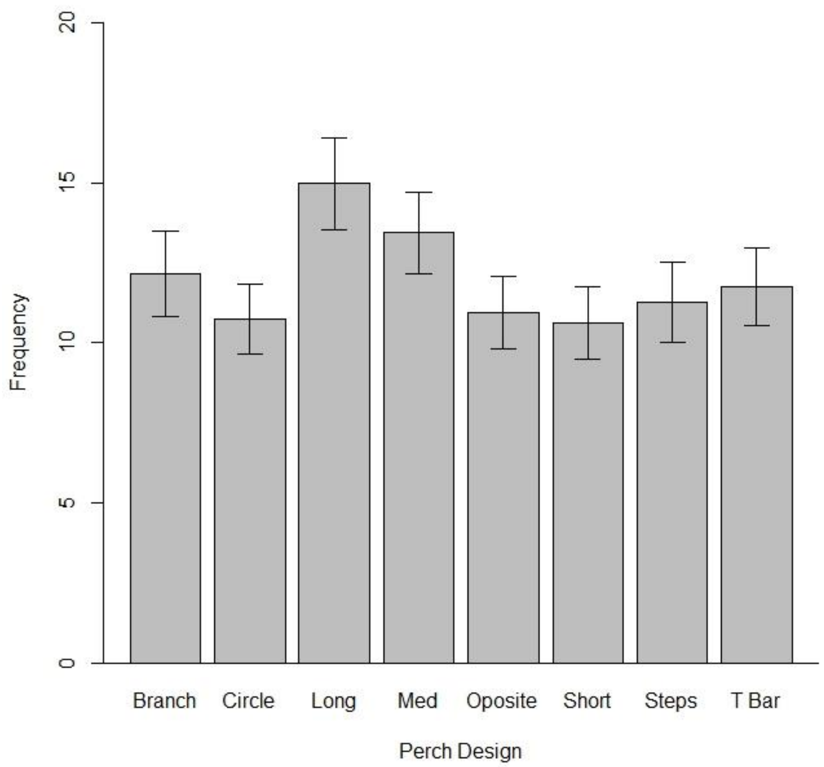


Figure 23: Mean frequency of visits to each perch design feeder per 30 minute observation period, pooled across all sample periods and all species. Error bars represent ±1 S.E.

Table 15: GLM output for pairwise comparison of visits to feeders of different perch designs (all sites and all species combined). The cells above the diagonal show the z value, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the estimate (effect size) and associated standard error.

Perch Totals	Branch	Circle	Long	Medium	Opposite	Short	Steps	T Bar
Branch	x	**z=-3.480 p=0.001 Adj p=0.001**	**z=6.320 p=<0.001 Adj p=<0.001**	**z=2.950 p=0.003 Adj p=0.005**	**z=-3.000 p=0.003 Adj p=0.005**	**z=-3.770 p=<0.001 Adj p=<0.001**	**z=-2.150 p=0.031 Adj p=0.046**	z=-1.000 p=0.319 Adj p=0.372
Circle	Est=-0.124 SE= 0.036	x	**z=9.750 p=<0.001 Adj p=<0.001**	**z=6.420 p=<0.001 Adj p=<0.001**	z=0.480 p=0.633 Adj p=0.657	z=-0.300 p=0.767 Adj p=0.767	z=1.330 p=0.184 Adj p=0.234	**z=2.490 p=0.013 Adj p=0.020**
Long	Est=0.208 SE=0.033	Est=0.333 SE=0.034	x	**z=-3.380 p=0.001 Adj p=0.001**	**z=-9.280 p=<0.001 Adj p=<0.001**	**z=-10.03 p=<0.001 Adj p=<0.001**	**z=-8.440 p=<0.001 Adj p=<0.001**	**z=-7.310 p=<0.001 Adj p=<0.001**
Medium	Est=0.100 SE=0.034	Est=0.224 SE=0.035	Est=-0.108 SE=0.032	x	**z=-5.940 p=<0.001 Adj p=<0.001**	**z=-6.710 p=<0.001 Adj p=<0.001**	**z=-5.100 p=<0.001 Adj p=<0.001**	**z=-3.950 p=<0.001 Adj p=<0.001**
Opposite	Est=-0.107 SE=0.036	Est=0.018 SE=0.037	Est=-0.315 SE=0.034	Est=-0.207 SE=0.035	x	z=-0.770 p=0.439 Adj p=0.473	z=0.850 p=0.394 Adj p=0.441	z=2.010 p=0.044 Adj p=0.062
Short	Est=-0.135 SE=0.036	Est=-0.011 SE=0.037	Est=-0.344 SE=0.034	Est=-0.235 SE=0.035	Est=-0.028 SE=0.037	x	z=1.630 p=0.104 Adj p=0.139	**z=2.780 p=0.005 Adj p=0.009**
Steps	Est=-0.076 SE=0.035	Est=0.048 SE=0.036	Est=-0.284 SE=0.034	Est=-0.176 SE=0.034	Est=0.031 SE=0.036	Est=0.059 SE=0.037	x	z=1.160 p=0.247 Adj p=0.301
T Bar	Est=-0.035 SE=0.035	Est=0.090 SE=0.036	Est=-0.243 SE=0.033	Est=-0.135 SE=0.034	Est=0.072 SE=0.036	Est=0.101 SE=0.0362	Est=0.0412 SE=0.0356	x

Species Specific Perch Design Preference

Blue Tit

There was a significant effect of perch design on the number of visits that Blue Tits made to the feeders containing different perch designs (LME, $F_{7, 189.92}$=5.4134, P <0.001; Figure 24a). Pairwise comparison of the number of visits to each perch designed feeder revealed that Blue Tits made significantly more visits to the long perch than to all other perch design (P <0.05), except medium in addition to making significantly more visits to the medium perch than the circle, short, steps and t-bar designs. There was no significant difference in the number of visits to the branch, circle, opposite, short, steps or t-bar feeders (Table 16).

Great Tit

There was a significant effect of perch design on the number of visits Great Tits made to bird feeders (LME, $F_{7, 189.91}$=2.173, P <0.05; figure 24b). Pairwise comparisons of the number of visits to each perch design revealed that Great Tits make significantly more visits to long perch feeders than to those with opposite or short perch designs (P=<0.005), however, Great Tits do not appear to have any preference between the branched, circle, medium, opposite, short, steps or t-bar perch designs (Table 17).

Coal Tit

There was no significant effect of perch design on the number of visits Coal Tits made to bird feeders ($F_{7, 175.75}$=0.64205, P=0.721; Figure 24c). Pairwise comparison shows that there is no significant difference between Coal Tit's preferences for any design of perch over others (Table 18).

Goldfinch

There was a significant effect of perch design on the number of visits Goldfinches made to the bird feeders ($F_{7, 190.11}$=4.5125, P <0.001; Figure 24d). Pairwise comparisons of the number of visits to each perch design feeder revealed that bird make significantly more visits to the long perch than to all others; with the exception of medium and t-bar (P <0.05) and make significantly more visits to the medium perch than to all others except long and t-bar (P <0.05). Goldfinch do not appear to have a preference between branch, circle, opposite, short, steps or t-bar designed perches (Table 19).

Species Specific Preference Graphs

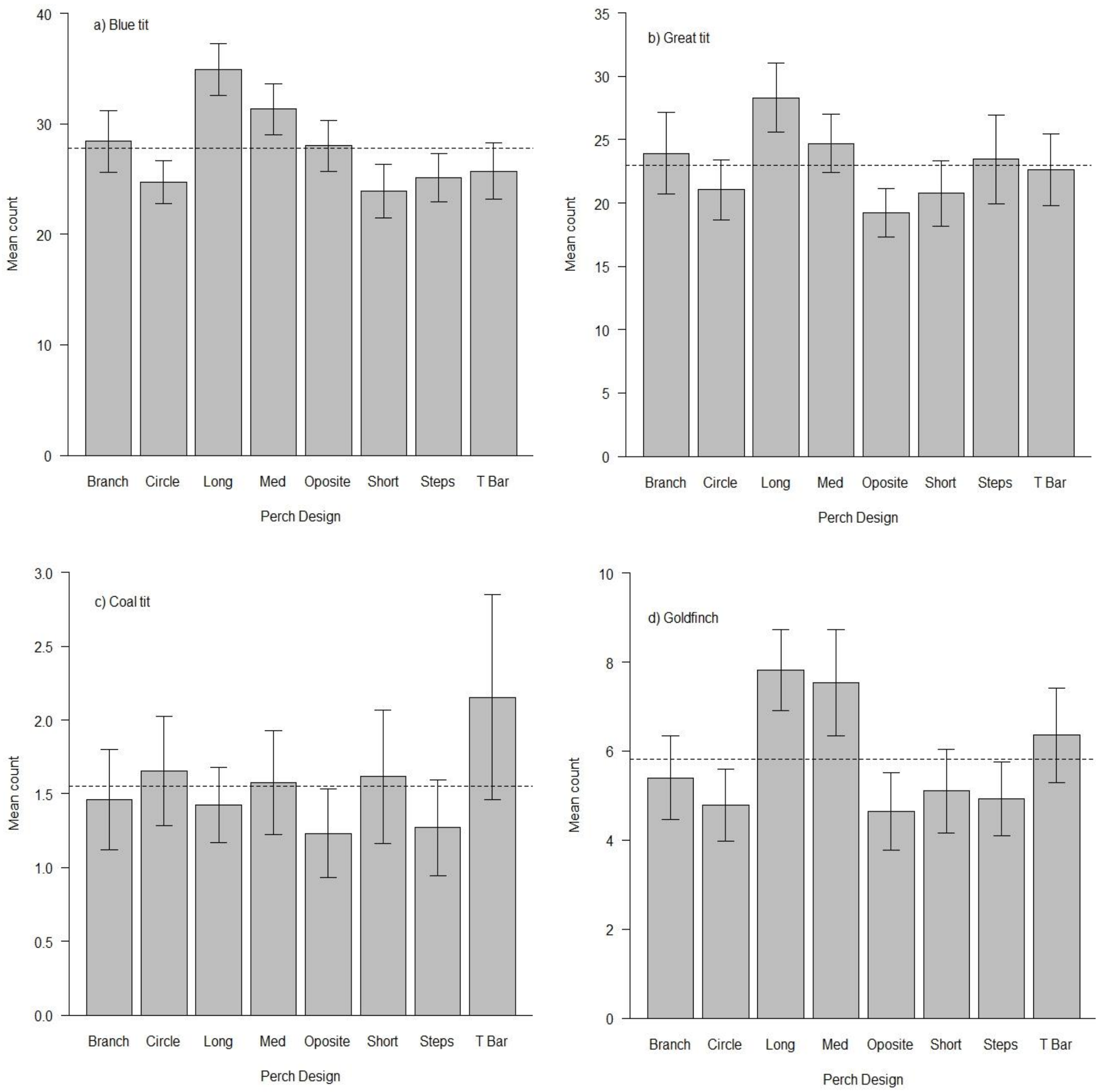


Figure 24: The average number of visits to feeders of all perch designs per observation period, pooled across all sample periods, for the 4 most frequently recorded species (with over 100 individual visitations). Blue Tit (*Cyanistes caeruleus*) (a), Great Tit (*Parus major*) (b), Coal Tit (*Periparus ater*) (c) and European Goldfinch (*Carduelis carduelis*) (d). Due to the differences in frequency of occurrence between species, note the difference in Y axis. The dashed line indicates the expected value for mean visitation to each feeder with a different perch design if the level of visitation was equal for each coloured feeder.

Species Specific Perch Design Preference: GLM output

Tables 16-19: The GLM output for pairwise comparison of visits to feeders of different perch designs for individually analysed species: Blue Tit (Table 16), Great Tit (Table 17), Coal Tit (Table 18) and Goldfinch (Table 19) from all data collection periods. For each GLM output, the cells above the diagonal show the z value, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the estimate (effect size) and associated standard error.

Table 16: GLM output of pairwise perch design comparison for Blue Tit (*Cyanistes caeruleus*)

Blue Tit	Branch	Circle	Long	Medium	Opposite	Short	Steps	T Bar
Branch	**x**	z=-1.550 p=0.120 Adj p=0.258	**z=2.680 p=0.007 Adj p=0.020**	z=1.430 p=0.151 Adj p=0.249	z=0.080 p=0.938 Adj p=0.938	z=-2.200 p=0.028 Adj p=0.071	z=-1.440 p=0.151 Adj p=0.265	z=-1.330 p=0.182 Adj p=0.268
Circle	Est=-0.135 SE= 0.086	**x**	**z=4.230 p=<0.001 Adj p=<0.001**	**z=2.990 p=0.003 Adj p=0.013**	z=1.480 p=0.139 Adj p=0.260	z=-0.650 p=0.519 Adj p=0.605	z=0.120 p=0.905 Adj p=0.975	z=0.220 p=0.827 Adj p=0.926
Long	Est=0.226 SE=0.084	Est=0.361 SE=0.085	**x**	z=-1.250 p=0.211 Adj p=0.281	**z=-2.760 p=0.006 Adj p=0.018**	**z=-4.870 p=<0.001 Adj p=<0.001**	**z=-4.110 p=<0.001 Adj p=<0.001**	**z=-4.010 p=<0.001 Adj p=<0.001**
Medium	Est=0.122 SE=0.084	Est=0.257 SE=0.089	Est=-0.104 SE=0.083	**x**	z=-1.510 p=0.131 Adj p=0.262	**z=-3.620 p=<0.001 Adj p=0.002**	**z=-2.870 p=0.004 Adj p=0.017**	**z=-2.760 p=0.006 Adj p=0.020**
Opposite	Est=-0.007 SE=0.085	Est=0.128 SE=0.087	Est=-0.233 SE=0.084	Est=-0.128 SE=0.849	**x**	z=-2.120 p=0.034 Adj p=0.079	z=-1.360 p=0.174 Adj p=0.271	z=-1.260 p=0.208 Adj p=0.292
Short	Est=-0.192 SE=0.087	Est=-0.057 SE=0.088	Est=-0.418 SE=0.086	Est=-0.314 SE=0.087	Est=-0.186 SE=0.087	**x**	z=0.766 p=0.444 Adj p=0.540	z=0.866 p=0.387 Adj p=0.492
Steps	Est=-0.125 SE=0.086	Est=0.010 SE=0.088	Est=-0.350 SE=0.085	Est=-0.247 SE=0.086	Est=-0.118 SE=0.087	Est=0.068 SE=0.088	**x**	z=0.100 p=0.920 Adj p=0.954
T Bar	Est=-0.116 SE=0.086	Est=0.019 SE=0.088	Est=-0.342 SE=0.085	Est=-0.237 SE=0.086	Est=-0.109 SE=0.087	Est=0.076 SE=0.088	Est=0.009 SE=0.088	**x**

Table 17: GLM output of pairwise perch design comparison for Great Tit (*Parus major*)

Great Tit	Branch	Circle	Long	Medium	Opposite	Short	Steps	T Bar
Branch	**x**	z=-0.792 p=0.428 Adj p=0.631	z=1.943 p=0.052 Adj p=0.182	z=0.908 p=0.364 Adj p=0.600	z=-1.231 p=0.218 Adj p=0.610	z=-1.049 p=0.294 Adj p=0.633	z=-0.219 p=0.827 Adj p=0.891	z=0.290 p=0.772 Adj p=0.901
Circle	Est=-0.093 SE= 0.118	**x**	z=2.737 p=0.006 Adj p=0.058	z=1.703 p=0.089 Adj p=0.276	z=-0.439 p=0.661 Adj p=0.804	z=-0.257 p=-0.797 Adj p=0.893	z=0.574 p=0.566 Adj p=0.755	z=0.503 p=0.615 Adj p=0.783
Long	Est=0.224 SE=0.115	Est=0.318 SE=0.116	**x**	z=-1.037 p=0.300 Adj p=0.599	**z=-3.176** **p=0.001** **Adj p=0.042**	**z=-2.992** **p=0.003** **Adj p=0.039**	z=-2.161 p=0.031 Adj p=0.172	z=-2.234 p=0.026 Adj p=0.179
Medium	Est=0.106 SE=0.116	Est=0.199 SE=0.117	Est=-0.119 SE=0.115	**x**	z=-2.142 p=0.032 Adj p=0.150	z=-1.958 p=0.050 Adj p=0.201	z=-1.127 p=0.260 Adj p=0.606	z=-1.199 p=0.230 Adj p=0.586
Opposite	Est=-0.145 SE=0.118	Est=-0.052 SE=0.119	Est=-0.370 SE=0.117	Est=-0.251 SE=0.117	**x**	z=0.181 p=0.856 Adj p=0.888	z=1.012 p=0.311 Adj p=0.581	z=0.942 p=0.346 Adj p=0.606
Short	Est=-0.124 SE=0.118	Est=-0.031 SE=0.119	Est=-0.348 SE=0.116	Est=-0.229 SE=0.117	Est=0.022 SE=0.119	**x**	z=0.830 p=0.406 Adj p=0.632	z=0.760 p=0.447 Adj p=0.626
Steps	Est=-0.026 SE=0.117	Est=0.068 SE=0.118	Est=-0.250 SE=0.116	Est=-0.131 SE=0.116	Est=0.120 SE=0.118	Est=0.098 SE=0.118	**x**	z=-0.071 p=0.943 Adj p=0.943
T Bar	Est=-0.034 SE=0.117	Est=0.059 SE=0.118	Est=-0.258 SE=0.116	Est=-0.140 SE=0.116	Est=0.111 SE=0.118	Est=0.090 SE=0.118	Est=-0.008 SE=0.118	**x**

Table 18: GLM output of pairwise perch design comparison of Coal Tit (*Periparus ater*)

Coal Tit	Branch	Circle	Long	Medium	Opposite	Short	Steps	T Bar
Branch	**x**	z=0.513 p=0.608 Adj p=1.000	z=0.129 p=0.897 Adj p=1.000	z=0.323 p=0.747 Adj p=1.000	z=-0.579 p=0.562 Adj p=1.000	z=0.208 p=0.835 Adj p=1.000	z=-0.493 p=0.622 Adj p=0.968	z=1.059 p=0.290 Adj p=1.000
Circle	Est=0.148 SE= 0.289	**x**	z=-0.383 p=0.702 Adj p=1.00	z=-0.190 p=0.849 Adj p=0.991	z=-1.087 p=0.277 Adj p=1.000	z=-0.306 p=0.760 Adj p=1.000	z=-1.002 p=0.316 Adj p=1.000	z=0.549 p=0.583 Adj p=1.000
Long	Est=0.038 SE=0.294	Est=-0.110 SE=0.288	**x**	z=0.193 p=0.847 Adj p=1.000	z=-0.706 p=0.480 Adj p=1.000	z=0.078 p=0.938 Adj p=0.938	z=-0.620 p=0.535 Adj p=1.000	z=0.928 p=0.353 Adj p=1.000
Medium	Est=0.094 SE=0.291	Est=-0.054 SE=0.285	Est=0.056 SE=0.290	**x**	z=-0.898 p=0.369 Adj p=1.000	z=-0.115 p=0.909 Adj p=0.979	z=-0.812 p=0.417 Adj p=1.000	z=0.737 p=0.461 Adj p=1.000
Opposite	Est=-0.176 SE=0.304	Est=-0.324 SE=0.298	Est=-0.214 SE=0.304	Est=-0.270 SE=0.301	**x**	z=0.785 p=0.432 Adj p=1.000	z=0.086 p=0.931 Adj p=0.965	z=1.628 p=0.104 Adj p=1.000
Short	Est=0.061 SE=0.292	Est=-0.087 SE=0.286	Est=0.023 SE=0.292	Est=-0.033 SE=0.289	Est=0.237 SE=0.302	**x**	z=-0.699 p=0.484 Adj p=1.000	z=0.852 p=0.394 Adj p=1.000
Steps	Est=-0.149 SE=0.303	Est=-0.298 SE=0.297	Est=-0.187 SE=0.302	Est=0.243 SE=0.300	Est=0.027 SE=0.312	Est=-0.210 SE=0.301	**x**	z=1.543 p=0.123 Adj p=1.000
T Bar	Est=0.230 SE=0.283	Est=0.152 SE=0.276	Est=0.262 SE=0.282	Est=0.206 SE=0.279	Est=0.476 SE=0.293	Est=0.239 SE=0.280	Est=0.449 SE=0.291	**x**

Table 19: GLM output of pairwise perch design comparison of Goldfinch (*Carduelis carduelis*)

Goldfinch	Branch	Circle	Long	Medium	Opposite	Short	Steps	T Bar
Branch	**x**	z=-0.901 p=0.367 Adj p=0.542	**z=2.987** **p=0.003** **Adj p=0.011**	z=2.179 p=0.029 Adj p=0.082	z=-1.123 p=0.261 Adj p=0.430	z=-0.478 p=0.633 Adj p=0.770	z=-0.650 p=0.515 Adj p=0.687	z=0.984 p=0.325 Adj p=0.506
Circle	Est=-0.141 SE= 0.156	**x**	**z=3.861** **p=<0.001** **Adj p=0.002**	**z=3.071** **p=0.002** **Adj p=0.010**	z=-0.224 p=0.823 Adj p=0.853	z=0.423 p=0.673 Adj p=0.753	z=0.250 p=0.802 Adj p=0.864	z=1.882 p=0.060 Adj p=0.129
Long	Est=0.435 SE=0.146	Est=0.576 SE=0.149	**x**	z=-0.829 p=0.407 Adj p=0.570	**z=-4.077** **p=<0.001** **Adj p=0.001**	**z=-3.454** **p=<0.001** **Adj p=0.004**	**z=-3.622** **p=<0.001** **Adj p=0.003**	z=-2.021 p=0.043 Adj p=0.101
Medium	Est=0.320 SE=0.147	Est=0.461 SE=0.150	Est=-0.115 SE=0.139	**x**	**z=-3.285** **p=0.001** **Adj p=0.006**	**z=-2.651** **p=0.008** **Adj p=0.025**	**z=-2.823** **p=0.005** **Adj p=0.017**	z=-1.202 p=0.229 Adj p=0.402
Opposite	Est=-0.177 SE=0.157	Est=-0.036 SE=0.160	Est=-0.612 SE=0.150	Est=-0.497 SE=0.151	**x**	z=0.646 p=0.518 Adj p=0.660	z=0.474 p=0.635 Adj p=0.741	z=2.102 p=0.036 Adj p=0.091
Short	Est=-0.074 SE=0.155	Est=0.067 SE=0.158	Est=-0.509 SE=0.147	Est=-0.394 SE=0.149	Est=0.103 SE=0.159	**x**	z=-0.172 p=0.863 Adj p=0.863	z=1.459 p=0.145 Adj p=0.270
Steps	Est=-0.101 SE=0.156	Est=0.040 SE=0.158	Est=-0.536 SE=0.148	Est=-0.421 SE=0.149	Est=0.076 SE=0.160	Est=-0.027 SE=0.157	**x**	z=1.631 p=0.103 Adj p=0.206
T Bar	Est=0.158 SE=0.150	Est=0.288 SE=0.153	Est=-0.288 SE=0.142	Est=-0.173 SE=0.144	Est=0.324 SE=0.154	Est=0.222 SE=0.152	Est=0.248 SE=0.152	**x**

Feeder Depletion (Perch)

There was not a significant effect of perch design on the mean depletion per hour made to the bird feeders, (ANOVA, $F_{1,7}$=1.053, P=>0.05; Figure 25). Pairwise comparison of the mean depletion per hour to each perch design feeder revealed that overall, relating to preference, birds do not appear to have a preference for any perch design over any other (Table 20).

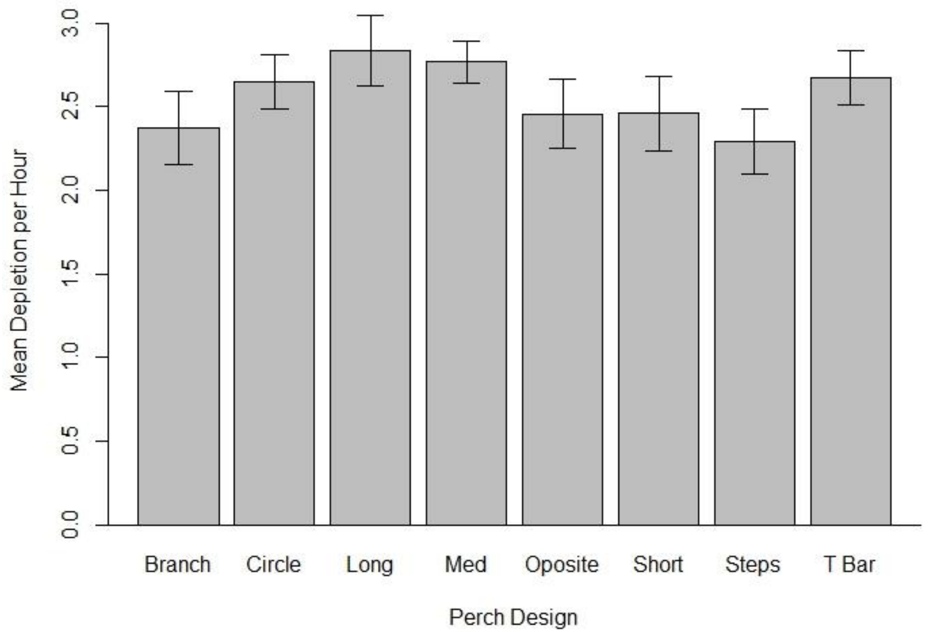


Figure 25: The mean depletion per hour for each perch design feeder, containing pooled data from all sample periods and is a summary of all species encountered. Table 14 includes all species encountered and the rates of visitation to all feeders

Table 20: LME output for pairwise comparison of depletion to feeders of differing perch design for all birds and all sites. The cells above the diagonal show the test statistic; t, the p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the test value (effect size) and associated standard error.

Perch Totals	Branch	Circle	Long	Medium	Opposite	Short	Steps	T Bar
Branch	**x**	t= 1.021 p=0.309 Adj p=0.721	t= 1.718 p=0.088 Adj p=0.819	t= 1.467 p=0.145 Adj p=1.000	t= 0.313 p=0.755 Adj p=0.880	t=0.324 p=0.746 Adj p=0.908	t= -0.302 p=0.763 Adj p=0.854	t= 1.116 p=0.266 Adj p=0.678
Circle	Value=0.276 SE= 0.270	**x**	t= 0.697 p=0.487 Adj p=0.852	t=0.446 p=0.656 Adj p=0.875	t= -0.708 p=0.480 Adj p=0.896	t= -0.697 p=0.487 Adj p=0.802	t= -1.323 p=0.188 Adj p=0.657	t= 0.095 p=0.924 Adj p=0.959
Long	Value=0.464 SE= 0.270	Value=0.188 SE= 0.270	**x**	t= -0.251 p=0.802 Adj p=0.864	t= -1.405 p=0.162 Adj p=0.756	t= -1.394 p=0.165 Adj p=0.662	t= -2.020 p=0.045 Adj p=1.000	t= -0.602 p=0.548 Adj p=0.767
Medium	Value=0.396 SE= 0.270	Value=0.120 SE= 0.270	Value=-0.068 SE= 0.270	**x**	t= -1.154 p=0.250 Adj p=0.779	t= -1.143 p=0.255 Adj p=0.714	t= -1.769 p=0.079 Adj p=1.000	t= -0.351 p=0.726 Adj p=0.924
Opposite	Value=0.084 SE= 0.270	Value=-0.191 SE= 0.270	Value=-0.379 SE= 0.270	Value=-0.311 SE= 0.270	**x**	t= 0.011 p=0.991 Adj p=0.991	t= -0.615 p=0.539 Adj p=0.795	t= 0.803 p=0.423 Adj p=0.912
Short	Value=0.087 SE= 0.270	Value=0.188 SE= 0.270	Value=-0.376 SE= 0.270	Value=-0.308 SE= 0.270	Value=0.003 SE= 0.270	**x**	t= -0.626 p=0.532 Adj p=0.828	t= 0.792 p=0.430 Adj p=0.859
Steps	Value=-0.082 SE= 0.270	Value=-0.357 SE= 0.270	Value=-0.545 SE= 0.270	Value=-0.477 SE= 0.270	Value=-0.166 SE= 0.270	Value=-0.169 SE= 0.270	**x**	t= 1.418 p=0.158 Adj p=0.886
T Bar	Value=0.301 SE= 0.270	Value=0.026 SE= 0.270	Value=-0.163 SE= 0.270	Value=0.095 SE= 0.270	Value=0.217 SE= 0.270	Value=0.214 SE= 0.270	Value=0.383 SE= 0.270	**x**

Experiment 4: UV Preference

Overall, 1042 individual visits to the bird feeders were recorded, representing 6 different species, although not all species were recorded during each individual recording session. The number of individual visits for each species are presented in Table 21. The data from all observation periods were combined prior to analysis to determine whether there is an overall preference for birds towards supplementary feeders with an additional UV coating. For those species with over 100 individual visitations recorded (in this case, just Great Tit), individual species preference analysis were also carried out.

Table 21. A summary of the species recorded at the Tophill Low Sample site during UV data collection. As discussed above, this is under the assumption that every visit to a feeder is a unique decision as the actual numbers of birds involved within each data collection experiment is unknown.

Species	Scientific Name	Occurrence
Chaffinch	*Fringilla coelebs*	19
Robin	*Erithacus rubecula*	19
Coal Tit	*Periparus ater*	12
Great Tit	*Parus major*	918
Blue Tit	*Cyanistes caeruleus*	21
Marsh Tit	*Poecile palustris*	53
Total		1042

Overall Avian UV Preference

There was no significant effect of UV on the number of visits birds made to bird feeders, (ANOVA, $F_{3,63}$=0.201, P=0.895; Figure 26). Pairwise comparisons of the number of visits to each colour revealed that birds overall did not appear to have any preference between any of the 4 options: blue (no UV), blue (with UV), red (no UV) (Table 22).

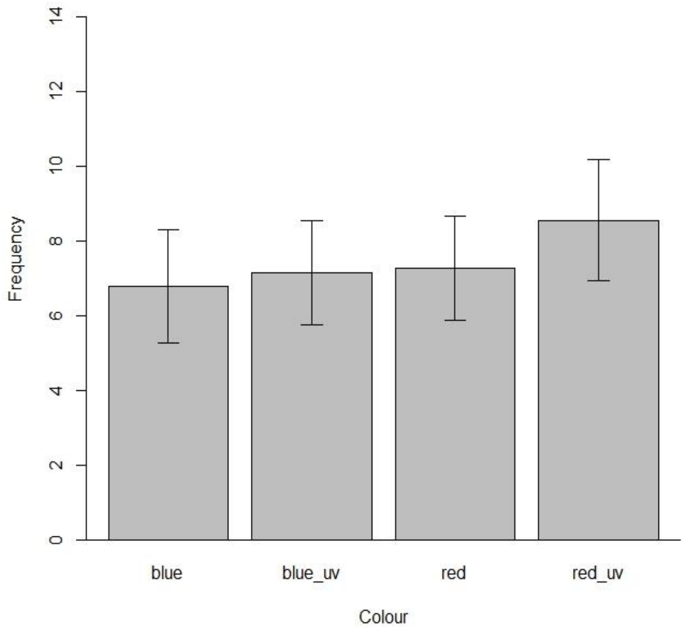


Figure 26: The mean frequency of visits to each feeder colour, with and without a UV coating per 15 minute observation period. Error bars represent ±1 S.E.

Table 22: GLM output for pairwise comparisons of visits to coloured feeders, with and without a UV coating (All species, all sample periods combined). The cells above the diagonal show the z value, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the estimate (effect size) and associated standard error.

UV_Colour	Blue	Blue_UV	Red	Red_UV
Blue	**x**	z=0.851 p=0.395 Adj p=1.185	z=0.397 p=0.691 Adj p=0.829	z=0.801 p=0.423 Adj p=0.846
Blue_UV	Est=0.075 SE= 0.088	**x**	z=0.083 p=0.933 Adj p=0.933	z=0.489 p=0.625 Adj p=0.938
Red	Est=0.095 SE= 0.238	Est=0.020 SE= 0.237	**x**	z=1.066 p=0.286 Adj p=1.716
Red_UV	Est=0.191 SE= 0.238	Est=0.116 SE= 0.237	Est=0.096 SE= 0.090	**X**

Species specific UV colour preference

Great Tit

There was not a significant effect of colour or addition of a UV coating on the number of visits Great Tits made to the different coloured/coated feeders (LME, $F_{3, 42.151}$=0.36038, P= 0.7819; Figure 27). Pairwise comparison of the number of visits to each coloured/UV feeder revealed that Great Tits do not show a significant difference in preference for any one colour over coloured feeder, either with or without the addition of a UV coat (Table 23).

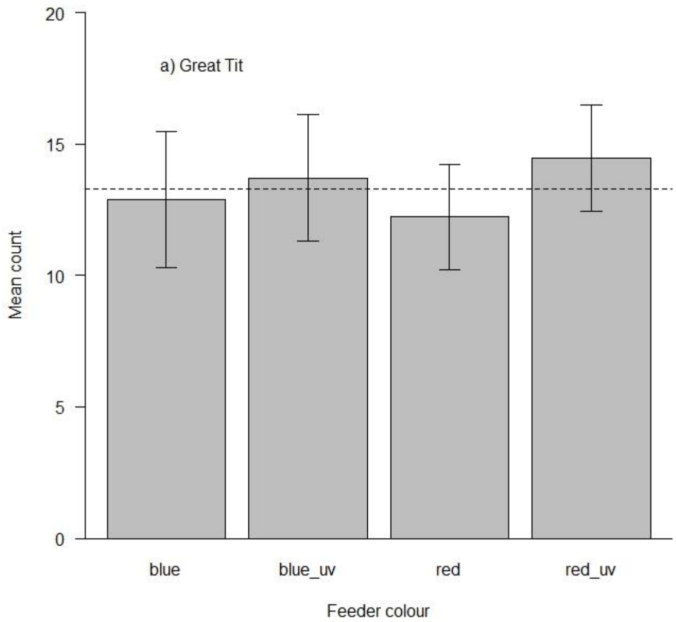


Figure 27: The average number of visits to feeders of all colours per observation period, pooled across all data collection periods for Great Tit (*Parus* major); the only species with over 100 individual visitations to the bird feeders.

Table 23: The GLM output for the pairwise comparison of visits to coloured and UV coated feeders for Great Tits from all data collection periods. The cells above the diagonal show the z value, p value and adjusted p value following post-hoc tests, with a bold font denoting significance. The cells below the diagonal show the estimate (effect size) and associated standard error.

Great Tit	Blue	Blue_UV	Red	Red_UV
Blue	**X**	z=0.622 p=0.508 Adj p=1.000	z=-0.226 p=0.821 Adj p=0.985	z=0.331 p=0.741 Adj p=1.000
Blue_UV	Est=0.0620 SE= 0.094	**X**	z=-0.476 p=0.634 Adj p=1.000	z=0.082 p=0.934 Adj p=0.934
Red	Est=-0.056 SE=0.249	Est=-0.118 SE=0.249	**X**	z=1.498 p=0.134 Adj p=0.804
Red_UV	Est=0.082 SE=0.249	Est=0.020 SE=0.249	Est=0.139 SE=0.093	**X**

Discussion

What are the overall preferences

Overall, there were significant differences in both the number of visits and depletion rate of seed between feeders of different colours and different perch designs. For colour, the silver feeders were most preferred over other colours, with the second most preferred colour being the green feeder, whereas the red and yellow coloured feeders were the least preferred overall. The addition of a UV coating to feeders had no effect on number of visits recorded both overall and at a species specific level. The pattern of colour preference differed between species, but with most closely related species exhibiting the most similar preference. For example, Blue Tits and Great Tits (Genus: *Parus*) visited the yellow and red feeders in lower numbers than the other feeders, while Coal Tits showed no preference between coloured feeders. House Sparrows (Genus: *Passer*) preferred the green feeder to many of the other colours, and also avoided yellow.

For perch design, overall the long, followed by the medium perch were most preferred over the other designs, whereas the circle, opposite and short were the least preferred designs of perches. In contrast to that of the avian colour preference experiments, although there were significant differences between the perch designs with regards visitation to each feeder, this was not the case for seed depletion as there was no significant difference between the amounts of seed depleted from feeders equipped with each perch design. There was also a slight variation in the pattern of colour preference between species. Although consistently the two most popular perch designs were long and medium, with regards the least popular designs, different species exhibited a lower level of preference for different perches than others. For example, Blue Tits showed a lower level of preference for the circle, opposite and short perches, whereas for Great Tits this was only opposite and short, or for Goldfinch also significantly preferring less the feeder with the steps perch design.

Overall for human colour preference, there was a significant difference in the recorded colour preference for different colours of feeders (denoted by placing tokens in coloured jars) with humans preferring the blue, red, green and yellow feeders over those painted black, purple, silver and white.. Due to the high overall proportion of votes cast being made by adults, adult preference closely matches overall preference however, this leads to large differences in the ranked preference for each of the colours between the two demographics. Whereas the feeders for adults are split into two groups; those with a high preference (blue, green, red and yellow) and those with a low preference (black, purple, silver and white), for children the most preferred colour overall was blue, with this the case almost exclusively in the demographic. The remaining seven coloured feeders each exhibited a very low preference for each of the remaining colours.

Colour preference: Why are silver and green preferred, and red and yellow avoided?

Several underlying factors may influence a bird's decision to feed at one colour feeder over another. These include perceived predation risk and crypsis, innate preferences for (or avoidance of), particular colours, avoidance of novel colours in the environment (neophobia), and the foraging decisions of con- and hetero-specifics (Foster, 1990).

Predation and Crypsis

Bright colours are documented to attract higher levels of predation than colours that increase an organism's crypsis in the environment. This is seen in a wide variety of species and habitats (Gotmark & Olsson, 1996, Haskell, 1996 & Stuart-Fox *et al*, 2003), and may explain why the red and yellow feeders were least preferred by birds in this investigation (Roper, 1990), if red and yellow could act to attract greater numbers of predators to the feeding site. In contrast, more cryptic colours (such as green) may experience a lower predation risk (Gotmark, 1996). In birds, darker and less conspicuous colours are commonly seen in plumage, particularly in females (Owens & Hartley, 1998). Brighter colours are often present on the ventral side to blend in with the canopy or sky when the bird is viewed from below, while darker colours on the dorsal side reduce detection when viewed from above (Gomez & Thery, 2007). At all sample sites, it is likely that the highest risk of predation was from avian predators.

High levels of conspicuousness in forageable resources have often been shown to increase foraging efficiency, especially by frugivorous or insectivorous species (Salzen *et al*, 1971) due to the increase in the resources' long distance advertisement (Willson *et al*, 1990). Good examples of this are in plants that often benefit from consumption to facilitate seed dispersal (Schaefer *et al*, 2007). In addition, juvenile or naïve birds have been shown to preferentially choose conspicuous prey (Roper and Wistow, 2007, Marples *et al*, 1998) while adults prefer more cryptic prey (Roper, 1990). It is not only the foraged items which are impacted by the colour and composition of the background (Galeotti *et al*, 2003), foraging species also exhibit a large amount of variation in plumage morphs dependant on environments (Galeotti, 2003, Delhey *et al*, 2010). This is seen both between species and within species where populations may occupy different niches (Gomez & Thery, 2007).

Innate preferences and avoidances of particular colours

A second explanation for the colour preferences observed by birds in our study is the innate avoidance of particular colours, perhaps due to their association with aposematic and warning colouration (Lindstrom *et al*, 1998). In some species, there is evidence of an underlying genetically fixed predisposition away from certain colours (Schuler & Hesse, 1985) or a learned avoidance during an individual's development or transition to maturity (Salzen *et al*, 1971, Avery, 1996) that results in the avoidance of organisms that naturally possess warning colouration (e.g. yellow and black Vespids (Wasps), red and black Coccinellids (Ladybirds)) (Rowe & Skelhorn, 2005). However, birds in ours study did visit the red and yellow feeders, but at a significantly lower level than the more preferred colours. This suggests that preferences towards certain colours can be altered following positive experiences or without negative reinforcement brought about by the action undertaken, as is documented in domestic chicks by Taylor *et al*, (1969). This may also be the case with coloured objects that do not resemble anything previously encountered (Roper & Wistow, 2007), this is due to testing of an object will often occur before an "avoidance image" for said object is generated. This may go some way to explaining why although a red insect might be avoided, a red bird feeder may not (Galeotti *et al*, 2003).

Neophobia:

In the selection of a food source, neophobia is likely to have a considerable role in decision making, and many species demonstrate a high level of short- (neophobia) or longer-term (dietary conservatism) avoidance in response to an unknown or novel prey item (Gotmark, 1996). However, at certain times of year; specifically winter or during times of low food availability an individual's level of neophobia is likely to be dependent on its hunger level and/or the effects of inter/intraspecific dominance and competition (Marples, 1998). Neophobia, therefore, can change due to differing levels of environmental stress (Barrows *et al*, 1980, Schuler & Hesse, 1985).

Red and yellow are uncommon as colours in garden bird feeders, and so neophobia may explain why birds chose to visit these colours less often. However, even juvenile birds in our study areas are likely to be familiar with the concept and use of supplementary feeders through their extensive use in gardens or as a tool in conservation management strategies, and thus may recognise feeders through their shape or other attributes, meaning that they visited feeders of colours that were less commonly encountered in their environment. Interactions between individuals, such as dominant individuals displacing subordinates from a preferred colour to a less preferred colour, may also explain why novel colours were not completely avoided. Birds were also able to view the food source (seed) within the feeder, which may also play a considerable role in reducing a neophobic response to a feeder, especially when a non-natural/anthropogenic food source is used (Pank, 1976).

Contrasts with previous studies

There are few previous studies of colour preference in relation to foraging (figure 1), and work on supplementary feeders in particular is subject to a high level of taxonomic bias towards Hummingbirds (family: *Trochilidae*), particularly Anna's Hummingbird (*Calypte anna*) (Grant, 1966, Stiles, 1976 & Wheeler, 1980). The observation (figure 1) that red is the most commonly reported colour in the literature, yet was one of the least preferred colours is our study, is likely due to differences in the diet between the study species. As Hummingbirds are nectivorous and are found predominantly in tropical regions (with exceptions), previous studies relating to supplementary feeders are of limited relevance to UK garden birds. Of the limited studies (5 species, 3 papers) on colour preferences in birds native to the UK, the majority focus on berries, usually concluding that the colours that symbolise the ripeness of the fruit often most commonly selected (e.g. Blackbird (*Turdus merula*) prefer red (ripe) berries over white (unripe) berries (Diesselhorst, 1972).

This study is the first to investigate the colour preference of omnivorous, (though predominantly granivorous in winter) species in a temperate region, specifically in the UK. In addition to this, it is also be the first study in a temperate region to use supplementary feeders in order to test colour preference, with the feeders identical in every aspect apart from their colour.

Producer-Scrounger Effect.

The producer-scrounger effect described a situation where an organism, rather than independently searching for its own food source, will be attracted to a particular area, due to the presence (David & Giraldeau, 2011) or behaviour of others (Morand-Ferron & Giraldeau, 2009). Producer-scrounger effects are commonly observed, especially among inexperienced or juvenile birds (Katsnelson *et al*, 2008) and may be a significant contributing factor in an individual's decision making. Foraging decisions at feeders in my study may be strongly influenced by producer-scrounger effects, particularly as birds form large (often mixed species) foraging flocks, especially in winter when natural resources are most depleted (Farine *et al*, 2014). These large flocks allow for extensive information (e.g. the location of a resource) and resource sharing (Beauchamp & Giraldeau, 1996). A notable downside of this technique is the increased competition for a highly desired resource (or coloured feeder) following its discovery due to the concentrated number of birds within an area. This may lead to increased aggressive behaviour from more dominant individuals causing the selection of less favourable food sources (or colours) by more submissive individuals.

Why is UV unimportant?

The addition of an ultraviolet coating to a bird feeder had no significant effect on the rate of visits by birds, in comparison to a feeder without a UV coating. Given that are birds visually sensitive at the UV end of the spectrum (Hunt *et al,* 2001) "probably the most advanced [visual system] of any vertebrate" (Goldsmith (in Church *et al*, 1998), we might have predicted an impact of UV on preference. UV is known to play a key role in a wide range of bird behaviours, including food choice, sexual selection (Bennett *et al*, 1997) and navigation (Church *et al*, 1998). Many avian-dispersed fruits possess a UV coating to increase their conspicuousness and attractiveness to birds (Maier, 1993), and UV has been shown to increase both foraging speed and efficiency in Blue Tits (Lyytinen *et al*, 2000). Many avian species also possess areas of UV plumage in order to increase their sexual attraction (Maier, 1993), with these patches often being sex specific (Eaton, 2007 & Sheldon *et* al, 1999). Examples include the UV crest of Blue Tits (Anderson *et al*, 1997) and a UV throat patch in Starlings (Bennett *et al*, 1997, Anderson & Amundsen, 1997). As UV provides an honest representation of a potential mates health and overall genetic condition (Hunt *et al*, 2001), UV and corresponding vision has an important role in many visually guided behaviours (Burkhardt & Maier, 1989).

Species difference in colour preference

Overall the preference for colour in avian species suggested that the silver and green feeders were significantly the most frequently visited with the yellow and red feeders receiving significantly less visitations. This is due, in part to the most common and frequently recorded species; Great Tit and Blue Tit sharing this preference; this trend was also seen in Coal Tit however, the differences in preferences were not significant. On the other hand, less abundant species such as House Sparrow and Greenfinch showed a significant preference (House Sparrow) for green feeders over less visited colours such as purple, red, white and yellow, however showing no significant difference in the visitation rates as compared to the black or silver feeders. A very similar trend can be seen in Greenfinch; however there is no overall significant difference in preference following post hock FDR tests. In addition to this, Robin and Starling both showed a preference for black (Robin significant against purple and white, Starling not significant after FDR). There are several potential explanations as to why these different colours may be preferred by different species. The first of these is likely due to the natural niche that an organism inhabits which will have a large impact on its colour preferences. Colour preference dependant on habitat has been documented in sexual selection through plumage variation across habitats (Galeotti, 2003 & Delhey *et al*, 2010) in addition to variation within a habitat, such as birds who occupy the understory are more likely to have a plumage of a darker colour than those species found in the canopy (Gomez & Thery, 2007). This matches the results of this investigation well with arboreal predominantly insectivorous *Paridae* species preferring (light) silver feeder as compared with predominantly granivorous species more associated with the understory (*Fringillidae, Passeridae, Sturnidae* or *Muscicapidae*) preferring darker less conspicuous colours. There may also be an impact with regards an individual's plumage effecting its colour preference, as can be seen in Vogelkop Bowerbird (*Amblyornis inornata*) who demonstrate a preference for colours most similar to their own plumage (as compared by human vision) (Diamond, 1987).

As colour (and UV) are often used as indicators for food quality; including nutrient content, ripeness (Willson *et al*, 1990) or toxicity (Rowe & Skelhorn, 2005), colour is likely to play a key role in decision making. However, colour preference is likely to be context specific (Galeotti *et al*, 2003) where recognition of the object, in addition to the colour will both have a role in food selection and the decision making process. As colour is a key deciding factor, by making the bird feeders identical in every way; except colours-with location factored in during data collection, this will allow for decisions purely based on colour to be recorded.

One potential explanation for the not significant result is that although it is known birds use their UV vision to forage (Siitari *et* al, 1999), they may not use UV cues to locate supplementary feeders as they are man-made and therefore not naturally occurring within the environment. A learnt behaviour may have been developed over time allowing species and individuals to associate these anthropogenic objects as a dependable source of food.

A further explanation as to the variation of preference between the feeders, rather than one colour being consistently favoured throughout is that, through the producer-scrounger effect and information sharing, an increased number of individuals are made aware of a resource causing a high density of foraging birds to be attracted to a specific area within a landscape. In order for individuals to utilise the most preferred resource/feeder, this will promote competition whereby submissive birds will be outcompeted and displaced to less preferred sites/locations or feeders by more dominant individuals; in this instance from preferred coloured feeders such as silver and green to less preferred feeders such as yellow and red. Another possible explanation for the array of visitation is that in all of the sample areas, though sustenance feeders were in place from the beginning of the winter season in order to attract birds to the area, in real terms, the use of supplementary feeders is likely to have only been in place for several generations of avian populations. This will mean that organisms and populations will have not been interacting with the feeders for long enough in order to evolve a response to the feeders, meaning that any decisions or behaviours around the feeders will have been individually learnt by the organism.

Why are longer perches preferred

Vigilance and visibility

The results suggest that the long perch was the most visited design both overall and in the majority of individually analysed species; including Blue Tit and Goldfinch , with visitation significantly higher than most (if not all) other perch designs. As discussed within the literature review, there is a remarkably small body of research with regards avian feet and perching with all passerines possessing a passive tendon locking mechanism (Quinn & Baumel, 1989) allowing an individual's foot to conform to the shape of a perch (Hutchinson, 2002 & Galton & Shepard, 2012), this therefore might go some way to explain the low level of significance in visitation between the perch designs. Although, with this in mind, there are likely other explanations as to why long perches are significantly preferred over other designs. In addition to the producer-scrounger effect as discussed above (regarding colour preference), potential vigilance and visibility with relation to each design are likely to strongly impact on an individual's decision.

Longer perches will allow birds to stand further away from the feeder (or feeding port) during antipredatory vigilance behaviour, with this in turn increasing the individuals' field of vision whilst on the feeder and thus decrease the overall predation threat (Lima & Bednekoff, 2011). There is much evidence suggesting that higher vigilance provides considerable benefit to foragers (Devereux *et al*, 2008) with a preference for longer (or higher) perches not only being recorded in avian species, but also in reptiles such as *Anolis aeneus* (Bronze anole lizard) who compete for more desirable territories that contain higher vantage points, with this a considerable portion of its antipredatory response (Stamps, 1987).

Escape Responses

Not only will longer perches allow for the potentially earlier alertness to a predation threat, it may also allow for a more rapid escape response. There are three main escape responses from a perch, these being: 1) rapid rate of climbing whilst in flight, 2) rapid horizontal flight and 3) high manoeuvrability (often not straight decent) diving (Hedenstrom & Rosen, 2001). For *Paridae* species, the escape tactic consists predominantly of a “woody cover escape”, common in many passerine species (Lima, 1993) with the same true for the majority of *Fringillidae* (finch) species. With all species, it is likely that following the recognition of a predation threat, an initial dive to cover will occur; as this will increase flight speed more rapidly than other escape techniques (Lima, 1993) with speed declining with increased take off angle (Deveraux *et al*, 2008). Although a higher perch has been shown to elicit a more successful antipredatory response (Cooper, 2010), there is currently no evidence to suggest a longer or more simply designed perch will be of a benefit in an escape, however Gotmark (1996) found that species of Birds of prey, such as Sparrowhawk (*Accipiter nisus*) have been documented attacking perching birds whilst at bird feeders, therefore; with a longer perch providing greater visibility of a potential threat, this may in turn lead to the further decrease in predation risk.

Perch orientation

The orientation of the perch, with regards to both the proximity and accessibility of cover provided by nearby foliage, in addition to the orientation of the food port of the feeder may also influence foraging decisions. For all species within this experiment, it is likely that due to their occupation of the same habitat and similar niches occupied that the visual capabilities will be very similar (Hart, 2001). Therefore, when a bird stands on a perch which protrudes out at a right angle to the feeder itself, the feeder will only occupy part of an individual’s monocular vision, with only a turn of the head required in order to feed. This means that the individual will still have use their binocular vision; the vision used to gauge distance and as such will be able to assess any predation threat which may occur. This in turn will prevent the unnecessary expenditure of energy (a highly important resource; especially in the winter period) by fleeing from a low level of predation threat; as it will allow the individual to assess the overall threat and thus respond with the appropriate response such as fleeing the feeder to cover, or remaining vigilant to an increased level until the threat is removed or diluted. On the other hand, perches which position the bird directly facing the feeder may have increased negative impacts for feeding birds. Although the bird only needs lean into the feeding port in order to feed, the supplementary feeder will occupy a large portion, if not all of the individual's binocular vision, thus leaving birds with only monocular or peripheral vision and as a result, removing their ability to gauge distance. This may lead to birds being easier to startle, therefore more likely to fly to cover given the presence of a predator -without necessarily being able to quantify the size or risk posed by the threat. In addition to this, in order to minimise the effect of loss of vision, a larger portion of an individual's time may be redirected towards vigilant behaviour rather than feeding- in order to retain the same level of antipredator vigilance of other perch designs. Therefore, this will not only decrease the amount of food consumed over the same amount of time as compared to straight perches, but will also increase the risk from predation as it is shown predators are more likely to attack organisms that exhibit any level of vulnerability (Cresswell *et al*, 2004) or any aspects which may single one individual out from the crowd (e.g. the Oddity effect (Landeau & Terborgh, 1986, Lima & Bednekoff, 2011) or aposematic selection (Allen, Raison & Weale, 1998))

Marketing Outcomes: Designing a bird feeder to attract more individuals or species

The results from the avian colour, avian UV, avian perch and human colour preference experiments suggest that a green coloured feeder with no UV coating and a long perch is the most preferred combination of colour and perch design taking into account both avian and human preference, however a silver coloured feeder, no UV coating with a long perch is most highly preferred combination overall purely by birds. This therefore could be marketed as "preferred by birds".

Individual species colour analysis suggest that different species have different preferences for certain colours, with this most apparent in species what occupy different niches in a habitat and species in different families, however, one drawback to the current research is that only sufficient data was collected in order to analyse the more common species independently, therefore meaning that species with only a few visitations across the whole data collection period were not able to be individually analysed.

With the current research, it may be possible to market certain feeder colours as targeted for some specific species. A good example of this is the silver feeder as it experienced a significantly higher level of visitation versus that of other coloured feeders by both Blue and Great Tits. This may mean that the silver feeder can be marketed as the most preferred by *Parus* species (that were individually analysed). On the other hand, due predominantly to the natural assemblage of the avian populations at the sample sites, some families were only represented by a single species in sufficient numbers in order to allow for individual species analysis. This is seen in House Sparrows who were the only member of their family (*Passeridae*) to be recorded and though their preference for green is significant against less visited feeders (e.g. purple and white in this case), there is not a statistically significant difference in visitation as compared to black, blue or silver feeders. The same problem is also seen for Robin, Greenfinch and Starling; species where there is an apparent preference for a certain colour, however the visitation rates for this are not always significantly different from that of other coloured feeders. This is in addition to them being the only member of their families with enough data to be individually analysed.

Therefore it can be concluded with confidence that for Blue and Great Tits, a silver coloured feeder with a long perch is the most preferred colour and perch design, however, for the majority of other species surveyed, due to the low levels of visitation or the absence of significant results, the overall preferences for other species cannot be confirmed, although the overall trend suggests that Green has the highest level of visitation in the majority of other species surveyed.

Opportunities for Future Research

Colour preference of less common or more desirable species.

In order to design species specific feeder for less common species, the following must be taken into account: if a species does not exist in the landscape, the habitat where the bird feeders are situated is not suitable (Evans *et al*, 2009) or the surrounding habitats does not have a sufficient network of biodiversity corridors allowing individuals (and therefore their genes) to pass along (Savard *et al*, 2000), this species will simply not occur at the experimental bird feeders. However at sites with existing populations, a feeder may be able to be designed in order to increase the frequency of visits. One way to collect sufficient data for less common species would be to undertake data collection (using an identical method) at sites with known populations of the desired species thereby allowing the colour preference of less common species to be recorded. In gardens frequented by these target species, this potential future research may encourage increasingly frequent visitations, however, this is highly dependent on both the individuals preferences and the condition of the surrounding landscape, including the availability of the natural food supply (specifically during the winter period).

Design perches to exclude larger species

When providing supplementary food for wildlife, there is often an aversion away from certain species, examples including Feral Pigeons or Squirrels due to the negative effect they impose on attractive/desirable species by preventing feeding and reducing the amount of resource (Bonnington *et* al, 2014), this leads to these species often being considered as pest species (Sheail, 1999). This is to the extent that Squirrel Proof feeders are manufactured to prevent squirrels feeding at "*bird"* feeders. On this tangent, it may be possible that although the large perch was the most popular amongst avian species in this experiment, it may also prove popular with "pest" species due to its design. Although on occasion grey squirrels (*Sciurus carolinensis*) were seen attempting to gain access to a bird feeder (personal obs) this often did not come to fruition due to the presence of anthropogenic disturbance in the area: which acted as a deterrent. In this investigation, Squirrel proof feeders; which would also deter larger birds from feeding were not considered.

Further research would aid this investigation by examining the perch preference for squirrels and large birds to see if a longer perch provides increased ease of access in comparison to smaller perches, in addition to whether the complexity of the design, (simple designs such a "long" and "medium" versus more complex designs such as "steps" or "branch") have any impact on the level of visitation; as a proxy for preference, before a solid conclusion can be made with regards the best perch for avian species.

Attracting birds to a new area.

This research examines the overall preference for 8 coloured bird feeders against one another in order to investigate whether one coloured feeder is preferentially chosen for or against versus the other 7 coloured feeders. However this research was undertaken at sites with historic and continuous use of bird feeders, where supplementary feeders are likely to be seen as a reliable food resource throughout the year by resident populations. One question arising from this is at a site which does not frequently provide supplementary food, specifically through the use of bird feeders, if there is a certain colour or design of feeder attracts foragers to a site quicker, and/or in greater numbers as compared to other coloured feeders. Although this is likely to be highly dependent on a species/flocks movement throughout the landscape- as passerines often form large mixed species flocks (Morse, 1977) and rarely forage independently during winter (Emlen, 1952, Barash, 1974, Farine *et al,* 2014) (foraging parties), this may provide some illustration as to the most preferred feeder colour both in close proximity and from a distance, illustrating certain colours conspicuousness within the environment and how in turn this effects visitation and preference.

Species preference relating to food source

Another question arising from this research is in regards to the different types of seed feeder. From this current research we can conclude that overall, silver was the most popular colour of feeder, however, this was conducted using a mixed seed feeder, containing a variety of different types of seed such as oats, sunflower hearts, millet and peanuts etc.. However, feeders designed specifically to accommodate different seed types (e.g. peanuts, sunflower seeds, nyjer seeds) often have comparatively differing designs and seed/resource dispensing port. . This in turn will affect the species attracted to each type feeder and as such, the colour preferences of these species. This may mean overall colour preference may differ in relation to food source due to the species attracted. Considering the potential implications of this, further research may be warranted in order to investigate if a species colour preference differs with food/feeder type. This may lead to the customisation of certain feeders for different species, more so than is available in the current market.

Further research into the effects of UV

As it is known, UV plays an important role in a wide variety of aspects in a bird's life, therefore, to fully understand the effects of UV with regards to a supplementary feeder, further research could be conducted both during the winter (suggesting all birds are mature/adults), and continuing this through the breeding season to juvenile fledgling in order to investigate whether there is a difference in UV preference between adult birds and juveniles and in turn whether this has any impact on feeder preference.

Competition at feeders

Dominance, hierarchy and competition are all likely to have a significant effect on an individual's food choice or foraging location (Beauchamp, 2000), often with access to food being highly dependent on social standing within the group (Patterson, 1977, Pravosudova *et al*, 2001). Dominant birds will often displace submissive individuals from sites (Krams, 1998) due to either their preference for that area (Stephens, 2008)/ the antipredatory benefits it provides (Ekman, 1987). Throughout the current research, an interspecies dominance hierarchy was seen, with this being predominantly size related (Goldfinch, Great Tit, Blue Tit, Coal Tit, Marsh Tit) (personal obs), however, this was not recorded or quantified. Further research may examine the overall first preferences of arriving birds, including the number of birds already at the feeder array and whether this leads to conflict or competition for certain feeders dependant on colour. The presence (or absence) of conspecifics may also be investigated to see if it has any effect on overall feeder preference by use of a model or stuffed bird on a perch in order to review whether this illicit a response from the approaching bird. The appearance of aggressive behaviour against the model may suggest that it is a preferred feeder, whereas if completion is avoided, it may either suggest a passive response to the feeder's colour or indicate where the approaching individual is within the social hierarchy, and in addition to this, if responses differ depending on the relative levels of natural food available within a landscape.

Predation risk and preference

The risk of predation is likely to have a strong impact on how, when and where a bird (or any organism) feeds, with adaptive foraging decisions often made in order to minimise an individual's risk (e.g. Foraging Location: Farine *et al*, 2014 or Escape Response: Devereux *et al,* 2008), specifically, it is shown that often there will be higher visitation to a feeder in a "safer" environment than ones in more exposed locations (Doherty *et al*, 2010 & Tsurim *et al*, 2010). Therefore, as location has an impact on the level of visitation, does this differ with colour/design and are birds more willing to undertake a higher level of risk for certain colours or designs than others?

Understanding the behaviour of how birds feed at supplementary feeders including their innate preferences could have far reaching implications for population level bird community structure in urban areas, with an increased understanding of these factors allowing us to better comprehend community dynamics. A deeper understanding of this would allow for improved support for displaced wildlife in our towns and cities, including the maintenance of biodiversity and species richness throughout.

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Appendix:

A1: The full spectral output for all feeder colours, using Red/Green/Blue ratios against a white standard.

Colour	R	G	B
Black	1135.364	1284.914	1850.015
Blue	1983.003	3518.524	7484.415
Green	1396.585	1653.837	2275.515
Purple	5184.187	4742.597	5565.397
Red	22307.89	5332.917	3457.663
Silver	20082.93	21979.92	23451.46
White	46517.11	46916.83	46676.79
Yellow	34504.56	24293.53	7352.043

A2: Example of poster displayed at each sample site during data collection

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As Part of my Master's Thesis, please do not touch.

If you would like to know more, or to report any Issue, please contact:

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