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Cognition and personality when deciding what to eat: foraging plasticity and diet in the great tit

Thesis presented by

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Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism and intellectual property.

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Jennifer Rose Coomes

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Abstract

Animal survival is highly dependent on consuming food resources, and many studies in behavioural ecology have investigated, for example, how animals optimise their foraging behaviour to increase their fitness. Yet recent work has shown that individuals differ consistently in their behaviours, known as animal personality, and therefore animals may be limited in their plasticity in response to different foraging opportunities. Similarly, individual differences in cognitive abilities may also drive foraging behaviour, but these mechanisms have rarely been explored under different ecological conditions. Advances in genetic sequencing of dietary components now make it possible to explore how animal personality and cognition influence foraging decisions and diet outcomes in wild birds. My thesis used the great tit to explore these ideas.

In Chapter 2, I examined how one cognitive mechanism (inhibitory control) and a behavioural trait (exploration behaviour) that is closely associated with the fast-slow exploration personality axis, were associated with foraging flexibility, a type of behavioural plasticity, in two ecologically relevant contexts. Both inhibitory control and exploration behaviour were associated with foraging flexibility, but only when the value of an alternative food source was high and there was a risk of predation, respectively. The results show that how cognition and personality affect foraging flexibility is only revealed when the ecological context changes.

While many studies of foraging behaviour quantify food choices, an alternative method is to look at the realised outcome of foraging choices – i.e. the diet, which represents multiple prey taxa consumed over multiple foraging events. In Chapter 3, I used DNA metabarcoding to describe the diet of adult and first year individuals in spring and winter, and the diet of nestlings in the nest, in coniferous and deciduous woodlands. I investigated the degree of dietary separation between demographic groups. Results suggest dietary differences between birds of different ages (adult, first year and nestling) and sexes, and that season and habitat play an important role. Investigating dietary variation advances our understanding of how individuals use resources across a heterogeneous landscape, and provides insight into how populations may adapt to environmental variation.

In Chapter 4, I investigated how inhibitory control measured in the wild was associated with the spring diet of adults and the diet of nestlings. I expected that inhibitory control would be important for parents when deciding on the prey to provision their young. Inhibitory control of males was associated with their own diet whereas inhibitory control of females was associated with the diet of their offspring. This result suggests that cognitive differences associated with parental care differ between the sexes. In Chapter 5, I investigated how three cognitive traits (innovation, inhibitory control and learning) and one behavioural trait (exploration behaviour) were associated with the winter diet. I expected that any effects of cognition and exploration behaviour may be especially pronounced in winter when the challenge of finding food is greater than in the spring. Innovation and inhibitory control were associated with the dietary composition of plants, and innovation and exploration behaviour were associated with the dietary composition of invertebrates.

My thesis represents the most comprehensive study on the diet of this key model species to date and by studying these wild birds in multiple contexts, I have demonstrated that foraging plasticity, and the extent to which animal personality and cognition drive behaviour and diet, are dependent on the environmental context, such as predation risk and season, and whether birds are foraging for themselves or their offspring. Understanding these dynamics will be important for future work, such as how individuals survive and populations persist in the face of environmental change.

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Great tit in the hand, Co. Cork

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Chapter 1

General Introduction

A pair of great tits, Meantán mór

by Becca Young

1.1 Foraging

Acquiring food is critical for the survival and fitness of wild animals, so understanding the processes driving variation in diet and foraging success is an important aim in ecology (Perry and Pianka, 1997; Weimerskirch, Gault and Cherel, 2005; Snijders *et al.*, 2018). Factors that drive variation in foraging behaviour include: genes (Sokolowski, Pereira and Hughes, 1997), social factors such as competition or producer-scrounger rules (Caraco and Giraldea, 1991; Svanbäck and Bolnick, 2007), and environmental factors such as weather, habitat or season (Fernández and Lank, 2008; Kowalczyk *et al.*, 2015; Fortune *et al.*, 2020). Furthermore, intrinsic factors such as age (Daunt *et al.*, 2007) and metabolic demands (Burton *et al.*, 2011) will lead to variation in behaviour whilst foraging. Foraging is a major aspect of behavioural ecology because the causes of variation are very diverse, and it is of great importance for animals.

Diet is a particularly important aspect of foraging behaviour, and influences a variety of ecological processes. Diet variation can lead to association behaviour (e.g.

sticklebacks prefer to associate with conspecifics fed the same prey; Ward, Hart and Krause, 2004), and assortative mating (Snowberg and Bolnick, 2008). The prey consumed by animals influences their energy intake and allows them to fulfil energetic demands (Spitz *et al.*, 2010). Moreover, diet can play a role in sexual selection. In species that advertise their health and condition to potential mates through feather or body colour, and where females choose partners based on this trait, the diet is a source of the carotenoids used for their bright colouration (Kodric-Brown, 1989). Prey resources are often limiting so animals must compete for food, either for their own consumption or to feed to their offspring (Alatalo, 1982). By consuming different foods or expanding the diversity of their diet, animals can reduce competition with conspecifics for resources, which can lead to dietary niche separation (Bolnick, 2001; Svanbäck and Bolnick, 2007).

Interspecific niche separation in diet has been studied extensively in many taxa including birds, fish and primates (Abbott, Abbott and Grant, 1977; Alatalo, 1982; Gladfelter and Johnson, 1983; Schreier *et al.*, 2009) and allows us to explain how species coexist in sympatry. However, intraspecific dietary niche separation is also important for ecological dynamics (Polis, 1984; Shine, 1989) and has a number of drivers, in addition to competition. Environmental factors such as habitat type and season will influence the diet due to variation in the abundance and diversity of prey that are available. For example, conifer plantations are expected to have a lower abundance and diversity of prey types than deciduous woodland (Gibb and Betts, 1963; van Balen, 1973), and the availability of prey in the winter compared to summer will be reduced (Alatalo, 1982). Diet differs between life stages and sexes, likely due to variation in energetic requirements and nutritional needs between parents and offspring (Munn and Dawson, 2003; Young *et al.*, 2010), and between males and females (Vasey, 2002; Thiemann *et al.*, 2011). Environmental factors can interact with intrinsic factors to influence the extent of dietary variation between demographic groups. For example, diet variation between the sexes may only be revealed during the breeding season when males and females have different reproductive demands (Coelho, 1974), and age differences in diet may be more pronounced in habitats that are more challenging to find food, if juveniles are less

efficient foragers than adults (Goss-Custard and Durell, 1987; Fayet *et al.*, 2015; Grecian *et al.*, 2018). Part of this thesis seeks to establish the extent of intraspecific dietary variation among ages and sexes, and between seasons and habitat types.

So far, I have mentioned factors that drive diet variation between groups of animals (e.g. females, or animals in deciduous habitats). However, even within an age group, or sex class, individuals may show variation in diet. Individual niche specialisation describes how individuals use a narrower subset of resources than the population as a whole, not due to age, sex, morphology or the availability of food (Bolnick *et al.*, 2003). For example, in a population of sea otters, 32 common prey types were discovered but most individuals only consumed up to four prey types and differed markedly from conspecifics in their diet (Estes *et al.*, 2003). The authors attribute these differences in diet between individual sea otters to differences in the sensory and motor skills required for different prey types (Estes *et al.*, 2003). Specialists are expected to be more efficient foragers than generalists and may have higher fitness under certain circumstances (Patrick and Weimerskirch, 2014a; but see Woo *et al.*, 2008), but generalists may be more flexible foragers and more able to respond to changes in prey availability (Terraube *et al.*, 2011; Stewart and Dudash, 2018; Korpimäki *et al.*, 2020). Many cognitive and personality traits are important for foraging (Toscano *et al.*, 2016; Rosati, 2017) and different abilities in these traits may determine the prey consumed by animals (MacLean *et al.*, 2014; Troxell-Smith and Mella, 2017).

1.2 Personality and foraging

Animals exhibit consistent differences in behaviour across time or context, known as personality (Sih *et al.*, 2004; Groothuis and Carere, 2005). There are many different terms used in the literature to describe personality, for example, temperament (Reale *et al.*, 2007), behavioural profiles (Groothuis and Carere, 2005), coping styles (Koolhaas *et al.*, 1999) and behavioural syndromes (suites of correlated behaviours; Sih *et al.*, 2004; Sih, Bell and Johnson, 2004). I will use animal personality for this thesis since it is the most widely used term (Gosling and

John, 1999; Gosling, 2001). Personality is widespread across the animal kingdom (Gosling, 2008; Réale and Dingemanse, 2012), from invertebrates, such as crickets and squid (Sinn and Moltschaniwskyj, 2005; Kralj-Fišer and Schuett, 2014), to fish (Toms, Echevarria and Jouandot, 2010), birds (Drent, van Oers and van Noordwijk, 2003; Herborn *et al.*, 2010; David, Auclair and Cézilly, 2011) and mammals (Freeman and Gosling, 2010; Schirmer *et al.*, 2019). Personality in animals is most commonly measured with certain traits (often called temperament traits, e.g. aggression, shyness/boldness; Wilson *et al.*, 1994; Reale *et al.*, 2007) which are indicators of variation in a whole variety of behaviours.

The 'fast-slow exploration' personality axis incorporates a variety of traits and defines individuals along a continuum with 'fast' individuals who are more exploratory and more predation-risk prone at one end, and 'slow' individuals who are less exploratory and predation-risk averse at the other (Verbeek, Drent and Wiepkema, 1994; Koolhaas *et al.*, 1999; Groothuis and Carere, 2005). This axis is defined mostly for birds and a similar continuum, the 'reactive-proactive' axis, has been described for small mammals (Groothuis and Carere, 2005; Reale *et al.*, 2007). Recent research on personality has placed focus on investigating how individual variation is maintained in populations, and the ecological and evolutionary consequences of personalities (Wolf and Weissing, 2012). The 'fast-slow' axis has been linked to life-history strategies that involve foraging (Biro and Stamps, 2008; Réale *et al.*, 2010). For example, fast explorers are likely to require a high food intake rate to maintain a higher metabolism (Careau *et al.*, 2008) and as a result may prioritise fast growth rates and high fecundity compared to slow explorers who consume food at a lower rate and prioritise slower growth rates and later fecundity (Biro and Stamps, 2008).

There are a variety of ways that personality has been shown to influence foraging behaviour, for example, there is evidence that bold and shy individuals forage in different locations (Patrick and Weimerskirch, 2014b), personality type can determine the propensity to forage in groups (Michelena *et al.*, 2009) and activity level (a personality trait) can determine the foraging strategy of predators (Sweeney *et al.*, 2013; Keiser *et al.*, 2020). In addition, certain personality traits (e.g.

exploration or boldness) correlate with predation-risk proneness (van Oers *et al.*, 2004; Ward *et al.*, 2004), and are likely to lead to individuals with different personality types assessing the 'food-fear' landscape differently (McArthur, Banks and Boonstra, 2014). For example, when faced with a choice between toxic or non-toxic food in a 'safe' location and non-toxic food in a 'risky' location, bold brushtail possums foraged at both the non-toxic feeders equally whereas shy individuals did not use the 'risky' feeder (Mella *et al.*, 2015). When investigating how personality influences foraging behaviour, the majority of studies quantify an observed behaviour, but, by taking this approach, the field may be missing the importance of the realised effect of foraging behaviour: the diet. Very few studies have investigated diet linked to personality due to methodological constraints (Han and Dingemanse, 2015; Toscano *et al.*, 2016; Troxell-Smith and Mella, 2017). Observing foraging choices in the wild is difficult and captive studies that provide subjects with simple food choices (Bergvall *et al.*, 2011) may be too simplistic to make inferences about the effect of personality on the diet of wild animals. Diet determines the energy available for growth and reproduction so investigating how personality is linked to the wild diet of individuals in complex environmental scenarios, furthers our understanding of the ecological consequences of consistent individual variation in behavioural traits.

1.2.1 Personality and individual variation in diet

There are conceivably many scenarios in which animal personality can drive individual differences in dietary components, but have yet to be tested explicitly (Troxell-Smith and Mella, 2017). First, animals of different personality types may occupy different habitats which hold varying resources (Patrick and Weimerskirch, 2014b). For example, bold red squirrels occupy a wider range of habitats than shy individuals (Boon, Réale and Boutin, 2008) and bold mud crabs use subtidal habitats, whereas shy mud crabs use intertidal habitats (Griffen, Toscano and Gatto, 2012). Additionally, the 'reactive-proactive' axis has been linked to habitat use (Schirmer *et al.*, 2019) and travel distances (van Overveld and Matthysen, 2010), which is likely to have impacts on the diet. Second, neophobia and boldness

are personality traits directly linked to eating novel food suggesting that personality will impact the diet (Exnerová *et al.*, 2010; Bergvall *et al.*, 2011). For example, bold deer are more likely to eat novel food than shy deer and bold great tits are more likely to eat aposematic prey than shy great tits (Exnerová *et al.*, 2010; Bergvall *et al.*, 2011). Third, personality has been linked to metabolic rate (Careau *et al.*, 2008) so bold or highly active individuals may have different energetic or dietary requirements from less active individuals.

Finally, personality determines how individuals act in social situations, and the role they play in foraging groups, which is likely to influence foraging opportunities and therefore consumption of prey. For instance, shy individuals are more likely to associate with conspecifics in feeding groups which may limit the resources available to them (sheep: Michelena *et al.*, 2009; cane toads: González-Bernal, Brown and Shine, 2014). Additionally, because they are more likely to join established patches rather than find new ones, shy barnacle geese are more likely to be scroungers than producers (Kurvers *et al.*, 2010). If an individual's diet consists of a subset of the diet items consumed by the population, and is consistent over time, this individual diet specialisation can be seen as part of an individual's personality (Araújo, Bolnick and Layman, 2011, Dall *et al.,* 2012).

The direction of causation between personality and diet could also occur in the opposite direction: diet may influence personality (Han and Dingemanse, 2015, 2017). For example, one study on great tits found an association between not diet *per se*, but the biomass of caterpillars delivered to nestlings and exploration behaviour later in life (van Oers *et al.*, 2015). This association was apparently mediated by the stress response as nestling great tits that received lower amounts of caterpillars, were more stressed, and were fast explorers after fledging (van Oers *et al.*, 2015). Personality has been linked directly to diet differences between individuals in only a handful of studies (Costantini *et al.,* 2005; Bergvall *et al.,* 2011; Kerr and Ingram, 2021) so more needs to be done to aid our understanding of the drivers of individual variation in resource use.

1.2.2 Personality and foraging plasticity

Animals have to forage under ecological conditions that are constantly changing and individuals should change their behaviour appropriately to match a given situation, that is, they should show behavioural plasticity (Dingemanse *et al.*, 2009; Stamps, 2016). However, research in the last few decades has shown that behavioural plasticity when conditions change is limited because it is costly for individuals to sample information from the environment and to flexibly adjust their behaviour (Komers, 1997; Dewitt, Sih and Wilson, 1998; Dall and Johnstone, 2002; Snell-Rood, 2013). Individuals will be impacted differently by these costs, because of differences in internal state (Dall, Houston and McNamara, 2004), leading to some individuals being more plastic than others (Dingemanse *et al.*, 2009; Coppens, De Boer and Koolhaas, 2010; Morand-Ferron, Varennes and Giraldeau, 2011). For example, bold rainbow trout are more plastic than shy trout, as bold individuals became more shy after losing a fight or watching a shy demonstrator, yet shy trout did not modify their response (Frost *et al.*, 2007). Similarly, more aggressive female Ural owls are more plastic in their nest defence than less aggressive females in response to changing food conditions (Kontiainen *et al.*, 2009). Understanding the drivers of individual variation in behavioural plasticity is a major focus of evolutionary ecology studies (Wolf, van Doorn and Weissing, 2008; Dingemanse *et al.*, 2009). Ecological context itself is likely to play a role in how plastic individuals are. For instance, under predation risk, individuals may need to be more plastic than when risk is low, because showing inflexible, inappropriate behaviour (e.g. continuing to forage) will result in being predated. Equally, if a new high-value food resource suddenly becomes available, individuals need to be plastic to adjust their behaviour to exploit the new resource. The extent to which individuals show individual variation in behavioural plasticity in a foraging context, and the potential drivers of this plasticity, remains poorly understood. In addition to examining their role in diet, this thesis seeks to unpick the underlying behavioural mechanisms that facilitate foraging plasticity when conditions change among individuals.

Specific facets of the 'fast-slow' axis (e.g. exploration and responsiveness), are linked to individual variation in plasticity among individuals when conditions change (Benus *et al.*, 1991; Koolhaas *et al.*, 1999; Marchetti and Drent, 2000; Dingemanse *et al.*, 2002; Quinn and Cresswell, 2005), but there is no clear consensus in the literature which end of the continuum is more associated with greater plasticity. This is particularly true for exploration behaviour, for example, some studies find evidence that slow explorers, those that make fewer movements around a novel environment compared to fast explorers, are more plastic when conditions change (Verbeek, Drent and Wiepkema, 1994; Marchetti and Drent, 2000), but more recent studies have found mixed support (no relationship: Arvidsson and Matthysen, 2016; fast explorers are more flexible: Rojas-Ferrer, Thompson and Morand-Ferron, 2019), with one study finding that both ends of the continuum can show flexible behaviour depending on context (Frost *et al*., 2007). How the fast-slow axis is linked to individual variation in behavioural plasticity of foraging decisions, when the environmental context changes, is poorly understood. Furthermore, studies are often limited in only looking at one potential mechanism driving individual variation in behavioural plasticity, without considering how, for example, cognition may play a role, either independently or dependently with personality traits.

1.3 Cognition and foraging

Although the influence of personality on foraging is a relatively recent development in behavioural ecology, the role that cognition plays in foraging has long been studied (Shettleworth, 2001). Cognition allows animals to acquire, process, store and act on information from their environment (Shettleworth, 2010) and success finding food depends on the ability of animals to carry out these processes and adjust their behaviour to different contexts. For example, animals may have to find and recall the profitability of a food patch, avoid aggressive competitors and be vigilant to the risk from predators (Stephens and Krebs, 1986; Godin and Smith, 1988; Lima and Dill, 1990; Hall and Fedigan, 1997; Lima and Bednekoff, 1999), all of which require information processing.

It is well established that individuals differ in their cognitive abilities (Thornton and Lukas, 2012; Boogert *et al.*, 2018) and many studies have investigated individual cognitive performance in a foraging context, both in captivity and in the wild. Traditionally, studies tested cognitive abilities related to foraging in a captive setting (Brown and Jenkins, 1968; Adams and Dickinson, 1981; Balda and Kamil, 1989; Kamil, Balda and Olson, 1994), which has the advantage of allowing control over external factors that can impact performance during testing. Research has now moved to assaying cognitive traits in the wild, in an ecologically relevant context for the species (Lipp *et al.*, 2001; Henderson, Hurly and Healy, 2006; Isden *et al.*, 2013; Morand-Ferron *et al.*, 2015; Pritchard *et al.*, 2016; Cauchoix *et al.*, 2017; Muth *et al.*, 2017) and has begun to assess the fitness consequences of cognition (Keagy, Savard and Borgia, 2009; Cole *et al.*, 2012; Cauchard *et al.*, 2013; Shaw *et al.*, 2019). Studies have focused on particular cognitive mechanisms thought to be involved in animal foraging in the wild, such as spatial learning and memory (Pravosudov and Roth II, 2013; Tello-Ramos *et al.*, 2018; Sonnenberg *et al.*, 2019), or on behaviour that has a 'wow-factor' like tool use (Bluff *et al.*, 2010). However, more recently there is growing appreciation of how executive functions such as inhibitory control are important for foraging (Rosati, 2017), as they are ubiquitous across vertebrates and there is likely to be individual variation in performance, that is, how well an animal executes tasks designed to test executive functions (Bray, Maclean and Hare, 2014; Kabadayi *et al.*, 2017).

1.3.1 Learning

Learning comes in many forms: classical conditioning refers to forming associations between environmental cues that occur in high congruity with positive (e.g. palatable food) or negative (e.g. toxic prey) outcomes. For example, animals may learn colours or patterns that are associated with palatable and or toxic food (Gittleman and Harvey, 1980; Ham *et al.*, 2006), or what cues indicate when a fruit is ripe or not (Korine and Kalko, 2005; Valenta *et al.*, 2016). Operant conditioning requires animals to learn to associate environmental cues with their own

behavioural actions and their co-occurrence with positive or negative outcomes. For example, animals may learn when it is most rewarding to remain at or move to a new foraging patch (Krebs and Inman, 1992; Warburton, 2003), that turning over leaf litter reveals hidden insects, or that waiting for prey to approach is the best hunting technique (Eaton, 1970). Tests of animal learning typically involve presenting subjects with a novel stimulus (e.g. colour or symbol), or training them to perform a behaviour (e.g. pressing a lever when the novel stimulus is presented), alongside a food reward (Wilkenfield *et al.*, 1992; Morand-Ferron *et al.*, 2015). Individual differences in learning performance can then be measured by counting how many presentations of these stimuli are required before the animal forms the association, for example, when colour or symbol choice errors are below a given threshold, or when an animal repeatedly and consistently performs the desired behavioural action (Boogert, Giraldeau and Lefebvre, 2008; Bonaparte, Riffle-Yokoi and Burley, 2011).

Often, a spatial component is involved in tests of learning to investigate the ability of animals to learn the location of rewards. Spatial learning performance has been measured in many taxa in captivity using a radial arm maze baited with food (Spetch and Edwards, 1986; Hughes and Blight, 1999; Bimonte and Denenberg, 2000; Lipp *et al.*, 2001; Samuelson *et al.*, 2016), and has been demonstrated in the wild using feeder arrays (Tello-Ramos *et al.*, 2015; Croston *et al.*, 2016; Sonnenberg *et al.*, 2019). The recent development of radio-frequency identification (RFID) technology allows large numbers of free-living individuals to be tested on their ability to learn a single rewarded location from an array of feeders. This has the advantage of gathering a large amount of data on many individuals simultaneously, without the need to bring them into captivity (Sonnenberg *et al.*, 2019; Reichert *et al.*, 2020). The ecological relevance of spatial learning for foraging has been demonstrated across animals that depend on learning the location of food and landmarks, such as hummingbirds and bees (Cartwright and Collett, 1983; González-Gómez and Vásquez, 2006). Moreover, not only do animals have to learn these locations, they may need to retain this knowledge for extended periods of time, for example, ravens and several species of jay must remember the location of food caches

hidden during the winter (Balda and Kamil, 1989; Bednekoff and Balda, 1996; Bugnyar and Kotrschal, 2002). Once caches are recovered, or foraging patches depleted, animals must continuously update this information by forming new associations, and ultimately being plastic in their foraging choices.

Although huge advances have been made in our understanding of animals' learning by observing when they make correct foraging choices (e.g. choosing the cue associated with palatable prey, or choosing the spatial location where food is available), these choices may not reflect successful foraging. For example, the richness (i.e. total number of different food items) or the composition (i.e. the taxonomic identity of food items consumed), may be a more informative indicator of foraging success. There are a few examples, mostly in primates, of spatial learning abilities being linked to aspects of diet or foraging ecology. For instance, ruffed lemurs which rely heavily on fruit, showed a more robust spatial memory than less frugivorous species (Rosati, Rodriguez and Hare, 2014). Additionally, a comparative study on golden lion tamarins and Weid's marmosets showed that tamarins have a more accurate spatial memory over a longer time, reflecting their diet of insects and patchily distributed fruit, compared to marmosets which are obligate gumnivores (Platt *et al.*, 1996; Rosati, Rodriguez and Hare, 2014). Only one study has looked at links between diet and spatial learning in birds (Arnold *et al.*, 2007). In this study, wild blue tit nestlings that were provided with a taurine supplement (an amino acid important for development) were more successful at a spatial learning task than controls (Arnold *et al.*, 2007). While it is intuitive to focus on learning when it comes to foraging success, there are many other behavioural and cognitive mechanisms that may drive foraging behaviour, such as innovation and inhibitory control.

1.3.2 Innovation

Innovation is a composite trait, likely underpinned by a number of cognitive processes, and refers to the process by which animals solve a novel problem or find a novel solution to an old problem (Reader and Laland, 2003). Innovation is mostly

investigated in a foraging context, as food is a strong motivator for animals to innovate. Early work on animal innovation consisted of chance observations of one or a small number of individuals performing a novel behaviour, such as lobtail feeding in humpback whales, sweet potato washing in Japanese macaques and blue tits pecking through milk bottle tops to get at the cream inside (Fisher and Hinde, 1949; Ennion, 1962; Kawai, 1965; Weinrich, Schilling and Belt, 1992). More recently, experimenters have developed problem-solving devices (e.g. puzzle boxes) to provide animals with an opportunity to innovate, so that the capacity to innovate is not reliant on biased, chance observations within natural populations (Griffin and Guez, 2014). Problem-solving devices can be deployed with captive animals, semi-natural populations or completely wild animals and to be considered an innovator, individuals must manipulate the device such that they gain access to the food reward inside (Cole and Quinn, 2012; Griffin and Guez, 2014; Benson-Amram *et al.*, 2016; Johnson-Ulrich, Holekamp and Hambrick, 2020). By testing many individuals on their problem-solving propensity, it is possible to investigate if certain classes of individuals are more likely to be innovators. For example, if competitive individuals monopolise resources, necessity may drive less competitive individuals to use innovative behaviours to obtain alternative food sources (Laland and Reader, 1999; Reader and Laland, 2001; Morand-Ferron *et al.*, 2011 but see also Boogert *et al.*, 2008). This provides insight into the evolutionary significance of individual variation in innovation tendencies (Morand-Ferron *et al.*, 2011). Consequently, competitive ability as well as cognitive performance (e.g. innovations) may together drive the food types animals can access. Therefore, through competition or cognition, animals are "successful" in foraging, but their strategies differ, so variation in diet among individuals may be a consequence of these different foraging strategies.

If innovation allows animals to exploit novel food resources, for example, using tools to fish for termites (Sanz, Morgan and Gulick, 2004), or washing sweet potatoes (Kawai, 1965), then innovators may have different diets to non-innovators. Several studies have classified innovation according to the acquisition of novel food types in the diet (Overington *et al.*, 2009; Navarrete *et al.*, 2016) but comparative studies investigating direct links between innovation and dietary diversity have

shown mixed results. One study showed that dietary generalists had higher innovation rates than specialists (Ducatez, Clavel and Lefebvre, 2015) but two others found no association (Overington *et al.*, 2011; Reader, Hager and Laland, 2011). These studies were all at the interspecific level and used broad diet categories as their measures of diet diversity. Empirical studies of single species investigating the association between individual variation in innovation propensity and the identity of prey in the diet are lacking, and I argue are necessary to make direct links between innovation and its consequences for foraging behaviour.

1.3.3 Inhibitory control

From a psychology perspective, inhibitory control is the ability to stop performing a prepotent, dominant behaviour and instead do something seemingly more appropriate (Diamond, 2013). This definition does not seek to explain inhibitory control from an adaptive point of view i.e. the fitness implications of having good or poor inhibitory control, and does not take into account the costs associated with developing this cognitive ability. However, I have chosen to use the definition most common in the literature that encompasses inhibitory control and its various forms (e.g. delayed gratification, motor inhibition etc.) most broadly. Inhibitory control, together with working memory and cognitive flexibility, are core processes for purposeful, goal-directed action, known as executive functions (Espy, 2004; Diamond, 2013). I will explore the hypothesis that inhibitory control is likely to be important when making foraging decisions in wild animals. For example, it may play a role when an animal has to make choices between different foods (e.g. low quality nearby or high quality further away) or where to feed, for instance avoiding returning to a depleted food patch. Individuals with high inhibitory control may be more efficient at avoiding unprofitable or unpalatable foods, may be better able to make choices between foods that differ in value and accessibility, and may avoid foods that do not have a high effort-to-payoff ratio (MacArthur and Pianka, 1966). In the first scenario above, animals must have enough information about different foraging options nearby and further away to provide them with a choice, which

then allows for the possibility that inhibitory control may be useful for decision making. In the other scenarios, even with only information about immediate foods, inhibitory control may still be important in a choice to eat the food or to search for something else. This leads to the expectation that variation in inhibitory control may have consequences for diet. Furthermore, in line with the expectation that inhibitory control will be involved in how individuals forage for themselves, altricial species may also need inhibitory control when provisioning their offspring. Inhibitory control may help parents better manage the trade-off between self-feeding and provisioning (Weimerskirch and Cherel, 1998; Weimerskirch *et al.*, 2003) or may mean they are better able to provision enough food of suitable quality for offspring development (Grieco, 2002; Ramsay and Houston, 2003; Arnold *et al.*, 2007; Pagani-Núñez *et al.*, 2011). How inhibitory control is involved in parental care has not been investigated.

Conceptually, there are many ways of measuring different components of inhibitory control, depending on what needs to be inhibited and why. For example, in humans, inhibiting unwanted thoughts (i.e. cognitive inhibition) may be distinct from inhibiting eating a tasty, but fattening food (i.e. response inhibition), although both scenarios require some level of self-control (Bari and Robbins, 2013). Consequently, there are many ways to test inhibitory control in humans and animals. One method is to test for delayed gratification, by presenting subjects with a choice between a small, immediate reward and a larger, future reward (Mischel, Shoda and Rodriguez, 1989; Diamond, 2013). Delayed gratification has been extensively examined in human children using the famous marshmallow test, and has been shown to have impacts in later life. For example, children that could wait longer for a reward had improved academic success and were better able to deal with stress and frustration as adolescents (Mischel, Shoda and Peake, 1988). Poor performance on delayed gratification tasks has been associated with ADHD (Costa Dias *et al.*, 2013), addiction (Mitchell and Potenza, 2014) and obesity (Epstein *et al.*, 2010), with the latter being one of the few empirical examples in which a food choice experiment with inhibitory control has a direct consequence on other aspects of an individual's life. A small number of non-human taxa, namely primates, corvids and

parrots, have been tested and have shown to succeed at, delayed gratification tasks (Dufour *et al.*, 2012; Auersperg, Laumer and Bugnyar, 2013; Beran, Rossettie and Parrish, 2016; Miller, Boeckle, *et al.*, 2019). While these studies have never looked at dietary consequences, they have demonstrated that subjects show improved inhibitory control when the quality, rather than the quantity, of food rewards varied (Hillemann *et al.*, 2014; Miller, Frohnwieser, *et al.*, 2019), which may be an indication that inhibitory control is involved in dietary choices.

Another commonly measured component of inhibitory control is motor inhibition, in which a subject has to stop a motor action that is irrelevant or inappropriate, in order to achieve a goal. For example, moving a food item to a new cupboard in the kitchen and having to stop oneself going to the old cupboard for that item. The 'detour-reaching' task, also called the 'cylinder' task, is commonly used to test motor inhibition (i.e. inhibiting a motor action) in animals. To succeed in the task, a subject must inhibit reaching directly for a food reward that is blocked by a transparent barrier and instead must reach or move around the barrier to get to the reward (Bray, Maclean and Hare, 2014; Kabadayi, Bobrowicz and Osvath, 2018). Recent research has moved beyond simply characterising variation in individual ability and comparing performance between species (reviewed in Kabadayi, Bobrowicz and Osvath, 2018), to examine how inhibitory control is related to fitness (Boogert *et al.*, 2011; Ashton *et al.*, 2018; MacKinlay and Shaw, 2019) and to employ comparative studies that investigate the evolution of cognitive skills (MacLean *et al.*, 2014; Kabadayi *et al.*, 2016, 2017). However, there is still a lack of research investigating how performance on the detour-reaching task, and how inhibitory control in general, is related to functional behaviour in an ecologically-relevant context.

Despite the expectation that inhibitory control will be related to foraging, there are few examples of inhibitory control being related to foraging success or diet. One study tested two primate species on a delayed gratification task and found that common marmosets waited longer for a reward than cotton-top tamarins, which the authors attribute to the feeding ecology of each species (Stevens, Hallinan and Hauser, 2005). Marmosets feed on tree sap, a slow release reward which requires

them to wait, so they are likely to value future rewards more than insectivorous tamarins (Stevens *et al.*, 2005). Two other studies used the detour-reaching task to investigate an association between inhibitory control and diet and found contrasting results. MacLean *et al.* (2014) found that primates with better inhibitory control had a higher dietary breadth, but the opposite correlation was found in pheasants (van Horik *et al.*, 2018). Dietary information in these studies was imprecise: in the primate study, broad dietary categories (e.g. leaves, fruit) were taken from the literature, and the pheasant study used dietary preference and not a natural measure of dietary breadth or composition (MacLean *et al.*, 2014; van Horik *et al.*, 2018). Studies are needed to investigate how variation in inhibitory control is related to individual composition of the natural diet, and how the inhibitory control of parents is related to provisioning. Part of this thesis seeks to investigate how cognitive mechanisms may drive variation in diet of individuals and their offspring.

Inhibitory control also has the potential to influence individual variation in behavioural plasticity when conditions change, since inhibitory control influences how individuals respond to new stimuli and controls impulsive, potentially inappropriate, changes in behaviour. These processes are vital in the appropriate adjustment of behaviour to environmental change. In addition, environmental context is likely to be important in revealing this association. For example, under risk of predation, any association between inhibitory control and behavioural plasticity may disappear due to stress that causes individuals to make inappropriate decisions (Schwabe and Wolf, 2009). Similarly, the association between inhibitory control and plasticity could depend on the value of food options. However, the role of inhibitory control in influencing individual behavioural plasticity, in a foraging context in particular, and the effects of environmental conditions on this relationship, is unknown.

1.4 Metabarcoding as a technique to characterise the diet

Characterising the diet of animals in the wild is challenging for a number of practical and ethical reasons. It is difficult to observe species when they are feeding, and to be able to observe the types of food they are consuming, particularly if they are generalist feeders. A number of traditional methods have identified prey invasively through gizzard or stomach dissection, which can only be carried out following death (Betts, 1955; Pierce and Boyle, 1991; Cuthbert *et al.*, 1999) and so are not useful for long term monitoring of diet over the lifetime of an individual. An alternative technique is morphological identification of prey from faecal material, which does not require the animal to be killed, but both this and the enteric dissection techniques require specialist skills to identify the remains of prey from undigested parts. Even with specialist training, prey may not be successfully identified to a high taxonomic resolution (e.g. only to family level). Moreover, dissection and morphological analysis are biased towards identifying hard-bodied organisms because soft-bodied prey will be completely digested (Arim and Naya, 2003; Pompanon *et al.*, 2012).

The pit-falls of morphological analysis of prey have resulted in the rapid expansion of molecular methods for dietary analysis, such as DNA metabarcoding, that overcome these challenges and provide greater taxonomic detail. DNA metabarcoding is an ideal approach for characterising the diet of wild animals as it identifies multiple taxa contained within many environmental DNA samples simultaneously, through the use of DNA barcodes and high-throughput sequencing (Shokralla *et al.*, 2012; Taberlet, Coissac, Hajibabaei, *et al.*, 2012; Taberlet, Coissac, Pompanon, *et al.*, 2012; Yu *et al.*, 2012). In diet studies, short fragments of prey DNA are determined from faecal samples which are then given a taxonomic assignment by matching the fragments to a reference database (e.g. GenBank or BOLD; Barcode of Life Data Systems, barcodinglife.org). DNA metabarcoding overcomes the challenges faced by morphological approaches because samples are collected non-invasively (e.g. faeces), specialist taxonomic identification skills are not necessary and even fragments in very degraded DNA can still be identified to a fine taxonomic resolution (Deagle, Eveson and Jarman, 2006; Elbrecht *et al.*, 2017).

Lower sequencing costs and the expansion of reference sequence databases have meant that the number of metabarcoding studies has rapidly increased in recent years (Ando *et al.*, 2020). DNA metabarcoding has been used to address a wide range of topics within diet studies, such as resource partitioning, diet overlap, competition and ecological impacts of changing populations (Crisol-Martínez *et al.*, 2016; reviewed in Ruppert, Kline and Rahman, 2019). Metabarcoding has been used on a number of species to date, but the diet of passerines has not been studied using this technique until recently (Jedlicka, Vo and Almeida, 2017; Rytkönen *et al.*, 2019; da Silva *et al.*, 2020; Shutt *et al.*, 2020).

1.5 The great tit as a model species

Great tits are one of the most widespread passerine bird species and are found across Europe down to northern Africa, and across the Middle East into central Asia (Cramp and Perrins, 1993; Gosler and Clement, 2007). They are one of the best-studied passerines throughout Europe thanks to their suitability in long-term study systems (van Balen, 1973; Wilkin *et al.*, 2006). They readily breed in nest boxes (Minot and Perrins, 1986; East and Perrins, 1988) and are tolerant of close observation by field workers, so nest attempts including measures of reproductive success and life history variables such as lay date, clutch size and fledgling number, can be easily recorded. Great tits are tolerant of equipment attached to the nest, for example mini surveillance cameras for recording parental provisioning rate (Royama, 1970; Naef-Daenzer, Naef-Daenzer and Nager, 2000; van Oers *et al.*, 2015) or equipment for assaying cognitive performance. Both adults and nestlings are easily trapped or temporarily removed from the nest allowing unique identifying rings to be fitted to the leg, morphometric and weight measurements to be taken, and samples collected for dietary analysis. As well as being easy to monitor in the wild, great tits also habituate well to captivity. Wild birds can be trapped and held in an aviary facility before being released back to the field site after a few weeks, providing opportunity for manipulation experiments on wild animals to be performed in a controlled setting (Dingemanse *et al.*, 2002; Davidson *et al.*, 2018).

Great tits have regularly been used as a model species to study personality and cognition (Marchetti and Drent, 2000; Cole, Cram and Quinn, 2011; Dingemanse *et al.*, 2012; Morand-Ferron *et al.*, 2015; Reichert *et al.*, 2020). One of the first studies investigating personality traits in great tits showed that hand-reared males had consistent within-individual differences in their response to a novel object and in their tendency to explore a novel environment (Verbeek, Drent and Wiepkema, 1994). This work became the basis for future studies that measured exploration behaviour in great tits and other species. Exploration behaviour is repeatable and heritable in wild and captive populations of great tits (Dingemanse *et al.*, 2002; Drent, van Oers and van Noordwijk, 2003; Quinn *et al.*, 2009) and bi-directional selection lines for fast and slow explorers have been established in the Netherlands (Drent, van Oers and van Noordwijk, 2003). This artificial selection approach is important for the identification of co-selected traits, for example morphological and physiological traits (e.g. stress) (Harri *et al.*, 2003; Baugh *et al.*, 2012). Exploration behaviour in great tits has been found to correlate with other behaviours such as boldness and risk-taking (van Oers *et al.*, 2004), which forms the basis for personality axes such as the 'fast-slow' and the 'reactive-proactive' axis (Koolhaas *et al.*, 1999; Groothuis and Carere, 2005; Quinn *et al.*, 2011).

In addition to personality, great tits are well suited to studying cognition as they are generally neophilic (Gibb, 1957) so do not require long, intensive habituation efforts, and are naturally innovative so will engage in cognitive tasks (Cole, Cram and Quinn, 2011; Cauchoix *et al.*, 2017). Additionally, there has been selection on genes related to neuronal function, learning and cognition in the great tit genome, when compared to other species (Laine *et al.*, 2016), providing support for the importance of enhanced cognitive function and further reason to study cognition in this species. Individual variation in cognition has been extensively investigated, with a focus on behaviours such as problem-solving performance (Cole, Cram and Quinn, 2011; Serrano-Davies, O'Shea and Quinn, 2017), learning (Morand-Ferron *et al.*, 2015; Cauchoix *et al.*, 2017; Reichert *et al.*, 2020) and inhibitory control (Davidson *et al.* 2021, Pre-print). Additionally, among-individual variation in cognition in great tits has been linked to fitness, (e.g. problem-solvers had larger clutches; Cole *et al.*,

2012), showing the importance of having a species that is easy to study in both captivity and the wild, and which tolerates disturbance so that fitness measures can be obtained.

1.5.1 Diet

There are relatively few detailed studies on dietary composition in adult great tits, despite many long-term studies on this species. Early work used gizzard analysis (Betts, 1955) and foraging observation (Gibb, 1954) to detail the diet across a number of years and illustrated the wide variety of prey consumed by great tits. As a species, the great tit is thought to have a generalist diet but recent work suggests there is dietary specialisation at the individual level (Pagani-Núñez, Valls and Senar, 2015; Pagani-Núñez *et al.*, 2016), indicating the importance of investigating among-individual variation in diet. Investigating the diet throughout the year, especially during winter, will be particularly relevant for my research aims. Foraging in winter is challenging and a high proportion of newly fledged birds perish at this time (Gibb, 1954), and therefore I would expect variation in cognition and personality to play a role in their survival. Attempts to investigate the natural diet of great tits in winter are particularly lacking and studies are mostly restricted to establishing the importance of natural beechmast and supplemental feeding for the diet (van Balen, 1980; Chamberlain, Gosler and Glue, 2007), as opposed to determining the range of prey, both plant and invertebrate, that are exploited by the great tit in the winter. In addition to Betts (1955), Vel'ký et al. (2011) provides one of the only studies detailing the winter diet and found that although plant material was the most dominant winter food, invertebrates such as moths, beetles and dipterans were also present. Investigating the diet in a variety of habitats may also reveal effects of cognition and personality on foraging behaviour since prey availability will not be universal and birds in different areas may rely to a greater or lesser degree on alternative prey (Pagani-Núñez *et al.*, 2011). van Balen (1973) compared deciduous woodland and conifer woodland and discussed a number of factors that differ between the two habitats that may cause differences in diet. For example, the density and abundance of caterpillars and the density of great tits is greater in

deciduous habitats compared to coniferous (van Balen, 1973), and investigating dietary differences between habitat types will further our understanding of how individuals use resources across a heterogeneous landscape.

Another limitation generally in the literature is that there is a disproportionate focus on nestling great tit diets (Royama, 1966; García-Navas and Sanz, 2011; Pagani-Núñez *et al.*, 2017), and very few studies that accurately characterise adult diet in the wild. Nestling diets have received a lot more attention than that of the adults, likely due to the ease of observing young at the nest. Neck collars were an early method of identifying the diet of young passerines and functioned to prevent nestlings swallowing prey, which the researcher would collect and identify after a few hours (Slagsvold and Lifjeld, 1985; Barba, López and Gil-Delgado, 1996). There are ethical concerns with this method and when the technology became available, putting up cameras at the nest provided a better alternative. Because great tits readily breed in nest boxes, it is easy to attach cameras to the inside or outside of a nest box and record the identity of prey and parental provisioning rate (Naef-Daenzer, Naef-Daenzer and Nager, 2000; Wilkin, King and Sheldon, 2009; Navalpotro *et al.*, 2016). There is a wealth of studies investigating the diet of nestling tits with the aim of identifying important prey groups (Royama, 1966, 1970; Naef-Daenzer, Naef-Daenzer and Nager, 2000; Pagani-Núñez *et al.*, 2011), linking nestling diet and condition (Naef-Daenzer and Keller, 1999; van Oers *et al.*, 2015; Serrano-Davies and Sanz, 2017), investigating how reproductive success is affected by composition of prey (García-Navas and Sanz, 2011) and identifying the importance of particular prey types at different stages of development (Ramsay and Houston, 2003; Arnold *et al.*, 2007; García-Navas, Ferrer and Sanz, 2013).

Video recordings at nests have been widely used to study diet but have a number of disadvantages. First, the lighting and position of the parent in the frame greatly influences identification of provisioned prey. Bright sunlight can wash out the colour of prey and small prey items obscured by the beak such as flies and spiders are challenging to identify with confidence. Even if the parent obligingly pauses on entry and is well lit, many prey items simply cannot be identified (pers. obs.; Wilkin *et al.*, 2009). Because of this, broad categories of prey are used, for example,

lepidopteran larvae, diptera, coleoptera and often a category of 'unidentified' (Nour *et al.*, 1998; Navalpotro *et al.*, 2016). Accurate identification of prey at a higher resolution than these broad categories requires at least a basic level of invertebrate ID knowledge. Second, there is evidence that great tit parents manipulate prey, for example removing the wings of flying insects, rendering prey ID difficult (Barba, López and Gil-Delgado, 1996). Third, watching video footage is very time-consuming even with the aid of programmes such as MotionMeerkat (Weinstein, 2015) that detect motion in video and produce still images of parent birds at the nest. Finally, we cannot know the extent of the diet that is brought to offspring and do not know if we are missing important prey taxa that either cannot be identified or are not caught on camera.

Molecular approaches can overcome the challenges of identifying prey from video footage but only a few studies have used molecular methods for dietary analysis in any tit species (blue tits: Jarrett *et al.*, 2020; Shutt *et al.*, 2020; Shutt, Trivedi and Nicholls, 2021), and only two studies have looked at great tits. Pagani-Núñez *et al.*, (2017) used stable isotope analysis to identify the nestling diet and assessed the reliability of this approach against data from video recordings. The second paper was the first to use DNA metabarcoding on insect frass and the faeces of four tit species to assess the identity of consumed prey and its availability (Rytkönen *et al.*, 2019). There are no studies that have established the full diversity of the great tit diet, across seasons and habitats, for adults and nestlings. The great tit is of great importance to ecological studies and DNA metabarcoding provides an opportunity to obtain detailed dietary information from different life stages throughout the year in different habitat types, providing greater understanding of dietary differences in this species.

1.5.2 The field sites and study populations in the Bandon Valley

This study was conducted in the Bandon Valley, county Cork, Ireland, where 12 nest box study sites are established; six mixed deciduous woodland and six conifer plantations. Seven of the 12 sites were set up in 2012 by William O'Shea (O'Shea,

2017) and the additional five were added after 2015. Table 1.1 shows the size of each site, the main habitat type and the number of nest boxes (all sites have a density of two boxes per hectare). All fieldwork in this thesis including collection of faecal samples, running of cognitive assays in the wild and capturing birds to take into captivity, was undertaken at these field sites. Sites are a maximum 45 minute drive to University College Cork, which ensures birds are not in transit for longer than necessary.

Table 1.1. The 12 study sites used in this thesis in the Bandon Valley, Co. Cork, Ireland. Habitat type was either mixed deciduous woodland ('mixed') or conifer plantation (six sites of each), the area of each site is given in hectares (total 199 ha), the number of boxes per site (total 395) and the location in decimal degrees (DD) is given.

Name	Habitat type	Area (ha)	Number of boxes	Coordinates (DD)
Ballinphelic	Coniferous	18	36	51.840074, -8.628249
Castle Bernard	Mixed	17	33	51.741821, -8.773443
Carrigeen	Coniferous	15	30	51.821298, -8.814267
Dunderrow	Mixed	14	28	51.719711, -8.604451
Dukes Wood	Mixed	16	31	51.787396, -8.755946
Farran	Coniferous	11	22	51.700448, -8.805728
Garretstown	Coniferous	25	51	51.654770, -8.616293
Inishannon	Mixed	10	20	51.763048, -8.662415
Kilbrittain	Mixed	25	49	51.671880, -8.683837
Lissarda	Coniferous	15	30	51.858086, -8.859128
Piercetown	Coniferous	15	30	51.788888, -8.456197
Shipool	Mixed	18	35	51.737620, -8.631437

1.6 Thesis aims and chapter structure

The chapters of my PhD thesis are presented in chronological order and my aims were to:

i. examine how cognition and a behavioural trait linked to the fast-slow personality axis are associated with individual variation in foraging plasticity, in two ecologically relevant contexts
ii. identify the invertebrate and plant taxa present in the diets of adults and first year individuals in spring and winter, and the invertebrates present in the diet of nestlings in the nest, using DNA metabarcoding
iii. establish the extent of intraspecific dietary variation among ages and sexes and between seasons and habitat types
iv. investigate cognition and personality as potential drivers of diet differences between individuals and their offspring

In **Chapter 2** I investigated how a measure of cognition (inhibitory control) and a behavioural trait closely linked to personality (exploration behaviour) were associated with individual variation in behavioural plasticity of foraging decisions. I examined how the value of food rewards and the presence of a predator affected food choice, and how these ecological factors interacted with cognition and personality to affect foraging flexibility. This chapter is published in the Journal of Animal Ecology.

In **Chapter 3** I examined the extent of variation in diet between age classes and sexes, across seasons and habitat types. I used DNA metabarcoding to identify the diet of adults, first years and nestlings in two habitats: conifer plantations and mixed deciduous woodland. I measured the composition (identity of taxa) and the richness (number of taxa) of dietary items. For adults and first years, I identified invertebrate and plant taxa in the diet in two seasons: spring and winter. For nestlings, I identified the invertebrates present in the diet in spring. I also compared the diets of adults with their own offspring. The aim of this chapter was to examine

age and sex as potential drivers of dietary differences to improve our understanding of how individuals fit into the niche occupied by the species as a whole.

In **Chapter 4** I investigated how a measure of inhibitory control in the wild is associated with the spring diet of adults and their nestlings. In addition, I explored if the association between parent inhibitory control and nestling diet can be explained by nestling mass and rate of food brought to the nest. The aim of this chapter was to i) investigate the association between diet and a cognitive trait assayed in the wild and ii) investigate cognitive differences between the sexes that are associated with parental care.

In **Chapter 5** I investigated how three measures of cognition (inhibitory control, innovation and learning) and one behavioural trait closely associated with personality (exploration behaviour), were associated with the winter diet of adults. I investigated the winter diet in this chapter because the four traits were measured in the winter and as there is evidence that cognitive performance can vary with age, consistency in time of year is important. In addition, I expected that effects of cognition and exploration behaviour may be especially pronounced in winter when finding food is more challenging.

Chapter 6 brings together the main findings of my thesis to discuss i) the importance of ecological context in revealing associations between variables of interest, ii) the consequences of and the direction of causation for, the association between behavioural traits linked to personality and cognition, and diet and iii) the influence of cognition on parental care and other behaviours, with a focus on inhibitory control. Finally, I suggest areas for further investigation.

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Chapter 2

Inhibitory control, exploration behaviour, and manipulated ecological context are associated with foraging flexibility in the great tit

Great tits participating in the foraging flexibility task

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2.1 Abstract

Organisms are constantly under selection to respond effectively to diverse, sometimes rapid, changes in their environment, but not all individuals are equally plastic in their behaviour. Although cognitive processes and personality are expected to influence individual behavioural plasticity, the effects reported are highly inconsistent, which we hypothesise is because ecological context is usually not considered. We explored how one type of behavioural plasticity, foraging flexibility, was associated with inhibitory control (assayed using a detour-reaching task) and exploration behaviour in a novel environment (a trait closely linked to the fast-slow personality axis). We investigated how these effects varied across two experimentally manipulated ecological contexts, food value and predation risk. In the first phase of the experiment, we trained great tits (*Parus major)* to retrieve high value (preferred) food that was hidden in sand so that this became the familiar food source. In the second phase, we offered them the same familiar hidden food at the same time as a new alternative option that was visible on the surface, which was either high or low value, and under either high or low perceived predation risk. Foraging flexibility was defined as the proportion of choices made during four minute trials that were for the new alternative food source. Our assays captured consistent differences among individuals in foraging flexibility. Inhibitory control was associated with foraging flexibility - birds with high inhibitory control were more flexible when the alternative food was high value, suggesting they inhibited the urge to select the familiar food and instead selected the new food option. Exploration behaviour also predicted flexibility – faster explorers were more flexible, supporting the information gathering hypothesis. This tendency was especially strong under high predation risk, suggesting risk aversion also influenced the observed flexibility because fast explorers are risk prone and the new unfamiliar food was perceived to be the risky option. Thus, both behaviours predicted flexibility, and these links were at least partly dependent on ecological conditions. Our results demonstrate that an executive cognitive function (inhibitory control) and a behavioural assay of a well-known personality axis are both associated with individual variation in the plasticity of a key functional behaviour. That their effects

on foraging flexibility were primarily observed as interactions with food value or predation risk treatments also suggests that the population level consequences of some behavioural mechanisms may only be revealed across key ecological conditions.

2.2 Introduction

Organisms are constantly under pressure to adapt to changes in their environment. Behavioural plasticity – that is, the reversible change in individual behaviour induced by environmental variation – allows individuals of many species to adapt throughout the course of their lives (Snell-Rood, 2013; Stamps, 2016). However, behavioural plasticity is constrained by a diversity of costs and mechanisms that differ among individuals, and consequently some individuals are more plastic than others (Dewitt, Sih and Wilson, 1998; Dall and Johnstone, 2002; Snell-Rood, 2013; Stamps, 2016). Explaining why this individual variation arises is a major focus of research in evolutionary ecological studies of behaviour (Dewitt, Sih and Wilson, 1998; Wolf, van Doorn and Weissing, 2008; Dingemanse *et al.*, 2009; Snell-Rood, 2013; Stamps, 2016). In particular, the role that cognition and personality (or behaviours associated with well-known personality axes) have in driving behavioural plasticity is receiving increasing attention (Dingemanse *et al.*, 2009; Snell-Rood, 2013; Spierer, Chavan and Manuel, 2013; MacLean *et al.*, 2014; Stamps, 2016; Dubois, 2019), but their role in doing so under realistic ecological scenarios is poorly understood.

Inhibitory control is an executive cognitive function that is central to decision making and allows animals to adapt to sudden changes in the environment (Aron, Robbins and Poldrack, 2004; Diamond, 2013). It is defined as the suppression of a dominant, prepotent or impulsive behaviour in favour of one that is more beneficial or appropriate (Diamond, 2013; but see also MacKillop *et al.,* 2016 for another definition). In psychology, inhibitory control is a form of self-regulation that is often studied in the context of emotional control and addiction to food or other substances (Bari and Robbins, 2013; Luijten *et al.*, 2014), and describes how individuals vary in their ability to ignore new stimuli that would otherwise lead to a potentially harmful change in behaviour. Very few ecological studies have linked inhibitory control to functional behaviour generally, and those that do have primarily studied inhibitory control in relation to foraging behaviour. Stevens, Hallinan and Hauser, (2005) examined a temporal form of inhibitory control (temporal discounting) and demonstrated that cotton-top tamarins (*Saguinus*

oedipus) in captivity discount future high-quality rewards in favour of immediate lower-quality rewards, a strategy that is likely beneficial given the temporal variability in the tamarins' natural diet, although the authors did not examine individual variation. Other studies have shown that inhibitory control predicts dietary breadth, although the direction of the effect is inconsistent and the analyses were primarily at the interspecific level (meta-analysis in MacLean *et al.*, 2014; but see van Horik *et al.*, 2018 for a study at the individual level). One possible reason for these contrasting results is that, in realistic ecological scenarios, the dominant or prepotent behaviour is difficult to predict due to conflicts between how the brain simultaneously processes information from past and present stimuli (Anderson and Weaver, 2009). Identifying the most appropriate behaviour is also difficult because the prepotent behaviour may be affected by trade-offs with other traits and individual state (Dall, Houston and McNamara, 2004). Even though inhibitory control influences how individuals respond to the sudden appearance of alternative stimuli, by controlling impulsive and potentially inappropriate changes in behaviour, its role in driving behavioural plasticity in a functional, ecological context when conditions change is largely unknown.

Behavioural plasticity is central to evolutionary and ecological studies of animal personality (Sih, Bell and Johnson, 2004; Dingemanse *et al.*, 2009; Herborn *et al.*, 2014). Animal personality refers to consistent differences between individuals in behaviour across time or context, or to correlations between different traits (Sih *et al.*, 2004; Groothuis and Carere, 2005). Recently, the field has also moved towards determining whether correlations between different traits arise at the between-individual rather than at the within-individual level (Reichert *et al.*, 2021; Dingemanse and Dochtermann, 2013; Mitchell and Houslay, 2021). Considerable focus in the field has been placed on behavioural axes that are known to predict many different behaviours (Réale *et al.*, 2007). For example, the 'fast-slow exploration' personality axis contrasts fast individuals who are more exploratory, more predation risk-prone and more routine like in their behaviour, with 'slow' individuals who are less exploratory, more predation risk-averse and more responsive to their environment (Groothuis and Carere, 2005). This axis has been

widely studied in birds and shows strong similarity to the reactive-proactive axis described in small mammals (Groothuis and Carere, 2005; Réale *et al.,* 2007). Individual variation in exploration behaviour has been linked to physiological, permanent environment, and additive genetic effects, and can predict a wide range of functional behaviours (Koolhaas *et al.*, 1999; Quinn *et al.*, 2009, 2011; Firth *et al.*, 2018). All of these correlations imply general constraints on behavioural plasticity, though the observed effects are often dependent on social or ecological context (Réale *et al.*, 2007; Webster and Ward, 2011). Furthermore, specific facets of the axis (e.g. responsiveness) suggest that some individuals are more responsive to changes in their environment than others (Benus *et al.*, 1991; Verbeek, Drent and Wiepkema, 1994; Koolhaas *et al.*, 1999; Quinn and Cresswell, 2005; Rojas-Ferrer, Thompson and Morand-Ferron, 2019). As such, ecological conditions and exploration behaviour may interact to affect behavioural plasticity.

This study investigated whether inhibitory control and exploration behaviour were associated with behavioural plasticity and whether these effects varied depending on ecological context. We focused on flexibility, a specific form of behavioural plasticity that involves changes in learned behaviour (following Stamps, 2016), in the context of foraging. Although there is growing interest (Sih and Del Giudice, 2012), and some evidence (Dougherty and Guillette, 2018) for links between behavioural traits associated with personality and cognition in general, there is little empirical evidence that inhibitory control and our assay of personality, exploration behaviour, are linked (Stow, Vernouillet and Kelly, 2018). We therefore expected them to have independent effects on foraging flexibility. We examined choices made between two food options while varying two variables: 1) the value of the alternative food options (high or low value), and 2) the perceived risk of predation (high or low risk). We did this using the great tit (*Parus major*), a model species for studies on individual variation in cognition (Cole, Cram and Quinn, 2011; Amy, van Oers and Naguib, 2012; Morand-Ferron *et al.*, 2015) and animal personality (Verbeek, Drent and Wiepkema, 1994; Marchetti and Drent, 2000; Dingemanse *et al.*, 2012). Initially, we assayed inhibitory control and exploration behaviour using a standard detour-reaching task and 'exploration behaviour of a novel environment'

(henceforth, exploration behaviour), respectively. Next, we trained individuals to retrieve patchy, high-value but hidden food. We then presented birds with the hidden food and an alternative visible food source simultaneously, and quantified the number of times the birds chose the alternative visible food, instead of continuing to retrieve the hidden food. We considered that choosing, that is switching to, the alternative visible option was the flexible response, and therefore the proportion of choices for the visible option during trials after training was a concise, simple measure of foraging flexibility. Although individual variation in plasticity is increasingly analysed using a random regression reaction-norm approach (Nussey, Wilson and Brommer, 2007; Araya-Ajoy, Mathot and Dingemanse, 2015), this is appropriate only when the gradient is continuous and replication is high (Stamps, 2016). When the 'gradient' is discrete, individual plasticity can be described by the difference between the individual mean scores for the discrete treatments (Auld, Agrawal and Relyea, 2010). Since all of our individuals behaved the same way in the training phase treatment, the proportion of choices in subsequent treatments can be viewed as a measure of flexibility. We made no assumption about which option was optimal, since our focus was the behavioural mechanisms underlying flexibility, a measure that does not necessarily reflect a single optimal behaviour because of state dependence, behavioural trade-offs and uncertainty (Dall, Houston and McNamara, 2004).

We had three main aims. First, we examined whether individuals differed consistently in their foraging flexibility by estimating repeatability across all four treatments. Second, we explored whether inhibitory control was associated with foraging flexibility (i.e. whether individuals tended to switch to the visible food option). We assumed that training made the hidden food the prepotent (dominant) stimulus because they had been trained to feed in this way before the trials, leading to the following prediction: individuals with high inhibitory control (as measured in the standard detour-reaching task) would show greater foraging flexibility because they would be more likely to inhibit searching for the hidden food and switch to feeding on the visible food, when the value of the latter was equal relative to the former. We expected little or no effect of inhibitory control on foraging flexibility

when the visible food was of lower value relative to the hidden food. Furthermore, given the expectation that the influence of inhibitory control on flexibility is likely dependent on contexts other than food quality (Stevens *et al.*, 2005; Sih and Del Giudice, 2012; Tsukayama, Duckworth and Kim, 2012; Cauchoix, Chaine and Barragan-Jason, 2020; Griffin *et al.*, 2020), we also explored the context of predation risk. Stress can suppress an animal's tendency to choose an alternative, potentially more rewarding behaviour (Schwabe and Wolf, 2009), and theory suggests that animals should choose the most easily available food when predation risk is higher in order to reduce search time and maximise vigilance (Stephens and Krebs, 1986; Lima and Bednekoff, 1999). Thus, we expected that any association between flexibility and inhibitory control in the low predation risk treatment could be weakened or disappear entirely under risk of predation. Specifically, we expected that all individuals would revert to the safest option - which we assumed would be to feed on the visible food, thus allowing them to be more vigilant than when searching for hidden and patchy food.

Third, we predicted exploration behaviour would also be associated with foraging flexibility in one of two contrasting ways. In line with the information-gathering strategy hypothesis (Arvidsson and Matthysen, 2016; Rojas-Ferrer, Thompson and Morand-Ferron, 2019), we expected fast explorers would be more likely to switch to an alternative, novel, visible food source (because of the higher sampling of novel options associated with their behavioural phenotype; Rojas-Ferrer, Thompson and Morand-Ferron, 2019; Smit and van Oers, 2019), primarily when the alternative food source was of high value. Alternatively, according to the behavioural flexibility hypothesis (Verbeek, Drent and Wiepkema, 1994; Koolhaas *et al.*, 1999; Coppens, De Boer and Koolhaas, 2010), we predicted slow explorers to be more responsive to the sudden availability of a new alternative food source and to switch to the alternative visible food, primarily when it was high value. Once again, we also explored how predation risk influenced the relationship between exploration behaviour and foraging flexibility, for the same reasons mentioned above for the analysis on inhibitory control, and with the same predictions. Together these three aims allowed us to explore whether our measure of foraging

flexibility captured intrinsic differences between individuals, whether this flexibility was influenced by inhibitory control and exploration behaviour, and how these relationships depended on the context of food value and predation risk.

2.3 Materials and methods

This study was conducted under licences from the Health Products Regulatory Authority (Project licence: AE19130/P017, Individual licence to JCoomes: AE19130/I250), the National Parks and Wildlife Service (Project licence: C02/2018, Individual licence to JCoomes: 11/2018) and the British Trust for Ornithology (individual ringing licences for Sam Bayley and Ivan de la Hera Fernandez). The research project received ethical approval from the Animal Welfare Body at University College Cork, and was in accordance with the ASAB (Association for the Study of Animal Behaviour) Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

2.3.1 Aviary housing

We caught wild great tits (22 females and 27 males) at seven field sites (three mixed deciduous and four coniferous woodland fragments from the same study population) in County Cork, Ireland and held them in an aviary on the university campus for a maximum of two weeks from January to March 2018. We fitted birds with a colour ring and a British Trust for Ornithology ring for identification, before placing them in individual plywood cages (62 x 50 x 60cm, H x W x D; Figure S2.1) where they could hear but not see each other. Each box had independent air circulatory systems to remove any risk of disease transmission. It is not a concern for the birds to be housed individually and there was never any indication that males being adjacent to another male caused any stress. When not participating in experiments, birds were fed *ad-libitum* sunflower seeds, peanuts and water with added vitamin drops (AviMix®). Live mealworms (*Tenebrio molitor*) were provided three times a day and during experimental training and tests. Before each experiment, we deprived birds of food, but not water, for one hour.

2.3.2 Exploration behaviour and inhibitory control assays

On the day after their arrival to the aviary, we released the birds individually into an experimental room (4.60 x 3.10 x 2.65m, W x L x H) to run the open field 'exploration behaviour in a novel environment' assay (Verbeek, Drent and Wiepkema, 1994). The experimental room was connected to the birds' individual cages via a sliding door that could be opened from the experimental room and had five wooden 'trees' (1.53 x 0.5m, H x W) spaced two metres apart from one another inside (Figure S2.2, S2.3). Trees were made of a wooden upright support and two thick branches running at right angles to each other (based on the design of Verbeek, Drent and Wiepkema, 1994). One branch is at the top of the upright support and the other is further down (Figure S2.3). The number of hops made within the tree from one of the four branches to another, and flights between trees within two minutes of entering the room was totalled to give each bird an 'exploration of a novel environment' score, henceforth referred to as 'exploration behaviour' (see Dingemanse *et al.,* 2002). This continuous measure is an indicator of the fast-slow personality axis in great tits - those with low scores represent slow explorers and those with high scores represent fast explorers. Demonstrating repeatability has become standard in animal personality studies; nevertheless, we were happy to refine this approach and assume repeatability in our sample because i) exploration behaviour has previously been shown to be repeatable in our population (O'Shea, Serrano-Davies and Quinn, 2017), as it has in many other populations (Dingemanse *et al.*, 2012), and indeed is true for most behaviour (Bell, Hankison and Laskowski, 2009); ii) doing so minimised the number of "procedures" individuals were exposed to, a key principle of animal welfare practice; iii) our aim was not to determine whether any association between behaviours occurred at the between or within individual level in this complex experimental design, when multiple measures of all behaviours would be required.

On the following day, we assayed inhibitory control using a detour-reaching task in the individual cages, following the methods described in MacLean *et al.* (2014). The detour-reaching task involved presenting a plastic cylinder (3.5 x 3cm, D x L), placed perpendicularly to the direction in which the bird approached the device, 20 cm in

front of a perch that was 5 cm high; thus the bird was positioned so that it faced the middle of the long edge of the cylinder before making an approach towards the cylinder (Figure S2.4). The assay had three phases: 1) Habituation – the birds had to acquire half a waxworm (*Galleria mellonella*) from the open end of an opaque cylinder three times within the same session; 2) Training – half a waxworm was placed in the centre of the cylinder and to complete training, birds had to retrieve the food without pecking at the cylinder, in four out of five consecutive attempts (Boogert *et al.*, 2011), indicating that they had learnt the task; and 3) Test – the opaque cylinder was replaced with a transparent but otherwise identical cylinder, and birds then attempted to retrieve half a waxworm from the centre. During the test phase, a successful trial was recorded when the bird moved around to the side of the cylinder and took the waxworm from the open end without touching the front of the cylinder, as in training (Figure S2.5 for distribution of scores). Any contact a bird had with the cylinder before retrieving the food was scored as a fail; birds that pecked at the cylinder front could still subsequently access the reward (>90% of failed trials resulted in the bird immediately moving to the side to access the worm) but this was still recorded as a fail. Following either a successful or a failed trial, the cylinder was removed from the cage, rebaited and put back for the next trial, of which there were 10 in total. All trials were performed on the same day. A bird's final score was the proportion of trials that were successful i.e., high scores indicate high inhibitory control. Note that although we generated a single measure of inhibitory control, this measure is repeatable temporally (across years) and contextually (breeding and non-breeding season) in our population (Davidson *et al.*, 2021, Pre-print).

2.3.3 Foraging flexibility

Before foraging flexibility was measured during four experimental treatments, birds first went through a series of stages: a food preference test, pre-training, and training. The food preference test consisted of presenting birds with three mealworms and three de-husked sunflower seeds, and recording the first food eaten. Four individuals did not choose either food in 5 minutes, so were given the

preference test again but with waxworms instead of mealworms, and all chose waxworms over seeds. Of 41 individuals who had the food preference test (the other eight that were in the aviary were not tested due to time constraints), 35 chose and ate a worm (either waxworm or mealworm) and six ate a seed as their first choice, demonstrating that the majority of the birds preferred worms to seeds. For the four birds that were given the preference test with waxworms and preferred them, they received waxworms for all of their following experimental trials and the other birds all received mealworms. For the remainder of the experiment, worms of any type were considered 'high value' and de-husked sunflower seeds were 'low value' based on the results of this preference test.

After the preference test, we gave the birds a pre-training task consisting of a 24-well tray filled with sand. We buried freshly dead mealworms underneath the sand in ten randomly chosen wells, scattered ten sunflower seeds (de-husked) randomly on the surface (Figure 2.1a), and recorded the first food chosen. We ran this task to confirm that the birds would forage on the tray, that the seeds were easier to access than the worms, and that the birds could not detect the buried worms, either visually or through smell. Of the 41 birds who received the food preference test, 39 were tested on the pre-training task (one bird was unwell and did not undertake any further behavioural tasks, the other would not participate) and of these, 38 chose a seed as their first choice, instead of searching in the sand, suggesting that the birds had to be trained to find the buried worms.

Next, we trained the birds to forage for the hidden food in sand so that they would know, when subsequently presented with a tray with sand during the main experimental trials, that their preferred food item (i.e. worms) could be found under the sand, albeit in a patchy distribution. Birds were trained in a step-wise progression. In the first step, all 24 wells were baited with hidden worms, two of which were partially visible to encourage birds to search. Birds progressed to the next step if they ate five hidden worms within one hour (N = 40). The second step was similar to the first, except only ten wells were baited (i.e. patchy distribution), one of which was partially visible. Birds progressed if they ate three hidden worms in one hour. The final step was the same as the second but the worms were hidden

in different wells. The birds completed training if they ate three hidden worms from this tray. Steps were repeated until birds progressed and completed the training (N = 35). Of the 41 individuals who received the food preference test, six did not complete training due to welfare concerns or time constraints and were excluded from the rest of the experiment. We assumed that any variation in the level of experience gained during the training (for example, the time taken to find food), did not bias our interpretation of the results from the experimental phase, though we acknowledge this could have happened if, for example, either inhibitory control or exploration behaviour influenced experience gained.

Birds then entered the experimental phase. All birds underwent four minute trials in each of four experimental treatments (described below), during which birds were offered a choice between food hidden in the sand and a new visible, alternative food source on the surface. Crucially, because birds had become familiar with searching through the sand during training when there was only one foraging option, which we considered to have then become part of the birds' behavioural repertoire, switching to choosing the visible food on the surface of the tray during the treatments when there were two options was considered to be the flexible response. We determined all of the food choices made during the four minute trials from video recordings, and scored food choices as either 'hidden' (two or more pecks in the sand in the same well), or 'visible'. Our main response variable, *foraging flexibility,* was defined as the proportion of choices where birds fed on the visible rather than the hidden food out of the total choices made during that four minute trial. A second coder (C.A.T) watched 20% of the videos to ensure the records of food choice were not biased. Strong agreement was found between coders (intraclass correlation coefficient: ICC = 0.977, 95% confidence interval = 0.938-0.994). See Figure S2.6 for the distribution of the total number of choices for each of the four tasks.

The treatments were organised in a 2 x 2 factorial design (Figure 2.1). Birds could hear but not see each other during treatments. The first factor was the type of alternative, visible food that was available on the surface (low or high value), and the second was predation risk (low or high). In all four treatments, we placed the

24-well tray, baited with ten dead, buried mealworms in randomly assigned wells (a single mealworm per well), on a stool (1m high) in the centre of the experimental room. We provided one artificial conifer tree (Figure S2.2) and one wooden tree as in the exploration assay (Figure S2.3) as perches, 1m from the stool, from which the trays could be observed. Visible food was also present on the surface of the tray for all four treatments, and was one of two types: low-value (ten randomly scattered de-husked sunflower seeds) (Figure 2.1a, c), or high-value, where mealworms were encased in two transparent, sealed cases (Figure 2.1b, d). The visible worms were encased to ensure that there was a cost to attempting to consume the worms, thus ensuring variation, in order to probe what factors explained individual variation in flexibility when an alternative food item of apparently similar value to the hidden familiar food became available. In the wild, great tits exploit both hidden and visible food resources (Gosler, 1993) so we considered these alternative choices to be ecologically relevant for this species. This design therefore reflected a realistic trade-off between the two foods; in the case of seeds, they were easy to access but less preferred, and in the case of the encased worms, they were more preferred but inaccessible. If birds chose a seed and removed it from the tray, or touched the transparent case containing the worm with foot or beak, this was scored as a choice for the visible food. Great tits sometimes flicked over the seeds with their beaks, which we did not count as a choice.

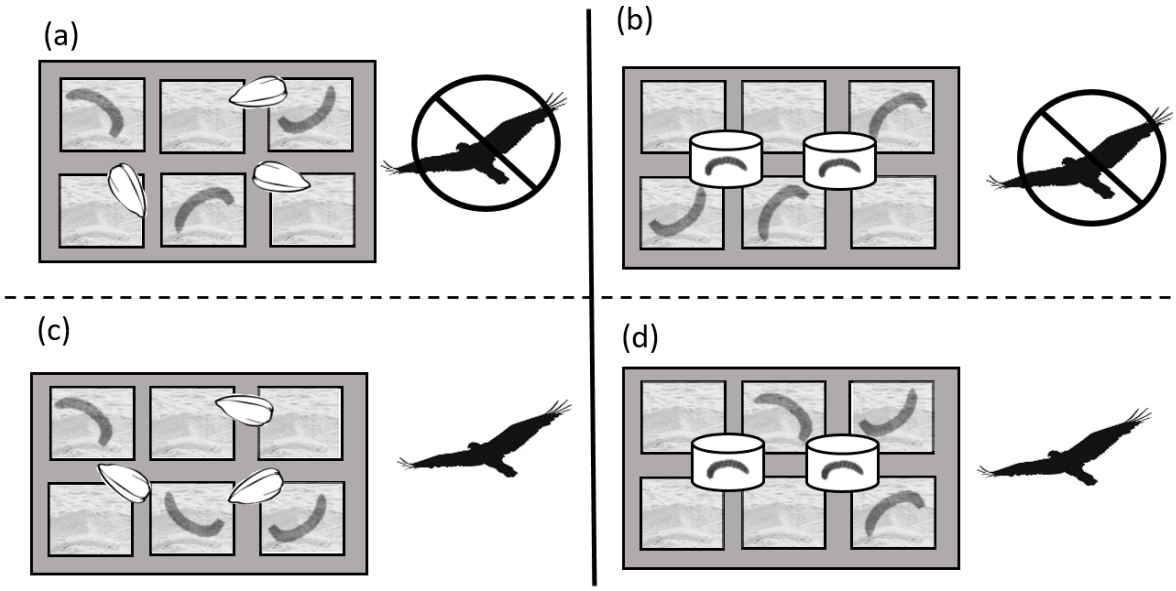


Figure 2.1. Schematic diagram showing the trays (six of 24 wells are shown here for illustrative purposes and clarity) used in the four treatments. In each treatment, we presented great tits with a tray filled with sand and buried mealworms underneath the sand in ten of the 24 wells. The first treatment a) had ten sunflower seeds (de-husked) on the surface and was presented as the pre-training task. The second b) had two mealworms in transparent cases on the surface. The third c) and fourth d) treatments were as in a) and b) but had the addition of a simulated attack by a model sparrowhawk.

The low predation risk treatments (in the absence of any model predator; see below) were run first (Figure 2.1a, b). The visible low-value and low risk treatment was considered to be the baseline response, and therefore we ran this treatment first; and the high-value, low risk treatment was run second for all individuals. We expected that potentially confounding carry-over effects from low-value food to high-value food treatments were much less likely than in the opposite direction (birds initially being presented with and choosing high value visible food leading to them by default choosing the low value visible food subsequently). The third and fourth treatments were run in the presence of a taxidermy sparrowhawk (*Accipiter nisus*) to simulate an increased perception of predation risk (Figure 2.1c, d), and the order in which the visible food alternatives were presented during the two predator treatments was chosen randomly to account for possible carry-over effects of predator attack on food choice. Taxidermic mounts are an effective way to simulate

predation risk (Carlson, Pargeter and Templeton, 2017), and have been used effectively on similar experiments in great tits (Kalb, Anger and Randler, 2019). During the third and fourth treatment, when an individual first landed on the tray to make a food choice, we released the 'hawk' from behind a sheet via a pulley system, to 'fly' across the room and 'hide' in a cardboard box. The four treatments were presented over a minimum of two days, with at least two hours between treatments, and birds that did not first participate in a treatment were given the treatment again once.

2.3.4 Statistical analysis

Data were analysed in R version 4.1.0 (R Core Team, 2021). To investigate if individuals were consistent in their foraging flexibility across treatments, and indeed whether it too might be viewed as a personality trait (as defined by Dingemanse and Dochtermann, 2013), we performed a repeatability analysis on foraging flexibility using the *rptR* package (Stoffel, Nakagawa and Schielzeth, 2017). Repeatability is the proportion of total variation that is reproducible among repeated measurements of the same subject or group (Nakagawa and Schielzeth 2010). It is calculated by dividing the between-group variance by the between-group variance plus the within-group variance. Statistical significance against the null hypothesis of R=0 is tested by likelihood ratio and permutation tests and the 95% confidence intervals are calculated by parametric bootstrapping. The unadjusted repeatability or 'agreement repeatability' (Nakagawa and Schielzeth, 2010; single variable of individual as a random effect) was calculated for the full dataset (N = 35; see below).

In the analyses for the second and third aims, we used the *lme4* package (Bates *et al.*, 2015) to create two models of foraging flexibility, with either detour-reaching score (model 1, N = 29) or exploration behaviour (model 2, N = 35) as the key explanatory variables. First we ran inhibitory control and exploration behaviour (and their interactions with the two main treatments central to the hypotheses being tested) in separate models to help limit over-parameterisation and to avoid a type II error, which would inevitably have occurred by including the main effects,

not least because doing so would reduce the sample size to the minimum (29 individuals in each 2 x 2 treatment, rather than 35). Furthermore, these two measures are not generally known to be interlinked and were not correlated in our population (Davidson *et al*., 2021, Pre-print), so we expected them to act on flexibility independently. Nevertheless we also explored whether their effects were truly independent by fitting a single model for both behaviours and their associated interactions, with the restricted dataset (N = 29 individuals tested across all four treatments), which we report along with the averaged model (see below) and make no adjustment for multiple testing. The response variable, foraging flexibility, was the proportion of choices for the visible food, weighted by the number of total choices (Thomas *et al.* 2017), and was modelled with a binomial error distribution and a logit link function, with individual ID fitted as a random effect. All models had predator treatment (yes or no), visible food type (seed or encased worm), and the interaction effect between these two included as explanatory variables. Our predictions were tested by the inclusion of detour-reaching score (a proportion out of ten, treated as continuous) in model 1, and exploration behaviour (continuous) in model 2, and their interactions with both visible food type and predation risk. To investigate the influence of confounding factors on foraging flexibility, we ran an analysis including sex, age, habitat, body condition and persistence separately to avoid over-complicating our main models, and found that none of these variables had an effect (for methodological details and results see Appendix A, section 2.6.1).

We used the *DHARMa* package (Hartig, 2021) to check model fit and to test model assumptions. We used the *dredge* function from the *MuMIn* package (Barton, 2020) and an information-theoretic approach in combination with model averaging (Grueber *et al.*, 2011) to generate the models with the most support, taken from the global model. The information-theoretic approach compares all possible combinations of models simultaneously and we calculated the amount of support for each model using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson, 2002). Models with a ΔAICc <2 were retained as the 'top' models that included the most important explanatory variables and since our global model only included variables that were directly relevant to answering our

question, the top models were considered biologically meaningful. We report the full averaged weighted parameter estimates across all models in the top set because this method takes into account that some variables are not present in all models. We ran posthoc analyses using the *emmeans* package (Lenth, 2021). Our figures were created with the *interactions* package (Long, 2019) and show the partial residuals from the binomial GLMMs. Each individual is represented with four points, one for each of the treatments (except where an individual did not complete a task), and the size of the points represents the number of total choices made during the four minute trials.

2.4 Results

The repeatability analyses confirmed that individuals differed consistently from one another in their foraging flexibility, across the four treatments (N = 35, R = 0.31, $P < 0.001$, 95% CI = 0.12-0.47). Foraging flexibility depended on both the value of the visible food and the predation risk treatment (Table 2.1; Figure 2.2). Birds were more flexible when the visible food was high value, and when there was no predator. Nevertheless, some birds were flexible even when the value of the visible food was low compared to the hidden food, and even when the predator was present, demonstrating individual variation in foraging flexibility.

There was no main effect of detour-reaching score, our assay of inhibitory control, on foraging flexibility (Table 2.1; for weights of the top models see Table 2.2). However, an interaction between detour-reaching with visible food type did predict flexibility (Detour-reaching score × Visible food: Table 2.1; Figure 2.3; for weights of the top models see Table 2.2). Birds that had a high score on the detour-reaching task were more flexible than birds that had a low score, but only when the visible food was high value (Posthoc test: Est. = 0.75, SE = 0.24, z = 3.10, $P = 0.002$; Figure 2.3). The effect of detour-reaching score on flexibility did not depend on predation risk (Detour-reaching score × Predation: Table 2.1).

Exploration behaviour had a positive main effect on foraging flexibility (Table 2.1, for weights of the top models see Table 2.2). Furthermore, faster explorers were more likely to be flexible than slower explorers, in the presence of a predator (Exploration × Predator: Table 2.1; Figure 2.4; for weights of the top models see Table 2.2; Posthoc test: Est. = 0.99, SE = 0.23, z = 4.34, $P < 0.001$). The relationship between exploration behaviour and flexibility was not dependent on the value of the visible food (Exploration × Visible food: Table 2.1).

When detour-reaching score and exploration behaviour were included as fixed effects, and as interactions with both of the main treatments, in the same model, the *P* values suggested all of the same effects remained significant and similar to those reported for the single models, despite the modest sample size relative to the number of parameters estimated (See Table S2.1). The averaged parameters from

the top four performing models, however, suggested the evidence for an independent effect of detour-reaching score (in its interaction with food value) on flexibility was weak because their averaged effects were not significant (Table S2.1). For a graphical representation of the results, see Figure S2.7.

Table 2.1. The choices made by the great tits in four minutes for detour-reaching score (N = 29) and exploration behaviour (N = 35) separately. Both models are binomial GLMMs (general linear mixed models) with the proportion of visible choices (out of the total number of choices made) as the response variable. The values shown are the full average of all the top models within two AICc of the best model. A positive value for the estimate means the visible food is more likely to be selected than the hidden food. For each categorical variable, the reference level is in brackets. The relative importance (averaged weight: sum of Akaike weights) for each parameter is shown.

	Estimate	**SE**	**95% Confidence interval**	**Averaged weight**	**P value**
Detour-reaching score					
Intercept	-0.28	0.74	-1.73; 1.17		0.71
Predator (no)	-2.35	0.41	-3.15; -1.55	1.0	**<0.001**
Visible food (encased worm)	-0.87	0.48	-1.81; 0.07	1.0	0.07
Detour	2.14	1.48	-0.76; 5.04	1.0	0.15
Predator × Visible food	2.47	0.50	1.49; 3.45	1.0	**<0.001**
Detour × Visible food	-2.54	0.96	-4.42; -0.66	1.0	**0.009**
Detour × Predator	-0.17	0.60	-1.35; 1.01	0.27	0.78
Exploration					
Intercept	0.23	0.28	-0.32; 0.78		0.42
Predator (no)	-2.93	0.25	-3.42; -2.44	1.0	**<0.001**
Visible food (encased worm)	-1.71	0.25	-2.20; -1.22	1.0	**<0.001**
Exploration	0.07	0.03	0.01; 0.13	1.0	**0.03**
Predator × Visible food	2.45	0.31	1.84; 3.06	1.0	**<0.001**
Exploration × Visible food	-0.04	0.03	-0.10; 0.02	0.54	0.27
Exploration × Predator	0.10	0.03	0.04; 0.16	1.0	**< 0.001**

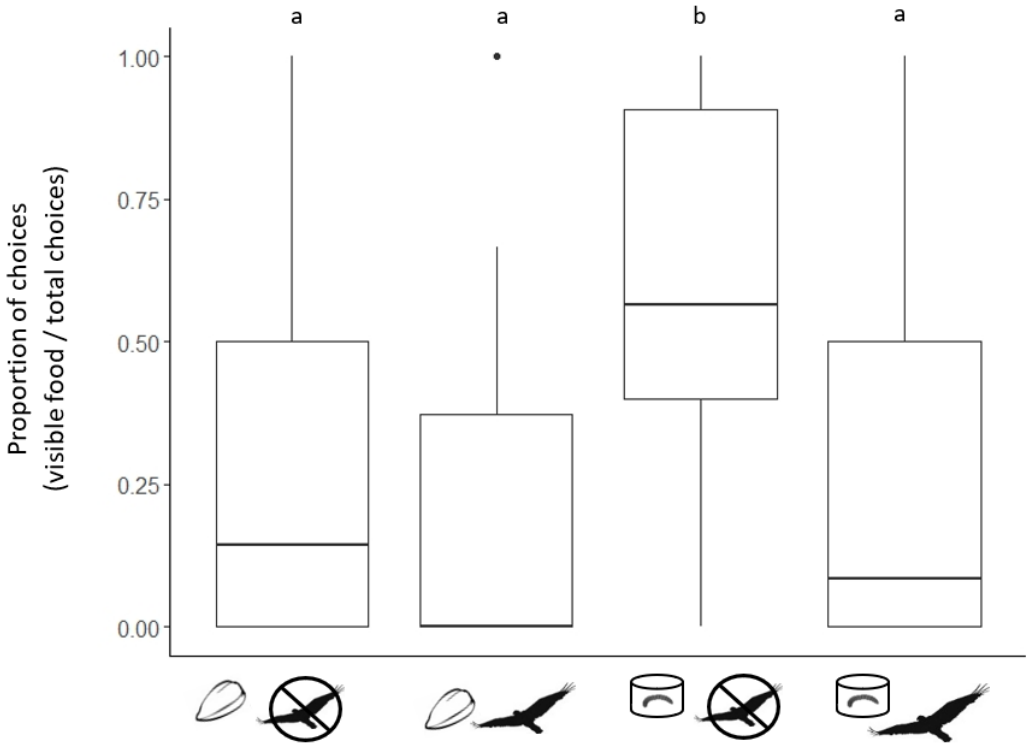


Figure 2.2. Foraging flexibility (the proportion of choices that were made for the visible option out of the total number of choices made in four minutes) in relation to the value of the visible food (low, seed; high, encased worm) and perceived predation risk (low or high). The median, 25th and 75th quartiles are shown; the whiskers are ±1.5 x IQR. Significant differences from post hoc tests are indicated by non-matching letters.

Table 2.2. The models in the top set for detour-reaching score and exploration behaviour as separate explanatory variables. The response variable was the proportion of choices for the visible food (out of all choices made) during four minutes. The table shows the variables, degrees of freedom (Df), AICc, delta AIC and Akaike weights (ω_i) for the top set of models within two AICc of the best model.

	Df	**AICc**	**Δ AIC**	**ω_i**
Detour-reaching score				
Predator × Visible Food + Detour × Visible Food	7	324.73	0.00	0.73
Predator × Visible Food + Detour × Visible Food + Detour × Predator	8	326.70	1.96	0.27
Exploration				
Predator × Visible Food + Exploration × Visible Food + Exploration × Predator	8	389.94	0.00	0.55
Predator × Visible Food + Exploration × Predator	7	390.38	0.44	0.45

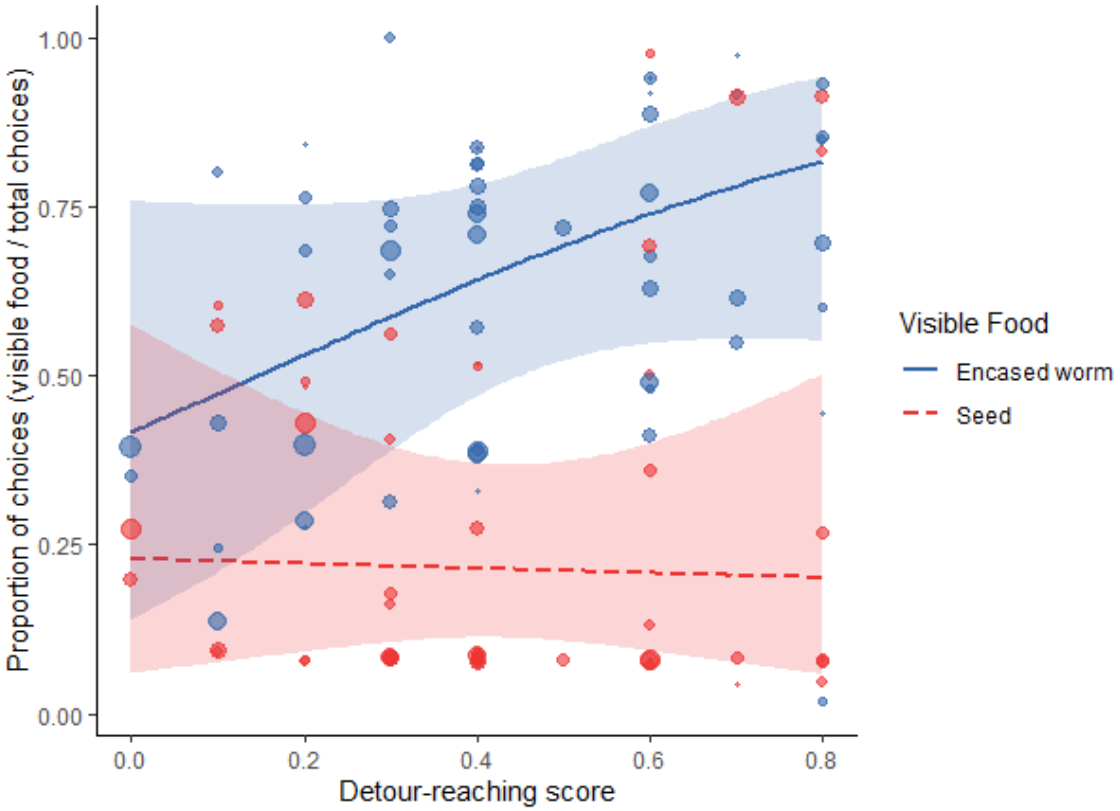


Figure 2.3. Foraging flexibility (the proportion of choices that were made for the visible option out of the total number of choices made in four minutes) in relation to detour-reaching score (an assay of inhibitory control), for each visible food value treatment (blue for encased worm, high value; red for seeds, low value). Each individual is represented by four data points, one for each treatment (except where an individual did not complete a task), with the size of the points indicating the number of total choices made. Data is the weighted partial residuals from the binomial GLMM (controls for additional effects in the model). 95% confidence intervals are shown. Sample sizes for each treatment: without predator, seed = 27; without predator, worm = 28; predator, seed = 26; predator, worm = 25.

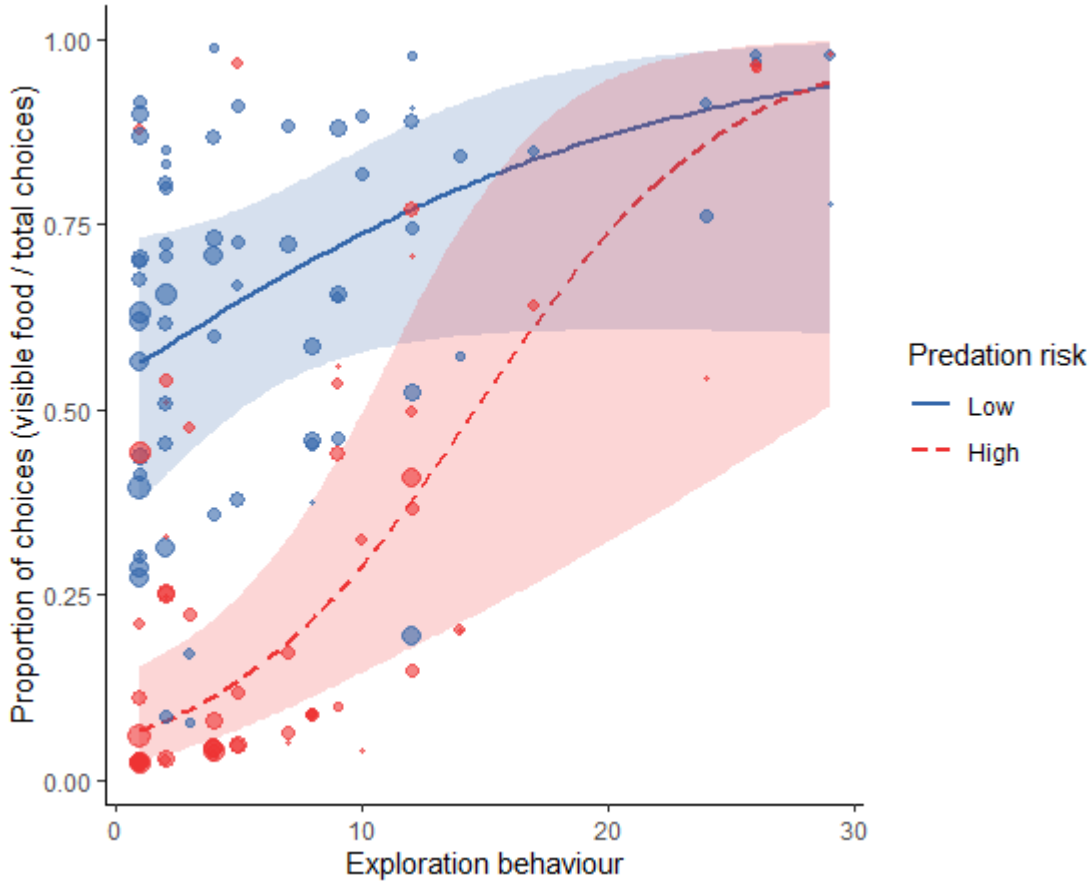


Figure 2.4. Foraging flexibility (the proportion of choices that were made for the visible option out of the total number of choices made in four minutes) in relation to exploration behaviour, for each predator treatment (blue for low perceived predation risk; red for high perceived predation risk). Each individual is represented by four data points, one for each treatment (except where an individual did not complete a task), with the size of the points indicating the number of total choices made. Data is weighted partial residuals from the binomial GLMM (controls for additional effects in the model). 95% confidence intervals are shown. Sample sizes for each treatment: without predator, seed = 33; without predator, worm = 34; predator, seed = 32; predator, worm = 30.

2.5 Discussion

Foraging flexibility – defined here as the proportion of choices that were made for the new alternative food option when offered at the same time as a familiar food – was observed among some individuals in all treatments. Furthermore, individuals differed consistently from one another in their foraging flexibility. When the visible food was of high value and when there was no risk of predation, individuals showed higher foraging flexibility. Foraging flexibility was also associated with both inhibitory control and exploration behaviour, though the effect of the former was weaker and dependent on food value, and the effect of the latter was especially strong when predation risk was high. Thus, individual differences in foraging flexibility were associated with individual differences in a cognitive trait (i.e. inhibitory control) as well as in a behavioural trait that is frequently used to assay the fast-slow personality axis, and these associations were moderated differentially by the ecological context.

2.5.1 Food value and predation risk

When the visible food was of lower value (non-preferred) and predation risk low, birds showed limited flexibility, primarily continuing to feed on the familiar, hidden and preferred food. This is as expected because birds had a high preference for mealworms over seeds, and assuming the birds were behaving optimally (MacArthur and Pianka, 1966; Milinski and Heller, 1978; Lima and Dill, 1990), it also suggests that the costs of having to find the hidden food were outweighed by their higher value relative to the low value visible food. Birds were more likely to show the flexible response when the visible food source was high value. That they continued to choose the encased worm (high value food) over their four minute trials, even though it was inaccessible, may be because in the wild great tits are known for their ability to acquire food from challenging and novel places (Aplin *et al.*, 2015; Serrano-Davies, O'Shea and Quinn, 2017). So they persisted in pecking at the plastic case to try and find a way to open it. Acquiring information about novel food likely serves as a way of generating new food sources and reducing future

uncertainty (Mathot *et al.*, 2012; Tebbich and Teschke, 2014), but these results suggest they primarily only do so when the risk of predation is low.

When predation risk increased, we expected birds to be more flexible by feeding on the visible food, because searching for hidden food would have reduced their vigilance and ability to detect an approaching predator. However, the opposite was the case: fewer birds chose the visible food when predation risk was high. One likely explanation for this finding is that great tits may have felt safer feeding on the familiar food, despite it taking more time to locate than the visible surface food, potentially compromising their vigilance. Whether animals are likely to disregard high value foods depends on risk, certainty and reward value (Holbrook and Schmitt, 1988; Mazur, 1988; Green and Myerson, 1996). In our study, the encased worm, though of relative high value, was likely too costly to choose when there was heightened risk because it was unfamiliar and difficult to obtain. In the case of the low-value seeds, any benefit of selecting this visible option was presumably outweighed by the cost of abandoning the preferred hidden food, even when under predation risk. An alternative explanation is that stress compromises the ability to assess changes in food value, as reported from a study on humans (Schwabe and Wolf, 2009). As such, when great tits were in the presence of a perceived predator, perhaps they could not accurately assess the relative value of the foods and so fell back on their trained behaviour of searching in the sand for the hidden worms. Whatever the explanation, the effects of predation and food type in our study highlight that manipulating ecologically relevant factors leads to differential patterns of foraging flexibility.

2.5.2 Inhibitory control

We found support for the hypothesis that inhibitory control, assayed using the detour-reaching task, is associated with flexibility when foraging. The association was only observed when the visible food was of high value. Individuals with high inhibitory control were more likely to switch to the visible food, but only when both options were of similarly high value. Birds with poor inhibitory control were less likely to override their trained behaviour and did not attempt to feed on the visible

food regardless of its value; that is, they were less flexible in their observed behaviour. We also predicted that this link could be dependent on predation risk because individual differences and habitual behaviour can be more pronounced under stress (Suomi, 2004; Schwabe and Wolf, 2009), or because severe predation risk could over-ride any effects of inhibitory control on behaviour (Quinn and Cresswell, 2005). We found no evidence for this, suggesting that the effect of this executive cognitive function on foraging flexibility is not influenced by an immediate extrinsic stressor like predation risk, although whether this is true for effects on functional behaviour generally, and whether this extends to other kinds of stressors, remains to be explored. Our modest sample size and complex models meant that the model average when inhibitory control, exploration behaviour, and their interactions with both of the main treatments were combined, provided weak support for an independent effect of inhibitory control (Table S2.1). This is likely due to limited power, however, so taken together our results suggest that inhibitory control does predict foraging flexibility, and that in natural systems this effect is most likely to be revealed when food availability changes.

One possible alternative explanation for birds with high inhibitory control being more flexible is that inhibitory control co-varied with neophobia, which then drove the effect. This seems unlikely in our sample where inhibitory control does not correlate with exploration behaviour (Davidson, *et al*., 2021, Pre-print), which itself is a predictor of neophobia (Carere, Caramaschi and Fawcett, 2010; see below under *Personality*). At the same time we cannot rule out an underlying causal effect of neophobia entirely because there is some suggestion of a link between inhibitory control and other personality traits (Regolin, Vallortigara and Zanforlin, 1994; Gomes *et al.*, 2020; Lucon-Xiccato, Montalbano and Bertolucci, 2020 but see Stow, Vernouillet and Kelly, 2018). Another possible explanation for the observed link between flexibility and inhibitory control is that the similarity between the transparent materials used in the inhibitory control and foraging tasks led to a carry-over effect. Again this is unlikely because the devices were otherwise very different (open-ended cylinder with access to food and circular case without

access), and all birds had similar experience with transparent objects before undertaking the food choice tasks.

Few studies have examined the ecological significance of inhibitory control. At the interspecific level, high inhibitory control in primates is associated with species that have pronounced fission-fusion dynamics (Amici, Aureli and Call, 2008, 2013) or wide dietary breath (MacLean *et al.*, 2014). At the intraspecific level, links between inhibitory control and behaviour are well established in humans (Bari and Robbins, 2013), but very few studies in non-human animals exist. Body condition was positively related to inhibitory control in New Zealand robins (*Petroica longipes)*, and although the author interpreted this to be because low glucose levels in the blood of birds in poor condition might have impaired cognitive performance (Shaw, 2017), causality could equally have been in the opposite direction: those with good inhibitory control could have been better foragers. In common pheasants (*Phasianus colchicus*), dietary diversity was negatively associated with inhibitory control (van Horik *et al.*, 2018), although the mechanisms underpinning such a link are difficult to interpret. Thus, the results presented here represent rare evidence for a link between inhibitory control and ecologically relevant behaviour, and the only example of a link with individual behavioural plasticity, not just foraging flexibility, when ecological conditions change.

2.5.3 Personality

Empirical studies predict that exploration behaviour correlates with flexibility, with some suggesting that fast explorers are more flexible (information gathering hypothesis; Frost *et al.*, 2007; Mathot *et al.*, 2012; Rojas-Ferrer, Thompson and Morand-Ferron, 2019), and others suggesting the opposite (behavioural flexibility hypothesis: Verbeek, Drent and Wiepkema, 1994; Wolf, van Doorn and Weissing, 2008; Coppens, de Boer and Koolhaas, 2010; Smit and van Oers, 2019). We found a significant positive main effect of exploration behaviour – faster explorers were more likely to prioritise the visible food and were therefore more flexible than the slower explorers – providing support for the information gathering hypothesis.

Differences in neophobia could also play a concurrent role here if the encased worm was perceived as a novel object - faster explorers also tend to be more neophilic (van Oers *et al.*, 2004). However, although we did not predict this *a priori*, given that the positive association between flexibility and exploration behaviour was especially pronounced under the high predation risk treatment (Figure 2.4), and that feeding on the familiar hidden food was perceived by birds to be the safest option (as discussed above), the stronger positive association in the high predation risk treatment is also likely explained in part by a differential response to predation risk since exploration behaviour also correlates positively with predation-risk proneness (Koolhaas *et al.*, 1999; Quinn *et al.*, 2009, 2011). Thus the potential ways that individual variation in behavioural flexibility might be influenced by the fast-slow exploration personality axis – and presumably by other axes and behavioural syndromes generally – are numerous and context dependent, but in our experiment are likely explained by a combination of how individuals collect information and manage risk.

Formally, it is widely considered that for a trait to reflect "personality", it should also be repeatable (Dingemanse and Dochtermann, 2013; Araya-Ajoy, Mathot and Dingemanse, 2015). Previously we demonstrated that exploration behaviour is repeatable in our study population (O'Shea, Serrano-Davies and Quinn, 2017), and along with a number of reasons specified in the methods, it was appropriate to assume that exploration was also repeatable in this sample of our population. We acknowledge that support for the hypothesis that foraging flexibility was associated with "personality", depends on this assumption. A natural extension to our analysis would be to establish whether the correlation between exploration behaviour and foraging flexibility, or indeed between inhibitory control and flexibility, occurred at the between- or within-individual level, the former of which would point to the correlations arising because of intrinsic differences among individuals and the latter to plasticity (Dingemanse and Dochtermann, 2013). The logistical challenge of estimating the phenotypic covariance in our system – generating large sample sizes and repeated measures over lengthy periods of time in captivity (see also Edwards *et al.*, 2013) – precluded us from taking this approach, though an increasing number

of studies are now doing so in other systems, even within a reaction-norm framework (e.g. Westneat, Schofield and Wright, 2013; Mitchell and Biro, 2017; Baškiera and Gvoždík, 2019; Hertel *et al.,* 2020).

Individual variation in behavioural plasticity is an important mechanism facilitating adaptation to ecological or environmental change. Our results show substantial and repeatable individual variation in foraging flexibility, a specific form of behavioural plasticity, and suggest that cognition and personality play context-dependent, independent roles simultaneously. They also suggest that the population level consequences of behavioural variation may only be revealed in the presence of specific ecological conditions, such as when individuals are under predation risk, or food types available vary over space and time.

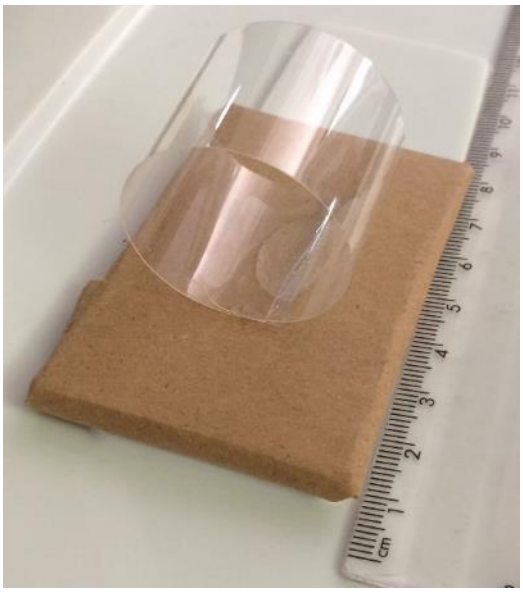
2.6 Appendix A – Supplementary material for Chapter 2

Figure S2.1. Birds were housed in plywood cages. The door at the front had three sections. The top section is a hole to put the bird into the cage. The middle section is a plastic window for observations. The bottom section is a flap so the base board on the floor can be removed to facilitate cleaning. Birds housed in the aviary could hear each other but could not see each other. Design of the cages followed Ihalainen *et al.,* 2012 and Hämäläinen *et al.,* 2017.

Figure S2.2. The wall of the experimental room showing the entrances from the cages. Each wooden frame holds a wooden door that slides to the left. Behind the door is an opening into the back wall of each box, so birds can move straight from the cage to the experimental room without handling.

Figure S2.3. A wooden tree that is 1.53m high and has four ‘perches’. Five of these ‘trees’ are used in the exploration assay.

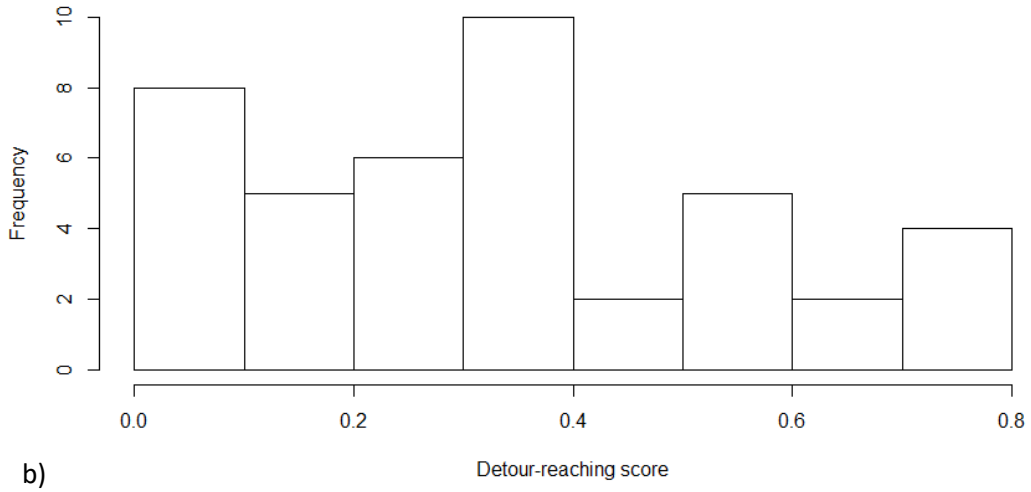
a)



b)

Figure S2.4. a) The cylinder used in the detour-reaching task and b) a great tit being presented with the detour-reaching task.

a)



b)

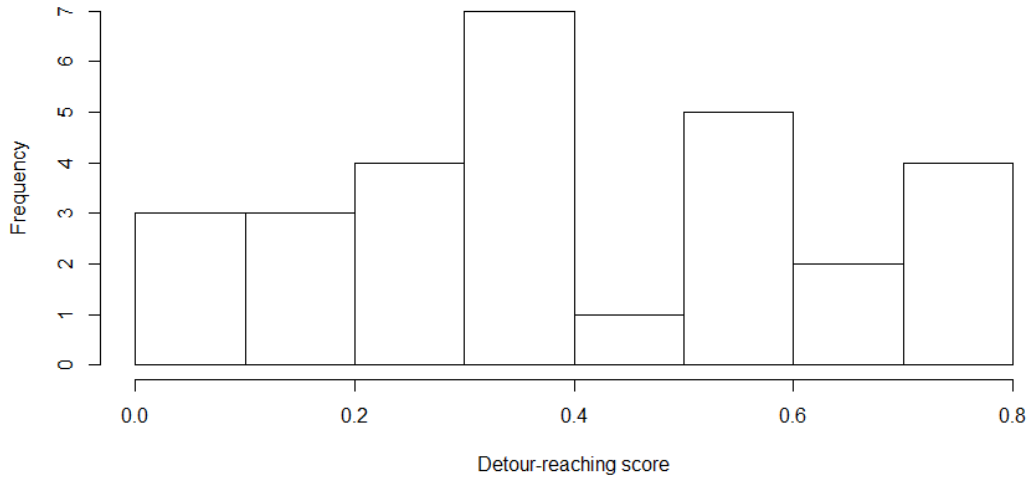


Figure S2.5. The distribution of scores on the detour-reaching task for a) all birds that participated in the task (N = 42) and b) only those birds that were present in our current analysis (N = 29).

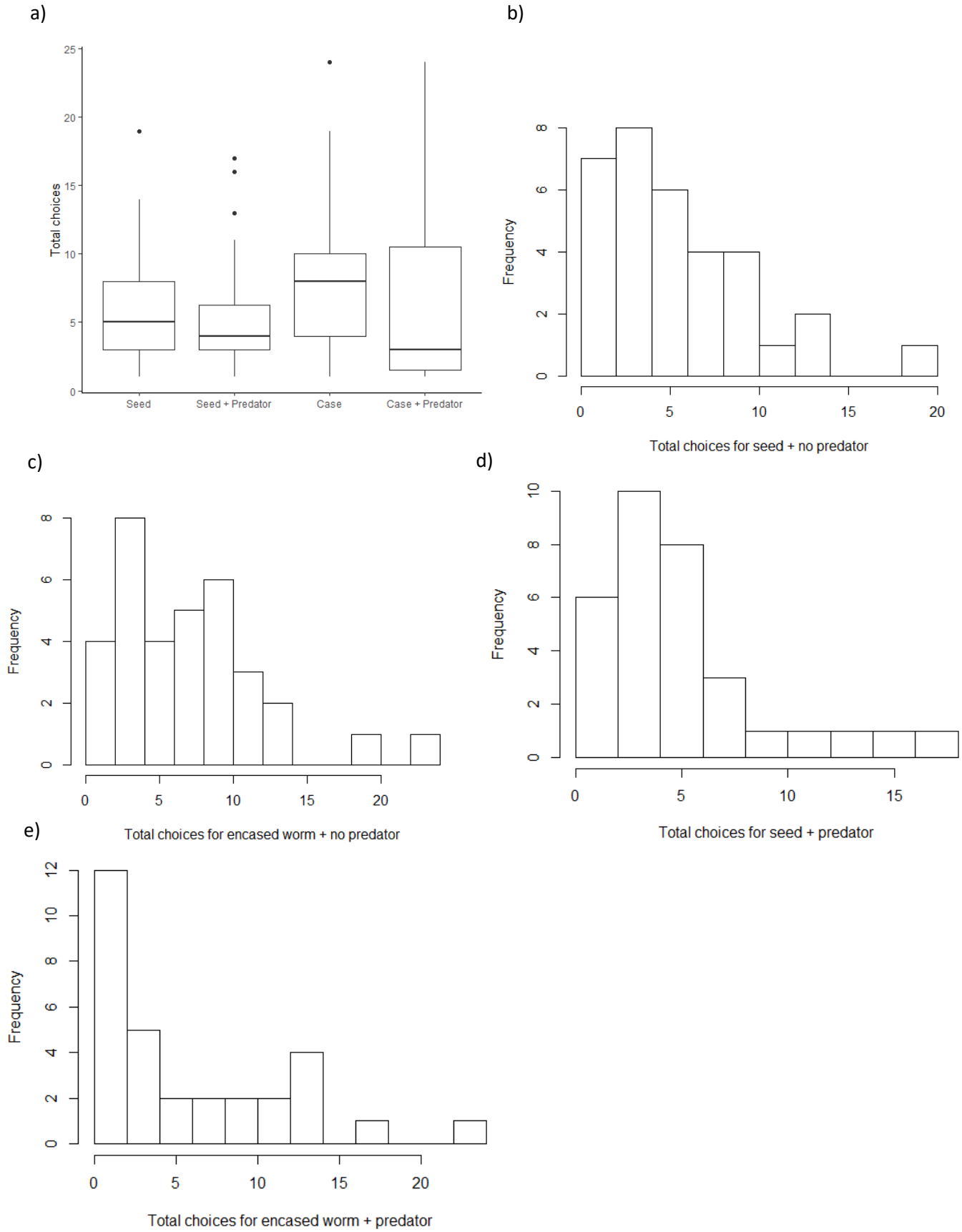


Figure S2.6. Distribution of total number of choices from a) all four treatments, b) seed as visible food and no predator, c) encased worm as visible food and no predator, d) seed as visible food with predator, e) encased worm as visible food

with predator. Figure a) shows the median, the 25th and 75th percentiles and the whiskers show ±1.5 × IQR. Figures b) – e) show the frequency of each number of total choices.

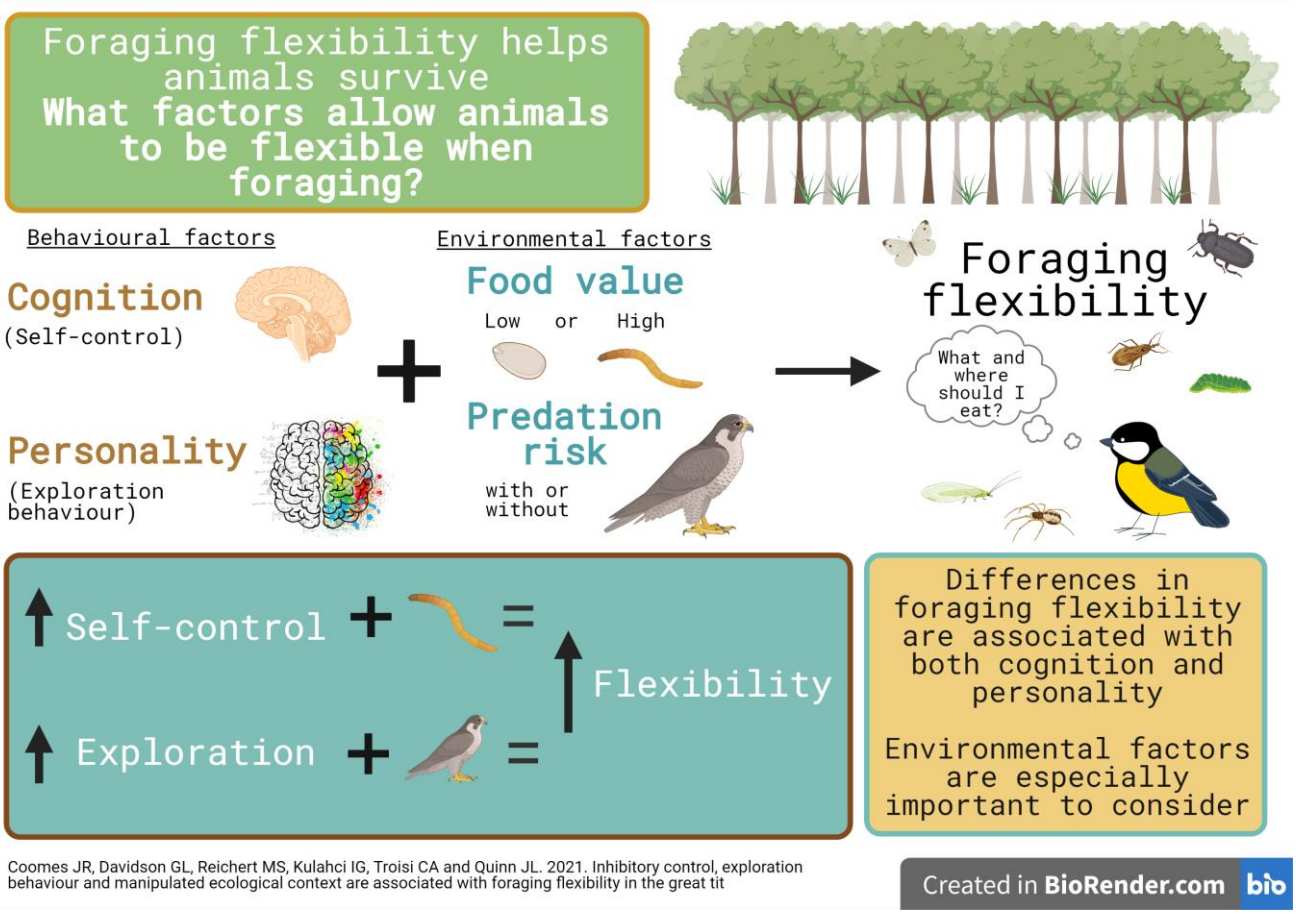


Figure S2.7. Graphical abstract. Being flexible when foraging is important for the survival of individuals. We investigated the factors that allow animals to be flexible when foraging. We found that ecological conditions (food value and predation risk) are important in revealing an association between foraging flexibility and individual variation in cognition and personality. Fast explorer great tits were more flexible when under predation risk and birds with high inhibitory control were more flexible when an alternative food source was high value.

Table S2.1. The proportion of choices made for the visible food in four minutes for both detour-reaching score and exploration behaviour (and their interactions) in the same model (N = 29). Results are shown for the full model and for the model average which reports an average of the models within two AICc of the top model. A positive value for the estimate means the visible food is more likely to be selected than the hidden food. The relative importance (averaged weight: sum of Akaike weights) for each parameter is shown. For each categorical variable, the reference level is shown in brackets.

Full model	**Estimate**	**SE**	**95% Confidence interval**	**Z value**	**P value**
Intercept	-0.57	0.75	-2.04; 0.90	-0.76	0.45
Predator (no)	-2.78	0.60	-3.96; -1.60	-4.67	**<0.001**
Visible food (encased worm)	-0.52	0.52	-1.54; 0.50	-1.01	0.31
Detour	2.22	1.47	-0.66; 5.10	1.51	0.13
Exploration	0.04	0.05	-0.06; 0.14	0.67	0.50
Predator × Visible food	2.41	0.51	1.41; 3.41	4.70	**<0.001**
Detour × Visible food	-2.07	0.99	-4.01; -0.13	-2.10	**0.04**
Detour × Predator	-1.05	1.05	-3.11; 1.01	-1.00	0.32
Exploration × Visible food	-0.10	0.05	-0.20; 0.00	-2.00	0.05
Exploration × Predator	0.15	0.05	0.05; 0.25	2.89	**0.004**

Model average	**Estimate**	**SE**	**95% Confidence interval**	**Averaged weight**	**P value**
Intercept	-0.25	0.55	-1.33; 0.83		0.66
Predator (no)	-3.06	0.35	-3.75; -2.37	1.0	**<0.001**
Visible food (encased worm)	0.78	0.45	-0.10; 1.66	1.0	0.08
Detour	1.46	1.22	-0.93; 3.85	0.75	0.24
Exploration	0.03	0.03	-0.03; 0.09	1.0	0.33
Predator × Visible food	2.39	0.31	1.78; 3.00	1.0	**<0.001**
Detour × Visible food	-1.62	1.11	-3.80; 0.56	0.75	0.15
Detour × Predator	-0.20	0.62	-1.42; 1.02	0.19	0.75
Exploration × Visible food	-0.08	0.04	-0.16; 0.00	0.83	0.06
Exploration × Predator	0.14	0.03	0.08; 0.20	1.0	**<0.001**

For an example of a great tit choosing each surface food type, see the video clips. https://figshare.com/s/dd27c6b7b48990e635fc

2.6.1 Sex, age, habitat, body condition and persistence statistical analyses and results

Data were analysed in R version 4.1.0 (R Core Team, 2021). We used the *lme4* package (Bates *et al.*, 2015) to create a general linear mixed model (GLMM) which included variables that were not of direct interest to the study but that may have been confounding. As in the main models, the response variable was the number of visible food choices out of the total number of choices made but here we had to use 'cbind(choices for visible food, total choices)' rather than using the 'weights' argument due to overdispersion issues. The model had a binomial error distribution and a logit link function, with individual ID fitted as a random effect and we used model averaging to report the average of the top models (see main text for methods). We included age (juvenile or adult), sex, habitat (deciduous or coniferous), body condition (weight divided by minimum tarsus length) and persistence (the number of pecks on the encased worm in four minutes in the non-predator task) as explanatory variables. We included habitat because it is known to affect food choice in our populations (Serrano-Davies, O'Shea and Quinn, 2017). We included body condition because it has been shown to confound performance in cognitive tasks and so may do the same in our foraging tasks (Shaw, 2017). Weight of the birds fluctuated throughout the period of captivity and for welfare reasons we only took weights if the birds were handled (i.e. when they were brought in and when they were released). The measurement of weight used here is on leaving the aviary. Finally, because individual persistence to gain access to the encased worm could affect our measure of foraging flexibility we included persistence as a confounding factor. The packages used to check model fit and for model averaging were the same as in the main models (see main text). Our analyses did not find an effect of any of our variables on food choice (Table S2.2).

Table S2.2. Supplementary analysis for the proportion of choices for the visible food including extra variables of interest. We show the full average of all the top models within two AICc of the best model. A positive value for the estimate means the visible food is more likely to be selected than the hidden food. The relative importance (averaged weight: sum of Akaike weights) for each parameter is shown. For each categorical variable, the reference level is shown in brackets.

	Estimate	**SE**	**95% Confidence interval**	**Averaged weight**	**P value**
Intercept	-0.95	0.23	-1.40; -0.50		<0.001
Age (adult)	-0.06	0.18	-0.41; 0.29	0.24	0.74
Sex (female)	-0.53	0.31	-1.14; 0.08	0.93	0.09
Habitat (conifer)	0.11	0.23	-0.34; 0.56	0.30	0.64
Body condition	0.02	0.08	-0.14; 0.18	0.17	0.78
Persistence	0.09	0.13	-0.16; 0.34	0.46	0.51

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Chapter 3

DNA metabarcoding suggests spatio-temporal variation in diet among great tits throughout the year

Great tits with prey, Wexford

Liam Ryan

Author contributions: Jenny R. Coomes and John L. Quinn designed the study, JRC collected the field data with help from others mentioned below. JRC undertook the laboratory work and analysed the data. JRC wrote the study with help from JLQ, Michael S. Reichert and Ipek G. Kulahci.

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3.1 Abstract

Niche separation is a major driver of evolution in nature. Within populations, dietary niche separation reduces competition between individuals for resources and affects how well they can adapt to environmental variation. Environmental factors affect the diet of individuals within a population but diet differences may arise even within, for example, the same habitat type or season. Intrinsic factors, such as age or sex, can be drivers of these individual differences in diet, which may lead to dietary niche separation. Establishing the degree of dietary differences is challenging in most taxa because of the difficulty in accurately identifying the food items consumed. DNA metabarcoding can overcome this challenge through identification of prey via DNA sequences from faecal samples. We used great tits (*Parus major*) to investigate differences in diet using two measures: dietary composition (identity of genera) and richness (number of genera) of invertebrates and plants. We investigated dietary differences between age classes (adults, first years, nestlings) and sexes, and across seasons (winter and spring) and habitats (mixed deciduous and conifer), controlling for site level effects. We found dietary differences between birds of different ages and sexes. Habitat and season interacted with age and sex to influence different dietary components, indicating that environmental factors play an important role in individual dietary variation. First years consumed more invertebrate genera than adults, supporting the idea that adults are more selective foragers. Variation in composition between the ages was particularly apparent in winter when food is more challenging to find. There was greater variation between the sexes in conifer compared to deciduous habitats, showing that sex is a strong driver of diet variation even in less densely populated habitats where we expect low competition and individual diets to converge. Season was also important for the sexes: females consumed less invertebrate genera than males in the spring, perhaps because they required more specific nutrients for reproduction. Nestlings had a lower richness than either adults or first years reflecting the nestlings' need for specific prey types at certain stages of development. Our results point to considerable separation in the diet composition and degree of specialisation depending on these key demographic parameters.

3.2 Introduction

Interspecific niche separation has long been the focus of foraging studies in ecology (Abbott, Abbott and Grant, 1977; Alatalo, 1982; Gladfelter and Johnson, 1983; Alatalo *et al.*, 1987; Schreier *et al.*, 2009) but intraspecific niche separation is also important for ecological dynamics (Polis, 1984; Shine, 1989). Competition for resources can drive intraspecific variation in diet (Svanbäck and Persson, 2004; Svanbäck and Bolnick, 2007). As competition increases, and preferred prey becomes scarce, less competitive individuals are forced to select alternative prey items (Robinson and Wilson, 1998; Svanbäck and Bolnick, 2007). Animals may have divergent foraging strategies when selecting alternative prey, which may lead to variation in dietary specialisations. Specialisation on prey has consequences for fitness (Ceia and Ramos, 2015; Pagani-Núñez, Valls and Senar, 2015; Balme *et al.*, 2020), for how well individuals cope in periods of resource unpredictability (Terraube *et al.*, 2011; Courbin *et al.*, 2018) and in response to changing environmental conditions (Bolnick *et al.*, 2003). Identifying the drivers of intraspecific niche separation and where individuals fall along the specialist-generalist continuum, improves our understanding of how individuals use resources, and of how they fit into the niche occupied by the species as a whole.

Drivers of intraspecific dietary differences can be intrinsic, such as age and sex, which may be linked to competition or specific dietary requirements. An individual's niche can change as it ages (Polis, 1984; Ebenman, 1987; Jones *et al.*, 2020), perhaps because of increased foraging experience (Estes *et al.*, 2003; Daunt *et al.*, 2007; Fayet *et al.*, 2015), changes in energetic requirements from growth to reproduction (Werner and Gilliam, 1984; Munn and Dawson, 2003), or changes in competitive ability (van Horne, 1982; Polis, 1984). Foraging strategies may change with age, for instance, juveniles may be less choosy and more generalist than adults who are more efficient foragers and show greater selectivity in their prey choice (Goss-Custard and Durell, 1987; Vander Zanden, Bjorndal and Bolten, 2013). Dietary differences and distinct foraging strategies can also occur among the sexes (Shine, 1989; Clarke *et al.*, 1998; Vasey, 2002; Kamilar, Jason M.; Poekmpner, 2008; Ratcliffe *et al.*, 2013), and be driven by competition, sexual size dimorphism and

other morphological differences (Mason, 1977; Birks and Dunstone, 1985; Rose, 1994; Weimerskirch *et al.*, 1997). Body size can affect the substrates on which an individual feeds (Boinski, 1989) and due to body size or the size of the appendages used for foraging, males and females can differ in the prey sizes and types that they can successfully catch or handle (Mason, 1977; Thiemann *et al.*, 2011). Furthermore, variation in diet between the sexes can arise from different reproductive needs (Coelho, 1974; Dunbar and Dunbar, 1988; Vasey, 2002) and reproductive strategies (Jones *et al.*, 2020). For instance, female fur seals have to stay close to their pups on the beach, so they forage in separate areas to males, resulting in variation in prey consumed between the sexes (Jones *et al.*, 2020). In addition, females require different nutrients during reproduction than males (Shine, 1989; Vasey, 2002) leading to divergent foraging strategies.

Variation in diet may occur between life stages (Werner and Gilliam, 1984), for example between parents and their offspring (Hodum and Hobson, 2000; Young *et al.*, 2010). Parents face a trade-off between finding food for themselves and providing for their young and this can lead to conflict, especially when food is limiting. Offspring need nutrients for rapid growth while adults need them for maintenance and reproduction (Munn and Dawson, 2003). As such, parents have the additional challenge of provisioning offspring with the necessary nutrients for development (Ramsay and Houston, 2003; Pagani-Núñez *et al.*, 2011), and they may develop separate foraging strategies when foraging for themselves and when foraging for their offspring (Cherel, Verdon and Ridoux, 1993; Markman *et al.*, 2004; Saraux *et al.*, 2011).

Environmental factors, including seasonal effects and habitat variation, drive general intraspecific variation in diet, due to changes in food availability. Different prey types will be available in spring versus winter as a result of organism life cycles (Betts, 1955). Similarly, habitat type can lead to general diet variation (Kemenes and Nechay, 1990; Newsome *et al.*, 2015), for example, deciduous woodland will host a greater diversity of invertebrate and plant prey than a monoculture of conifer plantation. In addition to driving general diet variation, environmental factors are also likely to play a role in the extent of dietary differences between

demographic groups. For example, variation among the sexes may only be apparent at specific times of year, for example during reproduction, for species that reproduce in only one season per year (Coelho, 1974; Dunbar and Dunbar, 1988). Variation in diet between age groups may also be influenced by season, since young individuals facing their first winter may struggle to find good quality food, more so than adults who have greater foraging experience. Similarly, within a single habitat, demographic groups may differ in diet, and a factor driving this is the density of conspecifics that will determine the amount of competition for food. For example, in deciduous woodland habitats, that support higher population densities (Kluyver and Tinbergen, 1954; O'Shea, O'Halloran and Quinn, 2018), individuals may have more distinct and specialised diets due to increased competition (Svanbäck and Persson, 2004). Moreover, in low density habitats such as conifer plantations (Kluyver and Tinbergen, 1954; O'Shea, O'Halloran and Quinn, 2018), there may be more overlap in diet between individuals, as they consume a wide variety of prey types and are less specialised due to decreased competition (Bolnick, 2001; Bolnick *et al.*, 2010). Quality and density of habitat types are likely to act in combination to affect the availability of different prey and feeding substrates, which affects the relative foraging success of adults and juveniles, and males and females.

Individual dietary differences in the majority of animal species is difficult to detect due to the challenge of identifying the prey species eaten. This is true in most species of birds, and especially in the most dominant taxonomic group, the passerines, many of which feed in difficult to observe habitats. Previous methods used to study diet have been invasive (Betts, 1955; van Balen, 1973), difficult to implement (identification of food items requires specialist training), strongly biased in what they detect (e.g. hard part analysis of faeces), or achieve poor taxonomic resolution (e.g. stable isotope analysis). These challenges can be overcome by using DNA metabarcoding. DNA metabarcoding is a process that involves identifying all or many taxa from DNA contained in environmental samples (eDNA) using high-throughput sequencing (Shokralla *et al.*, 2012; Taberlet, Coissac, Pompanon, *et al.*, 2012; Yu *et al.*, 2012). In dietary studies, this usually involves examining undigested DNA in faecal samples, which makes collecting samples easy and non-invasive. It

can also provide a high taxonomic resolution since items in the sample can be identified to species level if DNA profiles are available for those species in central databanks such as GenBank and BOLD (Barcode of Life Data Systems; barcodinglife.org) (Ratnasingham and Hebert, 2007; Taberlet, Coissac, Hajibabaei, *et al.*, 2012; Taberlet, Coissac, Pompanon, *et al.*, 2012).

The great tit (*Parus major*) is a small passerine that is widely used as a model species in ecological studies, and which feeds in woodland canopies and on the ground (Betts, 1955). Although it is assumed to have a generalist diet (Betts, 1955; Pagani-Núñez *et al.*, 2016), and the diet of adults, and primarily nestlings, has been well documented (Betts, 1995; Royama, 1970; Töröck, 1985; Naef-Daenzer, Naef-Daenzer and Nager, 2000; Vel'ký, Kaňuch and Krištín, 2011), the extent of dietary differences among the sexes and age classes is poorly known. We investigated the degree of variation in diet, as manifested by dietary composition (identity of genera) and richness (number of genera), in birds of different ages and sexes. Dietary composition provides a measure of the prey community, which is likely to reflect systematic differences in the locations and types of prey the birds are feeding on. Dietary richness allows us to examine the breadth of the diet and the extent of specialist or generalist foraging strategies since generally, individuals that are more specialist will consume fewer genera than generalists, though we note that this may not be the case if there is an abundance of a particular prey species that individuals exploit at certain times. Additionally, we investigated variation in two contexts; seasons (spring and winter) and habitat types (coniferous and deciduous).

First, we investigated dietary differences in seasons and habitats, between first year birds (<1 year old,) and adults (>1 year old), and between the sexes. Second, we investigated dietary differences in spring in both habitats between first years, adults and nestlings. Third, we compared the spring diets of parents and their own nestlings. In deciduous habitats, we predicted greater variation and specialisation in diet among the ages and sexes, due to high population density (Svanbäck and Persson, 2004; O'Shea, O'Halloran and Quinn, 2018), and subsequent potential for higher competition for food. Similarly, in conifer woodland we expected less

variation and specialisation in diets among the ages and sexes due to lower population densities (O'Shea, O'Halloran and Quinn, 2018) and individuals being released from competition to converge on similar diets (Bolnick *et al.*, 2010). We predicted diets to have greater variation and specialisation among ages and sexes in spring, when there is relatively more prey available than in the winter, and dietary niches can diverge. In winter, we expected diets to show less variation and specialisation, due to the relatively lower abundance of prey. See Figure 3.1 for an illustration of the factors that were examined with the diet and their predictions. By comparing the diets of different demographic groups across seasons and habitats, we aim to advance our understanding of how individuals use resources across a heterogeneous landscape, and provide insight into how populations may adapt to changing environmental conditions.

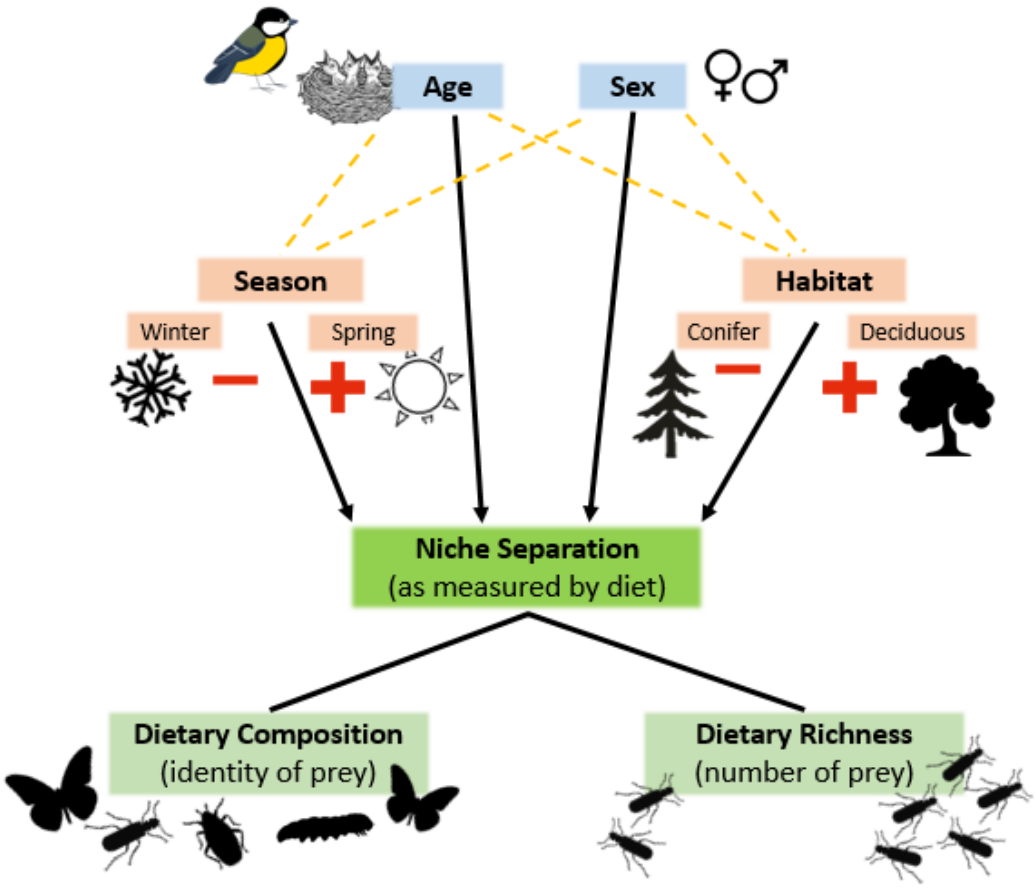


Figure 3.1. We investigated the influence of the intrinsic factors (blue) and the environmental factors (red) as main effects (black arrows) and in interactions (yellow dashed lines) on the diet (green) of great tits. Two components of the diet were considered, composition (identity of genera) and richness (number of genera) in three age categories: adults, first years and nestlings, and in both sexes. We examined the invertebrates and plants present in the diets of adults and first years, and the invertebrates present in the diet of nestlings. Dietary invertebrates were identified in both winter and spring and dietary plants were investigated in the winter only. Red plus (+) and minus (-) signs indicate the predicted direction of how the environmental factors could impact dietary differences. For example, we expected diets in winter and in conifer habitats to show less separation between the ages and sexes.

3.3 Methods

This study was conducted under licences from the Health Products Regulatory Authority (Project licence: AE19130/P017, Individual licence to JCoomes: AE19130/I250), the National Parks and Wildlife Service (Project licences: 004/2017, 001/2018, C02/2018; Individual licences to JCoomes: 70/2017, 11/2018) and the British Trust for Ornithology (individual ringing licences for JCoomes (C6597), Sam Bayley, Ivan de la Hera Fernandez). The research project received ethical approval from the Animal Welfare Body at University College Cork, and was in accordance with the ASAB (Association for the Study of Animal Behaviour) Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

3.3.1 Collection of samples

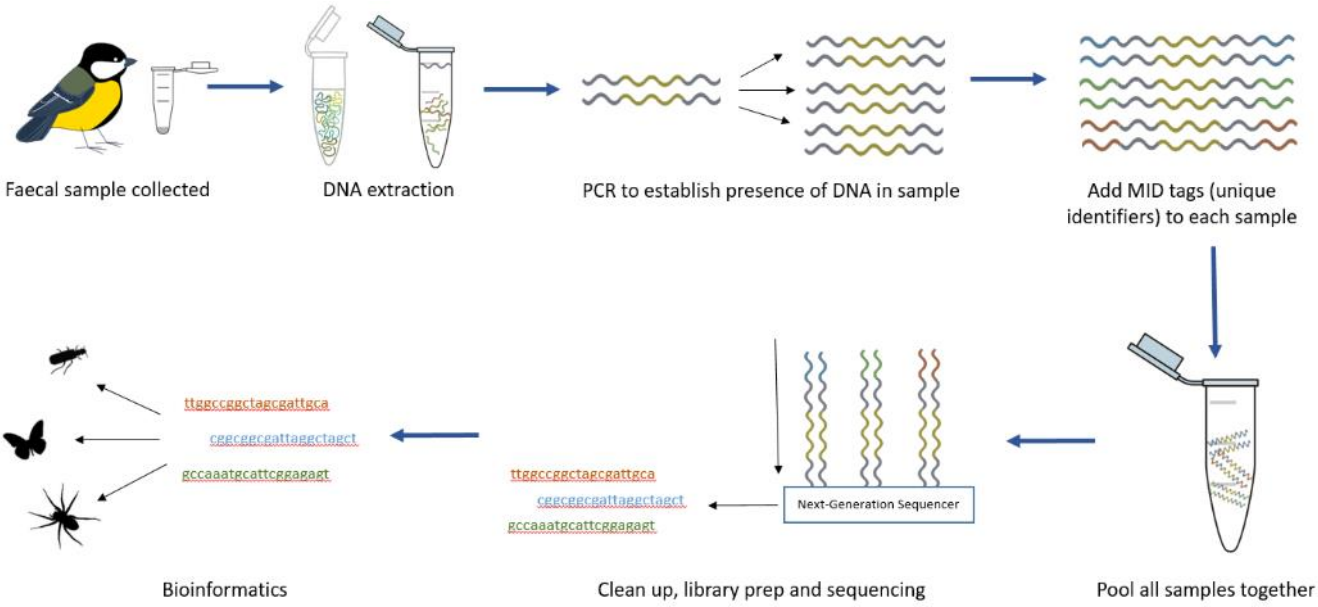
Faecal samples were collected from full-grown great tits in the spring and winter (N = 264), and from nestlings (N = 211) in the spring. The samples came from 12 field sites in the Bandon Valley, Ireland (Adults: 60 samples in conifer sites and 204 samples in deciduous sites; nestlings: 78 samples in conifer sites and 133 samples in deciduous sites; see Table S3.1 for number of samples from each field site). Samples were collected in May – June 2017 and 2018 (spring) and in November 2017 – February 2018 (winter). In the spring, a trap-door mechanism was used to trap full-grown birds on the nest, and mist nets were used to capture them in the winter. After capture by either method, birds were placed in coffee filters inside clean bags and were allowed time (not exceeding 30 minutes) to defecate. The coffee filter served to absorb liquid urea which can act as an inhibitor to amplifying DNA (Khan *et al.*, 1991). Each filter was used once and bird bags were sterilised between uses by washing in detergent. Following defecation, birds were fitted with a metal British Trust for Ornithology ring (if they had not been previously ringed for other ongoing studies) and were sexed and aged based on plumage (O'Connor, 1985). Faecal samples were removed from bird bags via sterilised plastic rods and were transferred into collection tubes with 1ml 100% ethanol. Nestling faecal

samples were collected when the nestlings were eight to nine days old, which was done by removing nestlings from the nest (for no more than 15 minutes), placing them into individual bags and transferring them singly to a plastic pot, where they were likely to defecate. Samples from different nestlings were kept in ethanol separately, and care was taken not to let a sample come into contact with any biological material. The maximum number of samples present in a single nest was 6, the minimum was 1 and the mean was 2.4. All equipment was sterilised between uses using bleach and ethanol. All samples were placed into a -20°C freezer at the end of the day and transferred to a -80°C freezer at the end of the season.

3.3.2 DNA Extraction

We established the invertebrates and plants present in the faecal samples of the great tits, through identification of DNA sequences (see Figure 3.2). JC undertook all laboratory work at Cardiff University in the UK. The first step was to extract DNA from the samples. Up to 18 faecal samples were extracted at once, and two extraction negatives were added per 18 samples. In one instance, only eight samples were extracted in one go and only a single extraction negative was included with that batch. In total, 475 samples were extracted: 137 adult spring samples (66 samples from 49 nests in 2017, and 71 samples from 49 nests in 2018), 127 adult winter samples, and 211 nestling samples from 83 nests. The Qiagen® Mini Stool Kit for DNA Extraction was used, together with the "DNA extraction from avian faeces stored in ethanol" protocol, incorporating modifications from Shutt *et al.*, (2020) (dx.doi.org/10.17504/protocols.io.ve6e3he) and from Sarah Davies (Davies, 2020) to deal with the small size and high levels of uric acid in avian faeces. Extractions were carried out under an air flow hood that was cleaned with bleach and ethanol between uses. Tubes and pestles were autoclaved before use and all equipment was cleaned with bleach and placed under UV light for 20 minutes prior to extraction.

a)



b)

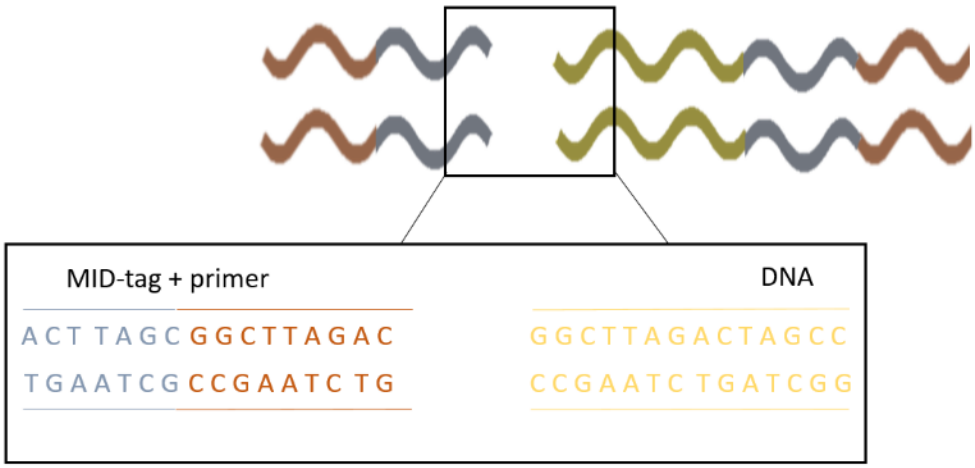


Figure 3.2. Illustration of the methods for determining diet are shown in panel a), and the addition of a unique identifier (MID-tag) is shown in panel b). Faecal samples were collected from the great tits and DNA was extracted from each sample. PCR was used to establish the presence of DNA. A unique identifier (MID-tag) was added to each sample using blunt-end ligation (shown in b) and the samples were pooled. Pooled samples were cleaned and sequenced using NGS (next-generation sequencing) to retrieve the sequences of each DNA fragment. The sequences were matched to a database (BOLD and GenBank) in a bioinformatics pipeline to determine the species/genera present.

Up to 220mg of each faecal sample was manually mixed with 1ml InhibitEX Buffer (Qiagen, Manchester, UK) using a plastic pestle (500µl at a time), vortexed for 3 minutes to homogenize the sample and incubated in a water bath for 15 minutes at 70°C. After another vortex for 2 minutes, samples were centrifuged for 3 minutes (every centrifuge step was at 13,000 rpm) to pellet the faecal particles. 400µl of the faecal supernatant was added to 20µl of proteinase K (Qiagen) and this was followed by adding 400µl of Buffer AL (Qiagen). The samples were then vortexed for 15 seconds to form a homogenous solution. The samples were incubated at 70°C for 15 minutes and then centrifuged for 1 minute to remove drops from the tube lid. 400µl of ethanol (96 - 100%) was added to the lysate and the sample was vortexed for 30 seconds and centrifuged for 1 minute. 600µl of each lysate was added to a QIAmp spin column (NBS Biologicals) and was centrifuged for 1 minute. The filtrate was then discarded. The remainder of the lysate was added to the spin column and centrifuged again for 1 minute. Following this, 500µl of the wash Buffer AW1 first, and Buffer AW2 second, was added to the spin column, with a 1 minute centrifuge after each addition and the filtrate discarded. A further 3 minute centrifuge followed this to eliminate Buffer AW2 carryover which could have caused problems in downstream analysis. 80µl of Buffer AE was added to the spin column membrane, incubated for 5 minutes at room temperature and then centrifuged for 1 minute to elute DNA. The solution was then passed through the spin column a second time to further concentrate the DNA and increase yield.

3.3.3 PCR amplification to establish presence of DNA

Following extraction, target DNA regions were amplified using PCR (SimpliAmp™ Thermal Cycler or Applied Biosystems Robocycler Veriti) and gel electrophoresis was used to establish the presence of DNA. In each PCR, 2µl of the extraction product was tested and this volume was dropped to 1µl part-way through the process to ensure ample volume would be left for sequencing. In addition to the DNA, 3 or 4µl of PCR reagents (for either 2µl or 1µl of DNA respectively) was added, which comprised 2.5µl Multiplex Master Mix (Qiagen), either 1.3µl or 0.3µl nuclease-free water (for either 1µl or 2µl of DNA respectively), and 0.1µl each of

the forward and reverse primers (concentration = 10µM). A PCR negative (nuclease-free water in place of the DNA) and a positive control (known DNA) was included with every PCR. All extraction negatives were also subject to PCR.

We tested all samples (winter, spring and nestling) for invertebrate DNA using primers that target the mitochondrial cytochrome c Oxidase subunit I gene (COI). DNA barcodes (unique identification markers) from COI are accepted as a standard for many groups of animals (Kress *et al.*, 2015) including invertebrates (Hebert *et al.*, 2003). The forward primer was "mlCOIintF" (Leray *et al.*, 2013) and the reverse was "C1-N-2191/Nancy" (Simon *et al.*, 1994). These primers were first used in combination by Jennifer Stockdale (Stockdale, 2018) and target a 306bp fragment of COI. The PCR cycle for COI was: 95°C for 15 minutes, 35 cycles of 94°C for 30 seconds, 55°C for 90 seconds, 72°C for 90 seconds, then an extension of 72°C for 10 minutes. We only searched for plant DNA in the winter samples as we did not expect plants to be a large component of either the nestling diet or the diet of adults in the spring. ITS2 (second internal transcribed spacer) primers were used to test for the presence of plant DNA. These primers target a short (160-320bp) region, which is ideal for dietary samples that are highly degraded. The forward primer was "UniplantF" and the reverse was "UniplantR" (see Moorhouse-Gann *et al.*, 2018 for details). The PCR cycle for ITS2 was: 95°C for 15 minutes, 40 cycles of 95°C for 30 seconds, 58°C for 30 seconds, 72°C for 60 seconds, then an extension of 72°C for 10 minutes. Following PCR for either primer set, gel electrophoresis was used to visualise the samples in which DNA had been amplified successfully. We used a 2% agarose gel with 1µl of SyberSafe to render the DNA visible under UV light. Samples that failed were re-PCRed once, and if failed a second time were dropped from further work. 94% of samples (576 out of 614) were successfully amplified. (614 is the number of samples amplified using either primer set. It is larger than the 475 samples extracted because the winter samples were analysed for both primer sets).

3.3.4 Adding unique tags to samples

Each successfully amplified sample was given a unique tag to differentiate it from every other sample. This allowed all samples to be pooled together and ensured sample identity would be known after sequencing. Following amplification, unique identifying (MID) tags (Eurofins©) of 10 unique base pairs long were added to the primers used in the previous step and were attached to the samples by blunt-end ligation in a PCR reaction (MID-tag-PCR). Blunt-end ligation means that there are no overhanging base pairs on the end of each sequence of DNA, and these sequences were ligated, or stuck, to the MID tag (see Figure 3.2b). Each sample and extraction negative were assigned a unique combination of forward and reverse tags. Each PCR plate of 96 wells had five extraction negatives, three PCR negatives and two positive controls (species that will be amplified by the primers but are not eaten by great tits), to identify contamination down the line. The positive controls for COI were whiteleg shrimp (*Penaeus vannamei*) and common mussel (*Mytilus edulis*) and for ITS2 were two species of native Mauritian plant, *Dombeya mauritiana* and *Dodonaea viscosa*. A 25µl reaction volume was used, and this consisted of 12.5µl of Multiplex Master Mix (Qiagen), 5µl of DNA solution and 2.5µl each of the forward and reverse primer with the added unique tag. Additionally, we added 2.5µl of nuclease-free water to reactions involving ITS2, and 2.25µl of nuclease-free water and 0.25µl of BSA (Bovine serum albumin; Yu and Morrison, 2004) to COI reactions. During testing, we found that the addition of BSA improved the brightness of bands on the gel image so it was added to all tagged PCRs for COI. The COI cycle was as follows: 95°C for 15 minutes, 35 cycles of 94°C for 30 seconds, 55°C for 90 seconds, 72°C for 90 seconds then an extension of 72°C for 10 minutes. The ITS2 cycle was as follows: 95°C for 15 minutes, 40 cycles of 95°C for 30 seconds, 56°C for 90 seconds, 72°C for 90 seconds then an extension of 72°C for 10 minutes (Moorhouse-Gann *et al.*, 2018). As with extractions, all equipment was autoclaved and/or cleaned with bleach and left under UV light before PCR setup commenced.

Following the MID-tag-PCR, the concentration (ng/µL) of the MID-tagged products was established by high-resolution capillary electrophoresis on a QIAxcel®

instrument (Qiagen). A DNA high-resolution cartridge (reference marker phix174) was used at initial testing and a DNA fast analysis cartridge (reference marker created for own samples) was used when the first one ran out. Failed samples were re-ran (to a maximum of three times) with a different tagged-primer combination. Tagged-primers were successfully attached to 90% (521 of 576) of samples.

3.3.5 Pooling

Following the addition of the unique identifiers, samples were pooled together by their MID-tag-PCR plate. The purpose of pooling by plate was to minimise potential differences in PCR conditions between plates, which may have influenced the detection of prey sequences. The concentration of the most concentrated sample in a plate was divided by the concentration of all the other samples in that plate to calculate the volume of each sample to be added to the pool. The most concentrated sample had 1µl added to the pool. Any sample that required greater than 25µl to be added to the pool was discarded, as there was only 25µl available from the MID-tag-PCR. Additionally, any samples that had a starting concentration of less than 2ng/µL were also discarded as adding too many samples of low-concentration would dilute the final pool. For plates in which the most concentrated sample was very high, we diluted the most concentrated sample with nuclease-free water to allow more samples in the plate to be pooled. Extraction and PCR negatives were pooled with a volume equal to the average for their whole plate and no more than 10% of each pool were negatives. 121 samples were pooled for ITS2 and 386 for COI. Because of the large number of COI samples and an insufficient number of tagged-primer combinations, it was necessary to have two groups that each contained the same tagged-primer combinations, but then would have a further unique identifying marker added, to identify the two groups and thus identify each sample. The final result was two pools for ITS2 (pool 1: 72 samples, 5 negatives, 2 positive controls and pool 2: 49 samples, 7 negatives and 2 positive controls) and eight pools for COI (12-71 samples, 2-7 negatives and 1-3 positive controls).

3.3.6 Clean-up, Library prep and Sequencing

The pools were taken by JC to the Genomics Research Hub at Cardiff University where they were cleaned and prepared for sequencing. SPRI (Solid Phase Reversible Immobilisation) beads were used in a ratio of 0.9 to select the DNA fragments of appropriate size (COI: 407bp and ITS2: 207-407bp) and to purify PCR products. The concentration of each of the ten pools was established using Qubit Fluorometric Quantification (ThermoFisher™ Scientific, Paisley, UK) and informed the volumes to be combined to end up with three final pools (COI Index 1, COI Index 2 and ITS2) ready for library prep. The NEXTflex® Rapid DNA sequence kit from Bioo Scientific© was used to prepare the samples and the protocol that did not require size selection of DNA fragments was followed. This protocol added the final unique identifiers (unique barcode adapter of 6 bp) to each of the three pools. The pools were cleaned with AMPure XP beads according to the Bioo Scientific© protocol and were run through a TapeStation that performs automated electrophoresis for sample quality control. The concentration of the pools were tested again with the Qubit Fluorometer and were loaded onto the Illumina® MiSeq to be sequenced. A V2 sequencing chip with 2x250bp paired-end reads was used for COI and a Nano chip with 2x250bp paired-end reads was used for ITS2. See Figure 3.2 for an illustration of the lab process.

3.3.7 Bioinformatics processing

JC used a bioinformatics pipeline developed by Lorna Drake (Drake, 2020) at Cardiff University to decode the sequencer output and to identify plant and invertebrate sequences. The process was carried out for each of the three indexes separately. First, the MID-tag primers were tested for truncation (shortening) by calculating the percentage of reads with less than 10bp of the MID-tag sequence attached to either end, and therefore would not be assigned to a sample identifier. For all indexes, the maximum was 20% and the average was 9%. 'FastP' (Chen *et al.*, 2018) version 0.20.1 was used to trim excess Illumina® adapter, align the forward and reverse reads, merge the paired-end reads and remove low-quality reads. The minimum sequence length was set to 125bp and the quality threshold to 33. After this, there

were 6,486,267 reads in COI index 1, 6,730,882 in COI index 2 and 772,865 in ITS2. 'Mothur' version 1.40.4 (Schloss *et al.*, 2009) was used to assign the sequences to their great tit sample by recognising their unique tag, and to trim off the tagged-primers, leaving only the fragment of DNA from the prey item. Due to the blunt-end ligation when adding the tagged-primers, the reads could be read in either direction so 'Mothur' split the sequences into two groups, one reading from forward primer to reverse, and the other the opposite. Only one mismatch was allowed when assigning sequences to their sample. Reads were then demultiplexed to obtain one file of prey sequences per unique tag combination (i.e per great tit sample).

The 'unoise3' command in Usearch v11 (Edgar, 2010) was used to identify and correct reads with sequencing errors, remove chimeras (a single DNA sequence originating from multiple sequences) and to create zOTUs (zero-radius operational taxonomic units) (Edgar and Flyvbjerg, 2015; Edgar, 2016). An Operational Taxonomic Unit (OTU) is a unique DNA sequence and a zOTU is a more taxonomically precise OTU with errors removed. zOTUs were clustered with 100% similarity. A 'closest species match' technique was used via the 'blastn' command in BLAST+ (Basic Local Alignment Search Tool, Camacho *et al.*, 2009) to obtain taxonomy for each zOTU by matching sequences from GenBank at the NCBI (National Centre for Biotechnology Information) using 97% similarity. Sequences with less than 100bp in length were removed as these were too short to be confidently assigned an identity. On completion of the pipeline, 10,503 unique zOTUs were left to be taxonomically assigned for COI Index 1, 7,304 for COI Index 2 and 792 for ITS2.

Before final assignment of taxonomic identities to each zOTU, only the top hit for each zOTU was retained, using *dplyr* in R (v0.7.8; Hadley *et al.,* 2019), based on bit-score (the required size of a sequence database in which the current match could be found by chance). MEGAN6 Community Edition© (MEtaGenome ANalyzer, v6.15.2, Huson *et al.*, 2016) was used to assign zOTUs to taxon name of the 'lowest common ancestor'. Any read counts less than 10 were removed as potential errors. The maximum amount of contamination was calculated for each index by finding the maximum number of reads in any one negative (extraction or PCR) or unused

MID-tag combination, and taking that number away from all the other read counts in the datasheet. All similar taxa were aggregated and read count was changed to presence/absence because biases in sequencing steps and in primer binding may lead to read counts that do not reflect the diet composition of a sample (Yu *et al.*, 2012; Deagle *et al.*, 2019). At this point, the two separate indexes for COI were aggregated. Non-prey items, such as feather mites, non-European species, marine species, water moulds and amoeba, were removed, as well as sunflower (*Helianthus*) and peanut (*Arachis*) which were used to bait the mist nets during capture. Furthermore, cockroach (*Blattella*) was removed because of a known contamination issue in the DNA extraction lab. The positive control species (i.e shrimp, mussel and the two Mauritian plant species) were checked to ensure they were not present in any sample above the read count of the positive control samples, and then were removed when this was found to be the case.

To maximise the number of taxa for statistical analysis, the presence/absence data for sequences assigned to species level were combined under their genus name, which allowed us to include sequences only assigned to genus. All analyses were performed at the level of the genus. For each different analysis, the following was removed: any taxa at family level or above, any sample that did not contain dietary data at genus level and any genera that were not present in any of the samples, for each analysis in turn. Additionally, three plant genera, *Citrus* (citrus fruits), *Cucumis* (cucumbers and melons) and *Embothrium* (Chilean firebush) were removed that may be present in private gardens but we do not believe were target prey items.

3.3.8 Statistical analysis

R version 3.6.1 and RStudio version 1.2.5019 (R Core Team, 2019; RStudio Team, 2019) were used to investigate both dietary composition and richness. Some genera were present only in one sample (singletons) and because the presence of these may skew the results, all composition and richness models on the full dataset were run both with the full number of genera and then with the removal of singletons. Results did not change with the removal of singletons. Below we describe how we

determined the diet composition results and then describe the variables included in our analysis.

Determining the composition of the diet using a 'manyglm'

To investigate differences in dietary composition, we used the package *mvabund* (v4.1.3) (Wang *et al.*, 2012) to produce multivariate models with a binomial family and 'cloglog' link function which were best suited for our presence/absence data and the large asymmetry between the 0s and 1s in our dataset. These were tested using the 'anova' function and montecarlo (parametric bootstrap) resampling as recommended in Wang *et al.* (2012) for presence/absence data. Model fit was checked using the 'plot' and 'qqnorm' functions in mvabund. Random effects cannot be incorporated into a manyglm, so duplicate samples from the same bird in each dataset were randomly removed. Results of the anova were visualised via NMDS (nonmetric multidimensional scaling) plots from the 'metaMDS' function in the *vegan* package (v 2.5-6) (Oksanen *et al.,* 2020) that use the Jaccard index (a similarity metric) to show how each individual (the points) differs from the mean (centroid) of their group. The further two individuals are from each other the more different their diets.

Invertebrate and plant composition and richness among adults and first years

To investigate dietary composition and richness of adults and first years we examined, first the invertebrate diet in the spring (two years: May to June in 2017 and 2018) and winter (single year: Nov 2017 to Feb 2018), and second the plant diet in the winter. The plant and invertebrate taxa were examined separately because plant data was only available for a single season while invertebrate data was available for two seasons. The manyglm model to determine invertebrate dietary composition included the main effects of age (adult: >1 year old, or first year: <1 year old), sex, habitat (coniferous or deciduous) and season (spring or winter), with the addition of age × season, age × habitat, sex × season, sex × habitat as interactions (Table S3.2, model a). In addition, the 2017 data only was investigated for both seasons, to check for a difference between seasons within the

same year (Table S3.2, model b). Finally, because the 2017 data included both seasons and the 2018 data was spring only, we tested for a difference in spring invertebrate composition between years (Table S3.2, model c). The winter plant data was used in a manyglm model with age, sex and habitat as main effects and age × habitat and sex × habitat as interactions (Table S3.2, model d). See Table S3.2 for the explanatory variables and the sample sizes for each composition model.

Posthoc tests cannot be run on interaction effects in manyglm models to determine the direction of the effect, so where a significant interaction was found, a separate manyglm was run on data subsets for habitat or season (depending on the variable in the interaction; see Results for models beginning 'X'). This approach allowed us to examine if the difference in age or sex was present in both groups for each environmental factor.

To investigate how the explanatory variables influenced dietary richness, a GLMM with a Poisson family and a log link function was used for the invertebrate data. The response variable was the total number of invertebrate genera consumed and included age × season, age × habitat, sex × season, sex × habitat as interactions and site and bird ID as random effects (Table S3.3, model f). See Table S3.3 for extra models on 2017 (model g) and spring (model h) only. For the plant data, a GLMM with a Conway-Maxwell Poisson distribution and a log link function was used (Table S3.3, model j). The response variable was the number of plant genera consumed and included age × habitat and sex × habitat as interactions and site as a random effect. See Table S3.3 for the model type, family and sample size used for each richness model. The package *emmeans* was used to examine significant interactions for the richness models (Lenth, 2019).

Invertebrate composition and richness among life stage; adults, first year and nestlings

To investigate the composition and dietary richness at different life stages, we examined the invertebrate diet of nestlings, first year birds and adults in the spring. The manyglm model to determine invertebrate dietary composition included the main effects of age (adult: >1 year old, first year: <1 year old and nestling: 8/9 days

old), habitat (coniferous or deciduous) and year (2017 or 2018) with the interaction age × habitat (Table S3.2, model e). The nestling data represents a single, randomly chosen nestling per nest because including pooled data for the nest would present unequal sampling effort between nests and individual adults and first years. Pooled nest data could inflate estimates of richness and frequency of occurrence of genera in nestlings. Additionally, a random effect of nest ID cannot be included in a manyglm and choosing a single nestling per nest avoids the issue of comparing an average richness (for all nestlings in a nest) against richness for single individuals (adults and first year birds).

To investigate the effect of explanatory factors on richness, a negative binomial GLMM was run which included the interaction age × habitat, year and sex as fixed effects and site as a random effect (Table S3.3, model k).

In addition to investigating differences in composition and richness of diet between adults, first years and nestlings in general, we conducted a within-nest comparison between the parental and nestling diets. For this, a Pearson correlation was run between the diet matrix for parents and for the total diet of nestlings in their nest. Not all nests had data for both parents (2017: 15 nests had data for a single parent and 8 nests had data for both parents, 2018: 19 nests had data for a single parent and 16 nests had data from both parents). We performed a separate correlation for each year to allow for the fact that diet differs between years. To investigate if parent richness is similar to nestling richness a GLM was run with a single randomly chosen parent richness as the response variable and a single randomly chosen nestling as the explanatory. Habitat, year and number of samples per nest were included as additional explanatory variables.

3.4 Results

3.4.1 NGS output

Of 436 identified sequences for invertebrate DNA (using COI), 256 were identified to species level (including subspecies) and 55 to genus level. Of 85 identified sequences for plant DNA (using ITS2), 45 were identified to species level (including subspecies) and 25 to genus level. The remaining sequences were assigned to a taxonomic level higher than genus.

After cleaning the data, from full-grown birds we had 187 invertebrate faecal samples (121 for both years of spring, 66 for winter) and 105 plant faecal samples. Tables 3.1 and 3.2 show the number of adult and first year samples in which each group of invertebrate and plant genera, were present. We had 192 samples from individual nestlings from 80 different nests (2017 and 2018 combined; Table 3.3). Below we first give an overall description of the diet and then expand on each result.

Table 3.1. The number and percentage of adult and first year samples, across both years, that had at least one genus of each group of invertebrates, for all 187 samples and split by season (N: spring = 121, winter = 66). In total, 148 invertebrate genera were identified. Groups are ordered according to percentage of samples for both seasons.

Invertebrates	**Group**		**Both seasons**		**Spring**		**Winter**	
		No. of genera	No. of samples	%	No. of samples	%	No. of samples	%
	Moths	65	165	88	121	100	44	67
	Spiders	13	88	47	55	45	33	50
	Hoverflies	6	78	42	69	57	9	14
	Parasitoid wasps	22	78	42	62	51	16	24
	Aphids	8	66	35	58	48	8	12
	Sac spiders	1	45	24	27	22	18	27
	Beetles	7	36	19	28	23	11	17
	True flies	6	36	19	17	14	19	29
	Moth flies	1	27	14	16	13	11	17
	Shield bugs	1	21	11	6	5	15	23
	Gall wasps	1	20	11	3	2	17	26
	Crane flies	1	18	10	15	12	3	5
	Biting midges	1	16	9	16	13	0	0
	Sawflies	2	15	8	15	12	0	0
	Spittlebugs	1	12	6	12	10	0	0
	Butterflies	3	9	5	9	7	0	0
	Gnats	1	9	5	1	1	8	12
	Bumblebees	1	7	4	7	6	0	0
	Mayflies	1	6	3	4	3	2	3
	Slugs	1	5	3	5	4	0	0
	Lacewings	1	4	2	3	2	1	2
	Weevils	1	4	2	4	3	0	0
	Springtails	1	3	2	1	1	2	3
	Cuckoo bees	1	1	1	1	1	0	0
	Earwigs	1	1	1	0	0	1	2

Table 3.2. The number and percentage of adult and first year samples that each plant genus was present in (N = 105).

Plants	**Common name**	**Genus**	**No. samples**	**%**
	Beech	Fagus	94	90
	Fruit bushes	Rubus	47	45
	Oak	Quercus	14	13
	Acer	Acer	13	12
	Plantain	Plantago	9	9
	Fruit trees	Prunus	9	9
	Elm	Ulmus	8	8
	Viola	Viola	8	8
	Fireweeds	Chamaenerion	7	7
	Yew	Taxus	7	7
	Ivy	Hedera	6	6
	Sowthistles	Sonchus	5	5
	Ash	Fraxinus	4	4
	Holly	Ilex	4	4
	Nettles	Urtica	4	4
	Alder	Alnus	3	3
	Cabbages	Brassica	3	3
	Spruce	Picea	3	3
	Willow	Salix	3	3
	Geraniums	Geranium	2	2
	Barley, rye, lyme grass	Hordeum	2	2
	Stinking willie	Jacobaea	2	2
	Walnut	Juglans	2	2
	Pine	Pinus	2	2
	Bentgrass	Agrostis	1	1
	Oat	Avena	1	1
	Heather	Caluna	1	1
	Cocksfoot grasses	Dactylis	1	1
	Stickyweed	Galium	1	1
	Water cresses	Helosciadium	1	1
	Privet	Ligustrum	1	1
	Flax	Linum	1	1
	Rhododendron	Rhododendron	1	1
	Rose	Rosa	1	1
	Elder	Sambucas	1	1
	Figwort	Scrophularia	1	1
	Wheat	Triticum	1	1
	Navelwort	Umbilicus	1	1
	Speedwell	Veronica	1	1

Table 3.3. The number and percentage of nestling samples that had at least one genus of each group of invertebrates, for all 192 individual samples and all 80 nests.

Nestling invertebrates	**Group**		**Individual nestlings**		**Whole nest**	
		No. genera	No. samples	%	No. samples	%
	Moths	98	192	100	80	100
	Crane flies	1	101	53	54	68
	Hoverflies	8	80	42	45	56
	Spiders	15	49	26	40	50
	Parasitoid wasps	22	39	20	25	31
	True flies	13	32	17	20	25
	Bumblebees	1	31	16	22	28
	Aphids	9	30	16	19	24
	Beetles	7	21	11	17	21
	Biting midges	1	19	10	9	11
	Sawflies	4	15	8	11	14
	Butterflies	3	4	2	4	5
	Cuckoo bees	1	4	2	4	5
	Slugs	3	4	2	4	5
	Moth flies	1	2	1	2	3
	Earwigs	1	1	1	1	1
	Honey bees	1	1	1	1	1
	Leafhoppers	1	1	1	1	1
	Social wasps	1	1	1	1	1

3.4.2 Description of the diet

Adults and first years

i) Invertebrates: A total of 148 genera of 25 groups of invertebrates were identified and used in the analysis, across seasons and years (Tables 3.1 and S3.4). Moths were represented by the largest number of genera (65 of 148 genera) followed by parasitoid wasps (22 genera) and spiders (13 genera). These groups were also most prevalent among samples across both seasons: moths (88% of samples), spiders (47% of samples) and parasitoid wasps (42% of samples). The maximum number of invertebrate genera present in any one sample was 25, the minimum was 1 and the mean was 8.3 (Figure 3.3). In spring, 124 different genera of 24 invertebrate groups were identified across both years, with the most prevalent among samples being

moths (100%), hoverflies (57%) and parasitoid wasps (51%) (Tables 3.1 and S3.4). In winter, 72 different genera of 17 groups of invertebrates were identified, with the most prevalent among samples being moths (67%), spiders (50%) and true flies (29%) (Tables 3.1 and S3.4).

ii) Plants: A total of 42 different plant genera were identified in winter samples taken from both habitats (Table 3.2), the most common of which was beech (*Fagus*) which was present in 90% of samples (94 of 105). *Rubus* (fruits such as blackberry and raspberry), *Quercus* (oak) and *Acer* (Japanese maple) were the next three most common genera and were present in 45%, 13% and 12% of samples respectively. Fewer plant genera were detected in winter samples than invertebrate genera (max = 8, min = 1, mean = 2.7, Figure 3.3). Many of the plant genera detected were rare with only four being in more than 12% of samples (Table 3.2).

Nestlings

Overall, 123 genera of 19 groups of invertebrates were identified and used in the nestling analysis (Tables 3.3 and S3.5). Of these 123 genera, 98 were moths and at least one moth genus was present in all 192 individual nestling samples. Similar to adults and first year birds, parasitoid wasps (22 genera) and spiders (15 genera) were the next two groups after the moths with the greatest number of genera identified. Although only one genus of crane flies (*Tipula*) was identified, it was present in 53% of individual samples and in 68% of nests (Tables 3.3), suggesting that it was an important food source for the nestlings. There was high number of invertebrate genera present in both individual samples and for all samples within a nest (individuals: max = 22, min = 2, mean = 8.2; whole nest: max = 34, min = 3, mean = 13.2; Figure 3.3).

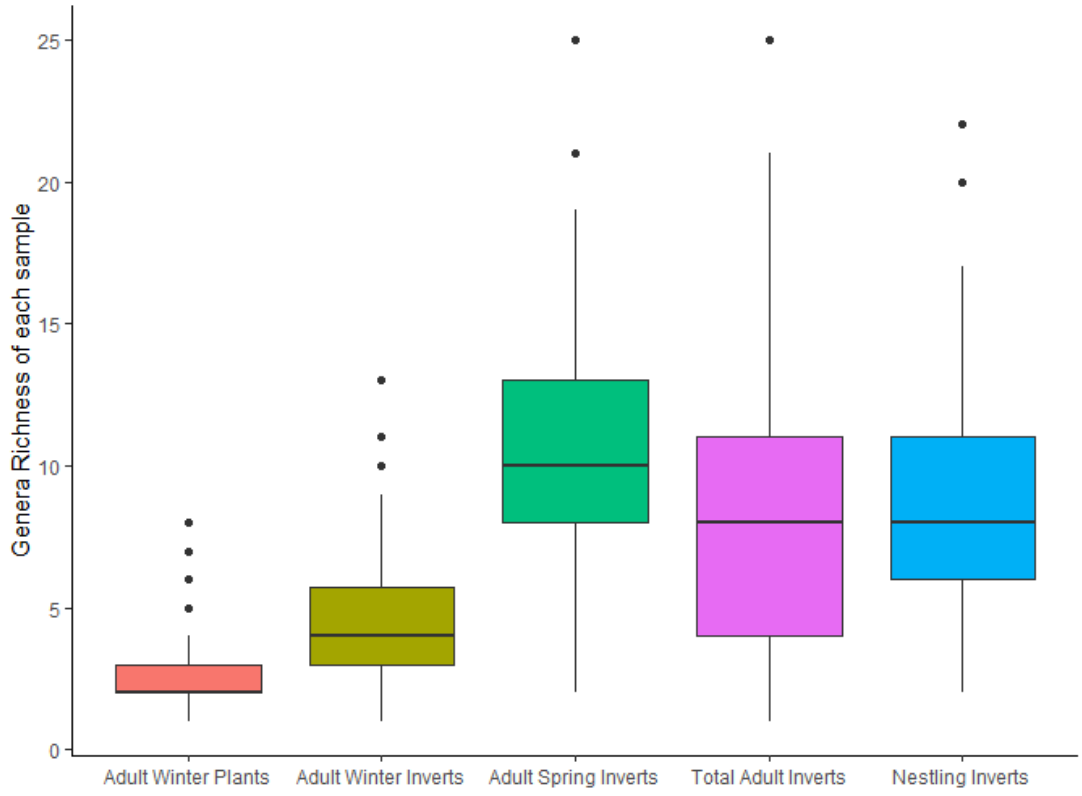


Figure 3.3. Genera richness (number of genera present in each sample) for winter plants (N = 105), winter invertebrates (N = 66), spring invertebrates (N = 121), total adult invertebrates (includes both winter and spring together, N = 187) and individual nestlings (N = 192). The total adult invertebrates includes both first year birds (<1 year old) and adults (>1 year old). Boxes show the median and the inter-quartile range with whiskers extending to 1.5*IQR above and below.

3.4.3 Correlates of invertebrate diet among full-grown birds

Season, year and habitat

Invertebrate composition of full-grown birds differed between seasons (LRT = 960.5, *P* = 0.001; Table 3.4, model a). Although the top five most commonly eaten genera in spring were all moths, in winter they included sac spiders, gall wasps and shield bugs. Groups that contained a higher percentage of samples in winter than in spring were spiders, beetles, flies, shield bugs, gall wasps and gnats (Table 3.1). Most of the genera identified were found in spring (84%), 52% of genera were found exclusively in spring and 30% of genera were common to both seasons. The most common genus eaten in spring was *Operophtera* (winter moth) which was entirely absent from the winter diet (Table S3.4).

Using the 2017 data alone, we confirmed the main season effect for dietary composition (LRT = 467.8, *P* = 0.001; Table 3.4, model b) and using the spring data alone we found that diet composition varied between 2017 and 2018 (Year: LRT = 336.4, *P* = 0.001; Table 3.4, model c). Richness of invertebrate genera differed between seasons and years. Great tits consumed fewer invertebrate genera in the winter than in the spring (Season: Est = -0.90, *P* < 0.001; Table 3.5, model f; Figure 3.3), and this season effect on richness was confirmed within 2017 (Est: -0.85, *P* < 0.001; Table 3.5, model g). There was a greater number of invertebrate genera found in the diets of birds in spring 2018 than in 2017 (Year: Est = 0.21, *P* = 0.016; Table 3.5, model h).

Invertebrate composition differed between conifer and deciduous habitats (LRT = 295.8, *P* = 0.001; Table 3.4, model a), yet there was no difference in richness between the two habitat types (Est = -0.06, *P* = 0.69; Table 3.5, model f). 52% of genera were found in both habitat types and there were more genera found exclusively in deciduous habitats than there were in coniferous habitats (38% compared to 7%).

Table 3.4. The model output for the *composition* (identity of genera consumed) models, for adults and first years (models a – d and X1 to X5) and adults, first years and nestlings (model e). Models X1 – X5 are the posthoc analyses to examine interactions between intrinsic and environmental variables. LRT is the likelihood ratio test.

Data	Model label	Data	Variable	LRT	P value	N
Adults and first years						
	Invertebrates					
	a	Winter and Spring	Age	337.7	**0.001**	160
			Sex	271.8	**0.001**	
			Season	960.5	**0.001**	
			Habitat	295.8	**0.001**	
			Age × season	69.1	**0.002**	
			Sex × season	54.4	0.062	
			Age × habitat	101.1	**0.028**	
			Sex × habitat	95.8	**0.023**	
	b	2017 only (winter and spring)	Age	492.7	**0.001**	113
			Sex	154.6	0.138	
			Season	467.8	**0.001**	
			Habitat	206.6	**0.001**	
	c	Spring only	Age	191.0	**0.001**	101
			Sex	233.1	**0.001**	
			Habitat	284.2	**0.001**	
			Year	336.4	**0.001**	
	X1	Winter only	Age	111.0	**0.001**	66
			Sex	92.1	0.098	
			Habitat	64.9	0.51	
	X2	Conifer only	Age	193.3	**0.001**	34
			Sex	136.6	**0.008**	
			Season	195.4	**0.001**	
			Year	154.2	**0.001**	
	X3	Deciduous only	Age	391.9	**0.001**	126
			Sex	247.3	**0.001**	
			Season	643.5	**0.001**	
			Year	276.6	**0.001**	
	Plants					
	d	Winter	Age	68.78	**0.001**	105
			Sex	50.22	0.131	
			Habitat	29.00	0.313	
			Age × habitat	13.91	0.151	
			Sex × habitat	39.73	**0.002**	
	X4	Conifer only	Age	33.2	**0.045**	18
			Sex	34.9	0.090	
	X5	Deciduous only	Age	24.6	0.111	87
			Sex	54.7	**0.003**	
Adults, first years and nestlings	Invertebrates					
	e	Spring	Age	1040.0	**0.001**	181
			Habitat	382.6	**0.001**	
			Year	489.2	**0.001**	
			Age × habitat	184.9	**0.001**	
	X6	Conifer only	Age	488.0	**0.001**	53
			Year	219.3	**0.001**	
	X7	Deciduous only	Age	754.9	**0.001**	128
			Year	385.2	**0.001**	

Table 3.5. The model output for the *richness* (number of invertebrate genera consumed) models, for adults and first year birds (models f – j) and adults, first years and nestlings (model k). The reference level is in brackets. Site as random effect: model f: variance (0.0053), standard deviation (0.073); model g: variance (0.009), standard deviation (0.095); model h: variance (0.0059), standard deviation (0.077); model j: variance (0.063), standard deviation (0.25); model k: variance (0.0016), standard deviation (0.040).

Data	Model label	Variable	Estimate	SE	Z value	P value
Adults and first year birds	f - Inverts	Intercept	2.18	0.13	16.58	**<0.001**
		Age (adult)	0.40	0.15	2.74	**0.006**
		Sex (female)	-0.001	0.14	-0.006	1.00
		Season (spring)	-0.90	0.18	-4.89	**<0.001**
		Habitat (conifer)	-0.06	0.15	-0.40	0.69
		Age × Season	0.21	0.20	1.02	0.31
		Sex × Season	-0.33	0.16	-2.09	**0.04**
		Age × Habitat	-0.25	0.17	-1.44	0.15
		Sex × Habitat	0.20	0.16	1.24	0.22
	g - 2017	Intercept	2.11	0.12	16.87	**<0.001**
		Age (adult)	0.24	0.12	2.03	**0.04**
		Sex (female)	0.08	0.09	0.87	0.39
		Habitat (conifer)	-0.03	0.14	-0.24	0.81
		Season (spring)	-0.85	0.11	-7.53	**<0.001**
	h – Spring	Intercept	2.16	0.10	20.56	**<0.001**
		Age (adult)	0.11	0.09	1.23	0.22
		Sex (female)	0.14	0.08	1.82	0.07
		Habitat (conifer)	-0.11	0.10	-1.16	0.25
		Year (2018)	0.21	0.09	2.41	**0.016**
	j - Plants	Intercept	0.88	0.22	4.06	**<0.001**
		Age (adult)	0.20	0.29	0.68	0.50
		Sex (female)	0.36	0.25	1.45	0.15
		Habitat (conifer)	-0.07	0.33	-0.2	0.84
		Age × Habitat	-0.03	0.36	-0.08	0.94
		Sex × Habitat	-0.42	0.27	-1.53	0.13
Adults, first years and nestlings	k	Intercept	2.23	0.12	18.91	**<0.001**
		Age (adult) – First year	0.31	0.15	2.07	**0.038**
		Age (adult) – Nestling	-0.34	0.14	-2.40	**0.016**
		Sex (female)	-0.13	0.08	-1.62	0.11
		Habitat (conifer)	0.01	0.12	0.084	0.93
		Year (2017)	0.18	0.065	2.83	**0.005**
		Age – First year × Habitat	-0.27	0.18	-1.48	0.14
		Age – Nestling × Habitat	0.09	0.16	0.56	0.57

Age

Dietary composition varied between adults and first years in both spring and in winter (age × season: LRT = 69.1, *P* = 0.002; Table 3.4, model a, c and X1; Figures 3.4a and 3.4b). Though not a significant difference, the proportion of genera found in the diet of both age groups (diet overlap) was higher in spring (67% of genera) than in winter (36%; Figure S3.1), suggesting their diet differences were more pronounced in winter. In the winter, a larger number of genera were consumed exclusively by first years (58%) than exclusively by adults (7%; Figure S3.1a), compared to the spring (22% for adults and 11% for first years, Figure S3.1b).

Dietary composition differences between adults and first years were habitat dependent (age × habitat: LRT = 101.1, *P* = 0.028; Table 3.4, model a). Age differences were especially pronounced in deciduous habitats (Table 3.4, model X2, X3; Figures 3.4c and 3.4d). Three of the most common genera (55%-73%) present in first year diets in conifer habitats were in less than 10% of adult diets. The top six genera present in the highest number of first year diets in deciduous habitats consisted of five different invertebrate groups (sac spider *Clubiona*, moth *Orthosia* and *Operophtera*, gall wasp *Neuroterus*, moth fly *Psychoda* and shield bug *Acanthosoma*) whereas the top five for adults were all moth genera. Additionally, though not significant, there was a tendency for more genera in conifer habitats to be eaten exclusively by adults than exclusively by first years (32% compared to 24%, Figure S3.2a) and in deciduous habitats a tendency for the reverse; slightly more genera were eaten exclusively by first years than by adults (22% compared to 12%, Figure S3.2b). Dietary richness differed between the two age groups; first years consumed a greater number of invertebrate genera than adults, irrespective of season or habitat (Age: Est = 0.4, *P* = 0.006; Table 3.5, model f).

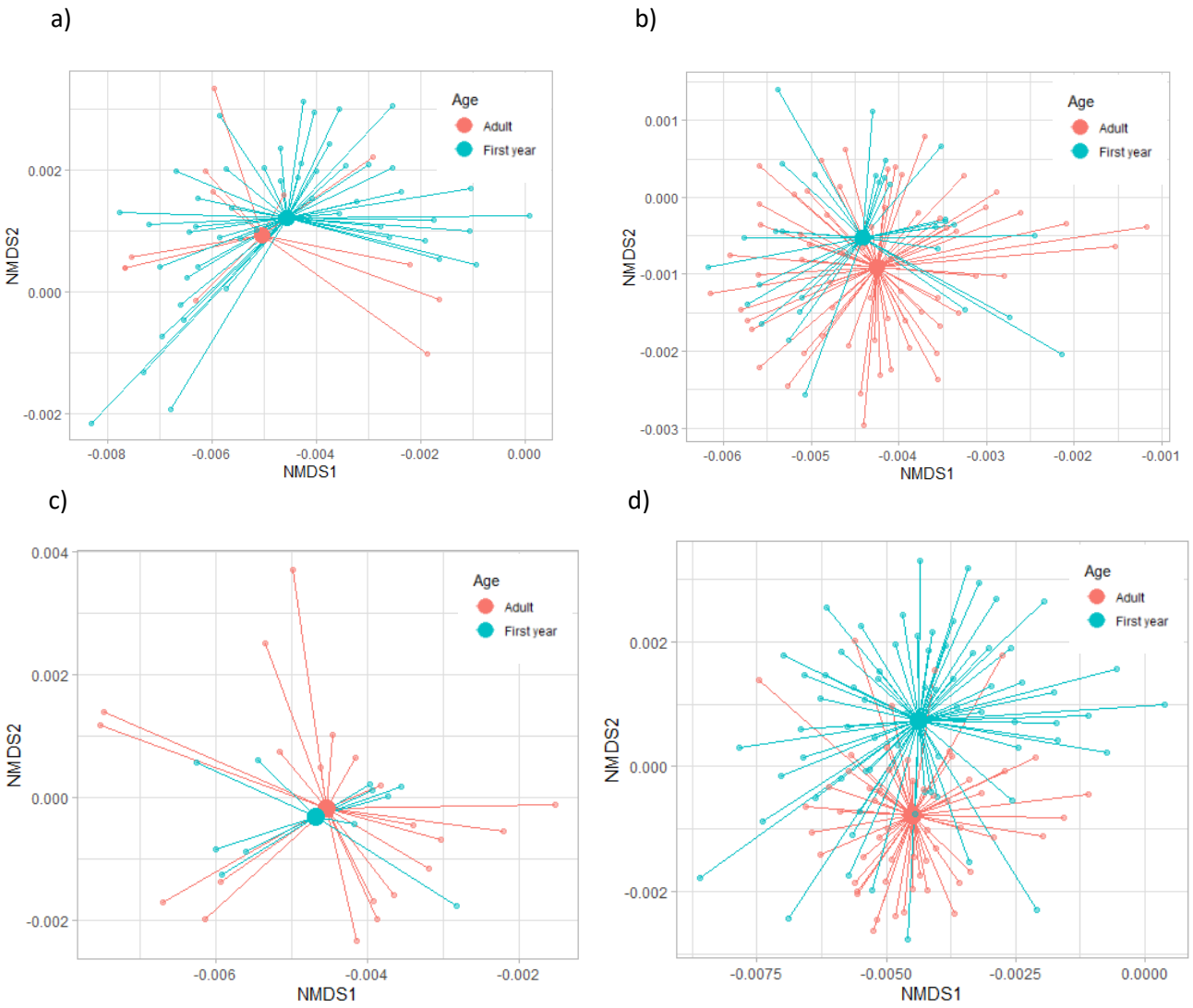


Figure 3.4. Nonmetric Multidimensional Scaling (NMDS) plots for the invertebrate genera composition of first years and adults for a) winter, b) spring, c) conifer habitats and d) deciduous habitats. Each point shows an individual and the connecting lines join the individual to the mean of its age group. The Jaccard index was used to calculate the distances between samples. Data includes both seasons together with no duplicates from the same individual and two outliers were removed (adults, both from the winter). Data contains: 13 adults and 51 first years in winter, 64 adults and 20 first years in spring, 21 adults and 11 first years in conifer, 56 adults and 70 first years in deciduous. NMDS values were created first and then plotted for each season and each habitat separately to allow comparison between graphs showing the same environmental factor.

Sex

Dietary composition differences between the sexes were habitat dependent (sex × habitat: LRT = 95.8, *P* = 0.023; Table 3.4, model a), and males and females differed in diet in both habitat types (Table 3.4, model X2, X3; Figure 3.5). There was a similar number of genera eaten only by a single sex in conifer sites (27% for males and 25% for females; Figure S3.3a). In deciduous habitats, males had 17% of the deciduous genera exclusively present in their diet compared to 10% for females (Figure S3.3b). The difference between the sexes in dietary invertebrate composition was not influenced by season (sex × season: LRT = 54.4, *P* = 0.062; Table 3.4, model a).

There was a marginally significant (*P* = 0.04) interaction between sex and season on invertebrate richness (sex × season: Est = -0.33, *P* = 0.04; Table 3.5, model f; Figure 3.6) which indicated that males had a higher richness than females in spring but not in winter. Furthermore, a posthoc test on this interaction found no difference in richness between the sexes within seasons (emmeans: spring: Est = -0.07, SE = 0.08, Z = -0.89, *P* = 0.38; winter: Est = 0.24, SE = 0.15, Z = 1.64, *P* = 0.10). Habitat type did not influence the dietary richness of males and females (sex × habitat: Est = 0.20, *P* = 0.22; Table 3.5, model f).

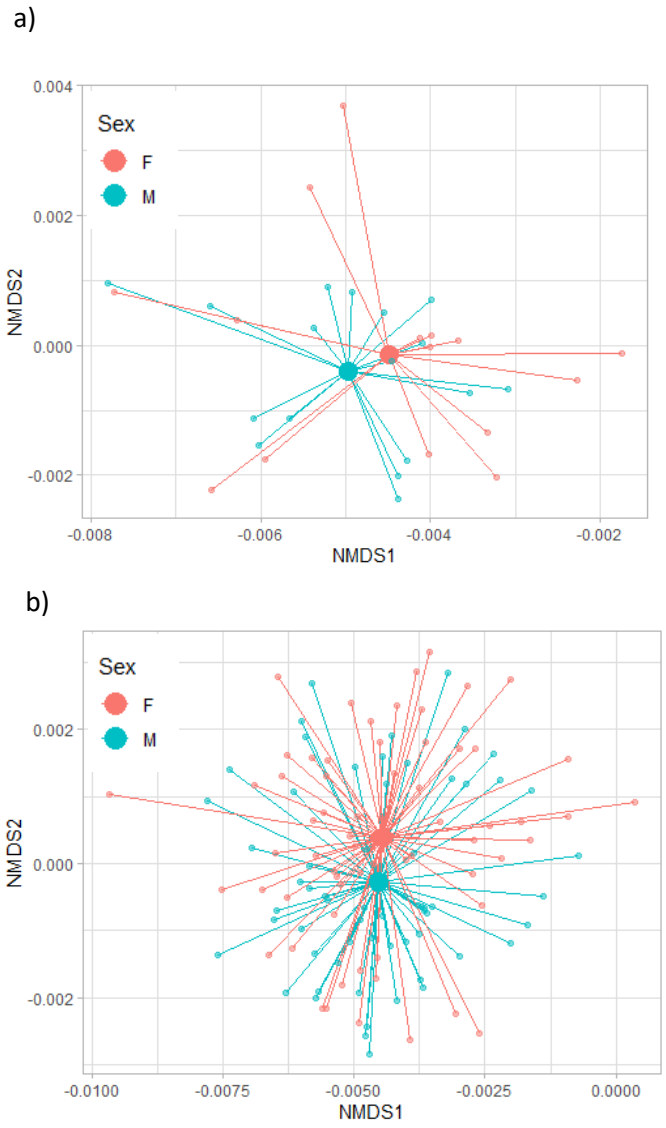


Figure 3.5. Nonmetric Multidimensional Scaling (NMDS) plots for the invertebrate genera consumed by males and females in a) conifer and b) deciduous habitats. Data includes both seasons together with no duplicates from the same individual and two outliers were removed (females, both from conifer habitats). Data contains 17 males and 15 females in conifer, 62 males and 64 females in deciduous. See Figure 3.4 for extra details on creation of the plot.

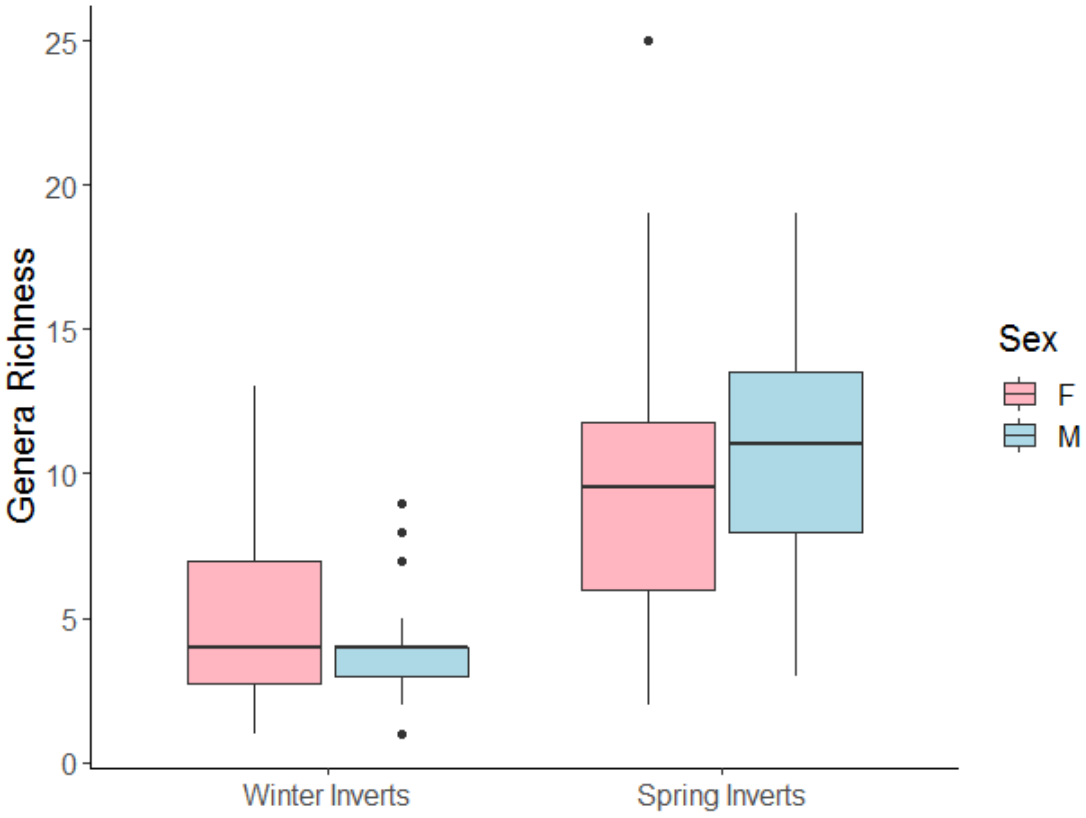


Figure 3.6. Invertebrate richness for males and females in winter and spring. Data contains 46 females and 55 males in the spring and 40 females and 26 males in the winter. See Figure 3.3 for extra details.

3.4.4 Correlates of plant diet in full-grown birds

Plant dietary composition differed between adults and first years (Age: LRT = 68.78, *P* = 0.001; Table 3.4, model d; Figure 3.7). Both adults and first years relied heavily on beech (*Fagus*; 62% and 96% respectively), while slightly more adults than first years consumed oak (*Quercus*; 24% and 11%) (Figure S3.4). In comparison to adult diets, more plant genera were eaten exclusively by first years (18 compared to four taxa, Figure S3.4) and these included ash, nettle, yew, plantains and ivy. Habitat did not influence differences in plant composition between the age groups (age × habitat: LRT = 13.91, *P* = 0.151; Table 3.4, model d).

Plant dietary composition differences between the sexes was observed in both habitats (sex × habitat: LRT = 39.73, *P* = 0.002; Table 3.4, model d; Figure 3.8) but there was more variation between male and female diets in conifer compared to deciduous (compare Figure 3.8a and 3.8b), although the effect of sex in conifer was marginally non-significant when running the model on the subset, most likely due to a small sample size (N = 18; Table 3.4, model X4, X5). In conifer habitats, 12 genera (of 24) were eaten exclusively by males (including spruces, pines and nettles), whereas six were eaten exclusively by females (including elm, heather and plantains; Figure S3.5a). In deciduous habitats, 11 genera (of 34) were found in the diet of both sexes with more females eating elm (*Ulmus*) and beech (*Fagus*) than males, and a similar number of plant genera were eaten by only one of the two sexes (13 genera for females and 10 for males; Figure S3.5b). There was no effect of age, habitat or sex on the richness of plants eaten in the winter, nor were there any significant interactions between them (Table 3.5, model j).

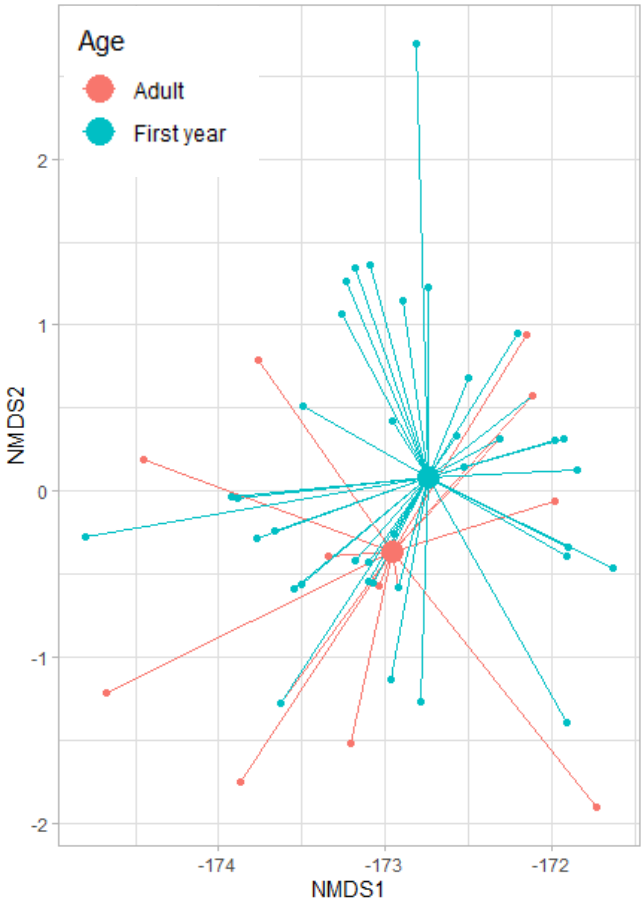
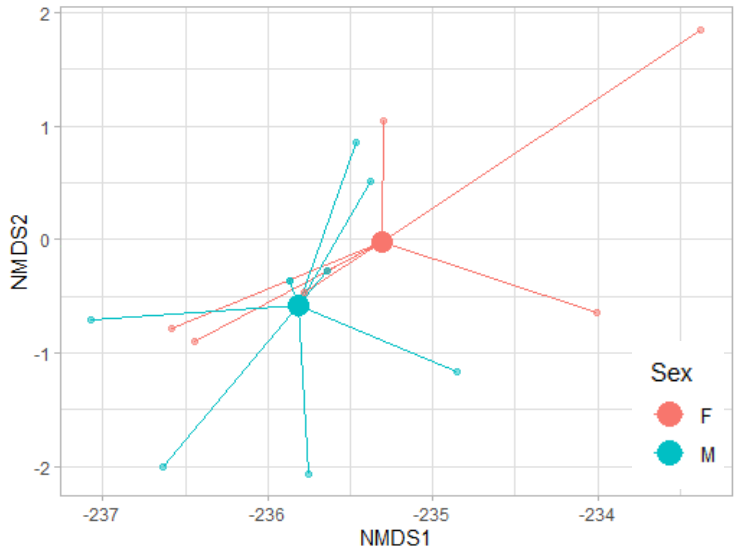


Figure 3.7. Nonmetric Multidimensional Scaling (NMDS) plot for the plant genera consumed by adults and first years. One outlier was removed (an adult). Data contains 20 adults and 84 first years. See Figure 3.4 for extra details on creation of the plot.

a)



b)

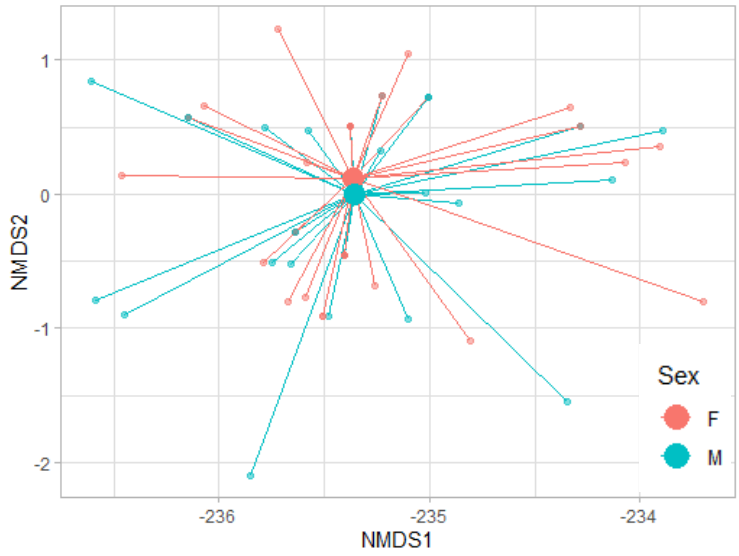


Figure 3.8. Nonmetric Multidimensional Scaling (NMDS) plots for the plant genera consumed by males and females in a) conifer and b) deciduous habitats. Two outliers have been removed (females, conifer). Data contains 10 males and 6 females in conifer, 36 males and 51 females in deciduous. See Figure 3.4 for extra details on creation of the plot.

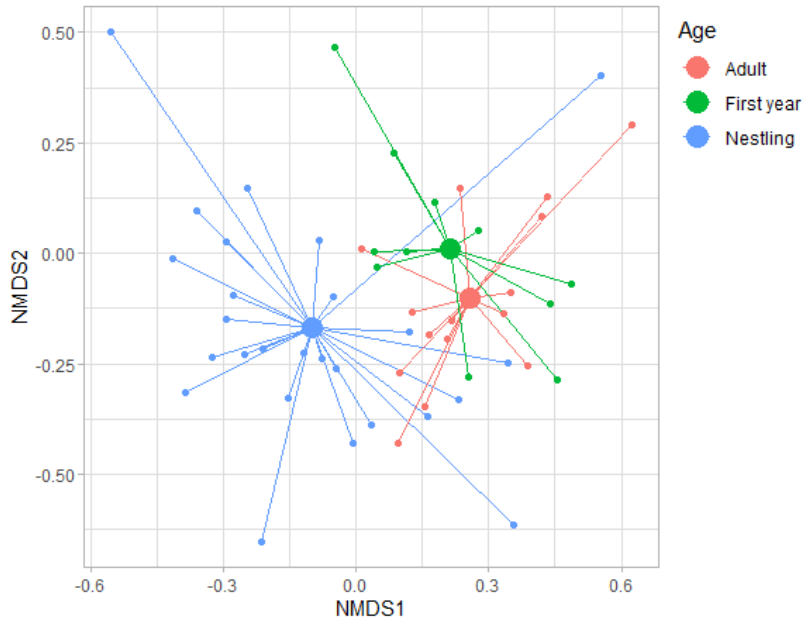
3.4.5 Differences in the (invertebrate) spring diet with life stage

Comparison among age classes

Adults, first years and nestlings all differed in the composition of dietary invertebrates (Age: LRT = 1040.0, *P* = 0.001; Table 3.4, model e) and tests on data subsets revealed a difference in composition between nestlings (a single nestling per nest) and first years (LRT = 626.9, *P* = 0.001) and between nestlings and adults (LRT = 662.3, *P* = 0.001). Additionally, the differences in composition between the three life stages were habitat dependent (age × habitat: LRT = 184.9, *P* = 0.001; Table 3.4, model e, X6, X7; Figure 3.9). In both habitats, the diet of the nestlings was equally distinct from adults and first year birds (Figure 3.9). 21% of genera in conifer habitats were present in the diet of all three age groups and 39% in deciduous (Figure S3.6).

Dietary richness of invertebrate genera differed between the age groups. Nestlings had a lower genera richness compared to adults (Est = -0.34, *P* = 0.016; Table 3.5, model k; Figure 3.10) and first years (Subset: Est = -0.50, SE = 0.11, Z = -4.40, *P* <0.001; Figure 3.10). Age differences in dietary richness were not habitat dependent (age × habitat: Table 3.5, model k). Dietary composition differed between the years (Table 3.4, model e) and more genera were consumed in 2018 than 2017 (Year: Est = 0.18, *P* = 0.005; Table 3.5, model k), confirming the result from the adult and first year data without nestlings. See Figure 3.11 for a summary of findings.

a)



b)

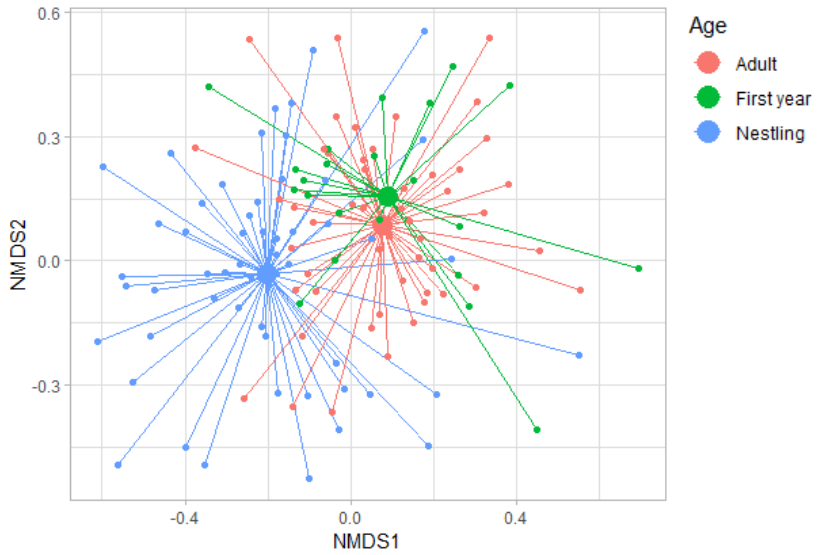


Figure 3.9. Nonmetric Multidimensional Scaling (NMDS) plots for the invertebrate genera consumed during the breeding season by adults (red), first year birds (green) and nestlings (blue) for a) conifer and b) deciduous habitats. One outlier in has been removed (first year, deciduous). Data contains 15 adults, 12 first years and 26 nestlings in conifer habitats and 51 adults, 22 first years and 54 nestlings in deciduous habitats. Data for nestlings represents a single nestling per nest. See Figure 3.4 for extra details on creation of the plot.

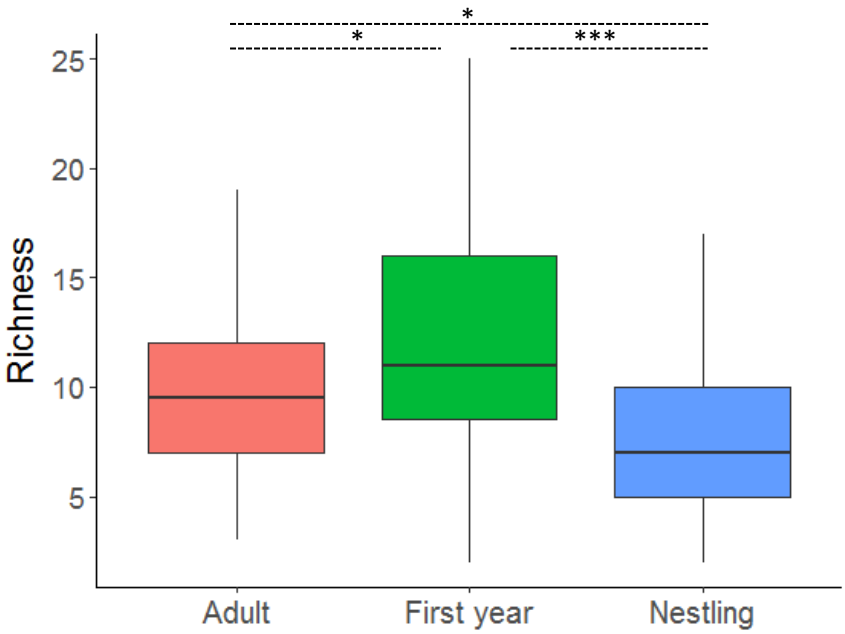


Figure 3.10. Invertebrate richness for adults, first years and nestlings in spring. Data contains 66 adults, 35 first years and 80 nestlings (single nestling from each nest). See Figure 3.3 for more details on plot creation.

a)

Invertebrates		Composition: Age	Composition: Sex	Richness: Age	Richness: Sex
Season	Spring	**less** variation / more overlap	No effect	Main effect only: First years = higher richness than adults	Males = **higher** richness than females
	Winter	**more** variation / less overlap			Both sexes equal
Habitat	Deciduous	**more** variation / less overlap	**slight less** variation / more overlap		No effect
	Conifer	**less** variation / more overlap	**slight more** variation / less overlap		

Plants					
Habitat	Deciduous	Main effect only: variation in diet of plants between the ages	**less** variation / more overlap	No effect	No effect
	Conifer		**more** variation / less overlap		

b)

Invertebrates		Composition: Age	Richness: Age
Habitat	Deciduous	Variation in diet between the ages	Main effect only: Nestlings = lower richness than adults and first years
	Conifer	Variation in diet between the ages	
Year		Main effect of year on composition	Main effect of year on richness: Higher richness in 2018

Figure 3.11. Summary of results that shows variation and overlap in diet for a) adults and first years and b) adults, first years and nestlings. Diet response variables are in green: composition is the identity of the prey items and richness is the number of genera detected in the diet. Demographic explanatory factors are in blue (age and sex) and environmental explanatory factors are in orange (habitat, season and year). Where the interaction between a demographic factor and an environmental factor was significant, there is a description of the effect, for example, in panel a), in the interaction between age and season, there was less variation and more overlap between adult and first year diets in the spring, compared to more variation and less overlap between adult and first year diets in the winter. In panel b), there was similar diet variation between the age groups in both habitat types. Where the interaction was not significant, the main effect is stated if found, and if not then there was 'no effect'. Note that in panel b) there was no interaction between year and age, the results stated for year are the main effect on dietary composition and richness.

Comparison between parents and their nestlings

The invertebrate dietary composition of parents was weakly similar to that of their nestlings (Pearson's product-moment correlation: 2017: cor = 0.18, t = 12.7, df = 4621, $P < 0.001$, 95% CI = 0.16 – 0.21; 2018: cor = 0.19, t = 16.6, df = 7033, $P < 0.001$, 95% CI = 0.17 – 0.22; Figure 3.12). We found a similar pattern when analysing the two habitat types separately (Pearson's product-moment correlation: conifer: cor = 0.18, t = 11.2, df = 3817, $P < 0.001$, 95% CI = 0.15 – 0.21; deciduous: cor = 0.20, t = 17.7, df = 7837, $P < 0.001$, 95% CI = 0.17 – 0.22). Additionally, there was no relationship between parent and nestling invertebrate richness; the richness of one parent did not predict the richness of one of its (randomly selected) nestlings (GLM: Est = 0.005, SE = 0.01, Z = 0.35 $P = 0.73$).

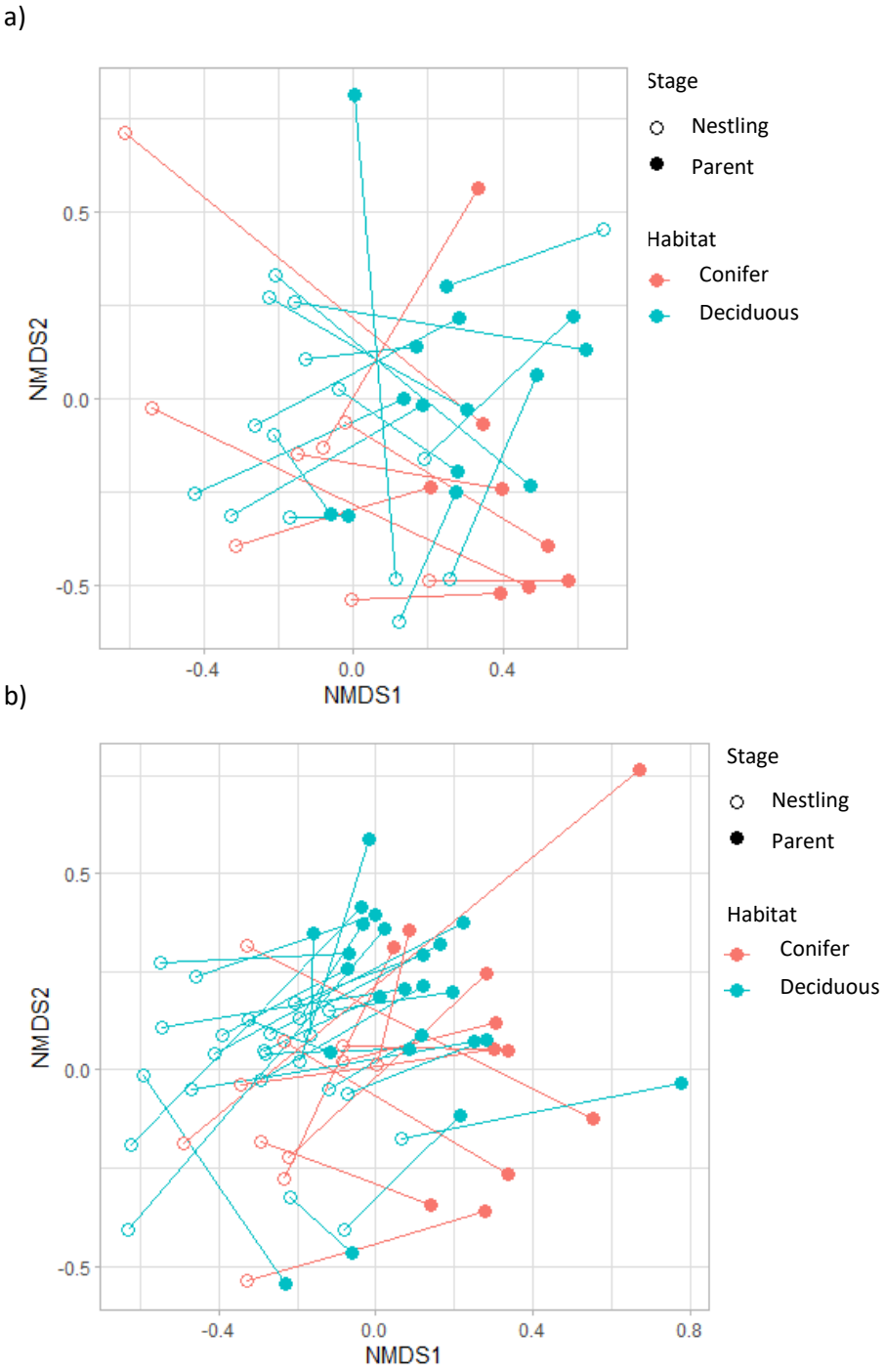


Figure 3.12. Nonmetric Multidimensional Scaling (NMDS) plots showing how separated the parent diet is from their nestlings for both habitat types a) 2017 and b) 2018. Conifer is in red and deciduous is in blue. Each point shows either the combined diet for the parent(s) or the combined diet for the nestlings. Data contains 23 nests for 2017 and 35 for 2018. Lines connect the parents of one nest box with their own nestlings.

3.5 Discussion

We compared dietary differences between age classes and sexes in great tits across different habitats and seasons. Our results show dietary variation in invertebrates and plants, between first year birds (<1 year old), adults (>1 year old) and nestlings, and between males and females (see Figure 3.11). We investigated dietary composition (identity of genera) and richness (number of genera) of invertebrates in both seasons, and plants in the winter only. Habitat type was particularly influential as it interacted with age and sex to influence the composition of invertebrate genera, and interacted with sex to influence plant genera, in the diet. In addition, season interacted with age to influence composition and with sex to influence richness. We expected diets between the ages and sexes in spring and deciduous habitats to show more variation compared to winter and conifer respectively. Our results provide mixed support for these predictions, which are discussed below. Our results parallel recent work that has found intraspecific variation in diet to be important in how we understand the niche occupied by whole populations (Bolnick *et al.*, 2007, 2011; Svanbäck and Bolnick, 2007).

3.5.1 Dietary differences among demographic groups with influences of season and habitat

Age

We found that adults and first year birds had different dietary compositions of both plants and invertebrates, and that adults had a lower dietary richness of invertebrates than first years. This shows patterns of variation in diet between the age classes and that adults have a more specialised diet than first years. There are two main possible reasons for this: experience and competition. First years are less experienced foragers than adults (Goss-Custard and Durell, 1987; Daunt *et al.*, 2007; Thornton, 2008; Fayet *et al.*, 2015) and will undertake a large amount of trial and error learning about different prey types (Marchetti and Price, 1989). This lack of experience may be particularly apparent in their first winter where invertebrate

and plant food types are unknown and invertebrates may be difficult to find (Goss-Custard and Durell, 1987). Indeed, we found that a lower proportion of invertebrate genera was eaten by both age groups (lower overlap) in winter than in spring (Figure S3.1), which is not as we predicted. Low overlap of diets in winter suggests that first years are sampling food types more broadly than adults to gain information, and is further supported by our result that more winter invertebrate and plant genera were consumed exclusively by first years than by adults. Further support for the idea that first years may be less experienced comes from looking at dietary differences dependent on habitat quality. In poor quality conifer habitats, there was a tendency for more invertebrate genera to be eaten exclusively by adults than by first years. However, in good quality deciduous habitats, the reverse was the case. This may be because adults can process difficult prey (Thornton and McAuliffe, 2006) and find high quality food, irrespective of habitat quality. First years, on the other hand, may struggle to forage successfully in a challenging habitat like a conifer woodland where prey abundance is low (van Balen, 1973). Indeed, our results show some suggestion of this as two of the genera consumed only by first years in conifer habitats were parasitoid wasps (*Dusona and Zele*) which include a number of species that have a venomous sting (Moreau and Asgari, 2015) and may not be very palatable. Moreover, in food-rich habitats, it may be easier for first years to find food and they can sample a variety of types to gain information about them (Marchetti and Price, 1989). Our results add to the multitude of studies demonstrating that juveniles are less experienced foragers than adults (Marchetti and Price, 1989; Daunt *et al.*, 2007; Thornton, 2008; Breed, Bowen and Leonard, 2011; Fayet *et al.*, 2015; Grecian *et al.*, 2018) and show some indication that first years may consume lower quality food in challenging foraging habitats.

A second reason for dietary variation between the age classes and greater dietary specialisation in adults is competition. Adults are likely to be more dominant than first years (Hogstad, 1989) and may be monopolising resources (van Horne, 1982). If first years need to avoid adults who are more dominant, they may frequent different foraging locations (Radford and Du Plessis, 2003; van den Hout *et al.*,

2014) and exploit a wider variety of suboptimal food types than adults (Sol *et al.*, 2005). Our result agrees with a study on green woodhoopoes where dominant birds had a narrower niche breadth than subordinates, perhaps due to them monopolising preferred foraging patches (Radford and Du Plessis, 2003). In our study, adults and first years did not differ in the richness of plant genera they consumed which may be explained by plants not being as challenging to acquire as invertebrate prey.

Further support for competition leading to variation in diet comes from our finding that dietary differences in invertebrate prey were season and habitat dependent. We found more variation in winter diets than spring diets, suggesting that because tits move in large flocks in winter, competition is more prevalent, leading to divergence in dietary niches (Gibb, 1954). Moreover, in spring, birds occupy territories, and are less likely to compete for food (Gibb, 1954), so diets overlap more. Differences in diet were also dependent on habitat type: there was less variation between the diets of adults and first years in conifer than in deciduous habitats and this supports our prediction. Deciduous habitats have a higher population density (O'Shea, O'Halloran and Quinn, 2018) and subsequent potential for increased competition. As competition increases and preferred prey becomes scarce, individuals must select alternative prey, leading to greater distinction between the age classes (Robinson and Wilson, 1998; Svanbäck and Bolnick, 2007). In less densely populated conifer habitats, individuals experience competitive release (Bolnick *et al.*, 2010) and individual niches include more prey types, leading to a greater overlap among individuals' diets.

Although competitive release is commonly described in the context of interspecific competition (Bolnick *et al.*, 2010), our results support the growing evidence that it also applies within populations (Bolnick, 2001; Svanbäck *et al.*, 2008). In combination with density, prey quality (abundance and diversity) can contribute to dietary differences. Increased variation in diet between adults and first years in deciduous habitats compared to conifer may be due to the higher abundance or diversity of prey (van Balen, 1973; Mänd *et al.*, 2005), which allows dietary niches to diverge because there is less competition for any one type of prey (Araújo,

Bolnick and Layman, 2011). Our results for the two environmental factors showed support for both the experience and competition hypotheses and we cannot separate the two. It is likely that both these drivers are contributing to variation in diet between adults and first years and are not mutually exclusive. Our results show that environmental context is important in revealing dietary differences of invertebrate prey between individuals of different age classes.

Sex

Males and females showed variation in the invertebrates present in the diet and habitat influenced this pattern. Dietary variation between the sexes may reflect different requirements for growth and reproduction. Male great tits are larger than females (van Balen, 1967) and so will require more food for their increased maintenance costs. While males may be able to catch and handle larger prey items due to their larger body size (Mason, 1977; Thiemann *et al.*, 2011), females may be able to access substrates that males cannot (Boinski, 1989; Radford and Du Plessis, 2003). For example, females may be able to catch different types of prey by reaching the fragile ends of branches in the canopy (Ebenman and Nilsson, 1982). The dominant plant species may influence how males and females can use a habitat, and indeed, we found that differences in composition of plant and invertebrate prey between the sexes were influenced by habitat. We predicted less dietary variation in conifer habitats compared to deciduous but we found dietary differences in both habitat types. Sex is a strong driver of intraspecific diet differences and sexual dimorphism in features such as nutrient requirements, prey capture size and access to certain substrates may override any effects of habitat that might have favoured dietary convergence between the sexes.

Season did not influence differences in composition of dietary invertebrates between males and females and it had only a marginal effect on invertebrate richness, since posthoc tests on the interaction were not significant. Females are likely to have more specific nutrient requirements than males, especially in the breeding season for egg production (Houston, Donnan and Jones, 1995). There was a tendency for females to have a lower invertebrate richness in the spring compared to males, but the types of prey that both sexes consumed did not differ.

This suggests that females may have a more specialised diet than males. In addition, there was no difference in dietary richness of invertebrates between the sexes in the winter, and no difference between the sexes in richness of plants, supporting the idea that dietary specialisation of females in the spring is due to nutrients needed for reproduction. Females require excess protein for egg production and animal protein from invertebrates is of higher quality than plant protein (Houston, Donnan and Jones, 1995) which may explain why females did not have a lower plant richness than males. Primate studies have found dietary niche separation between the sexes in the reproductive season (Coelho, 1974; Dunbar and Dunbar, 1988; Vasey, 2002) but our study suggests this could also be the case for birds.

Environmental factors

The environmental factors were important in influencing diet composition and richness, both as main effects and in interactions with age and sex. Great tits showed variation in the composition of invertebrates consumed between seasons, habitats and years, and showed variation in richness of invertebrates between seasons and years but not habitats. Invertebrate composition varies throughout the year with many species reproducing in spring leading to large population increases, and many hibernating or dying off over winter. Our results reflect this pattern as many more invertebrate genera were found in the spring diet compared to the winter. A number of other studies have found an effect of environmental variables on intraspecific dietary richness (Schafer *et al.*, 2002; Shutt *et al.*, 2020). For instance, there was an increase in dietary richness of blue tits with advancement of spring in Scottish woodlands (Shutt *et al.*, 2020). We found that moths were the dominant group consumed across the year and all spring samples had at least one moth genus present compared to just over half of winter samples. Moths were also the group with the highest number of genera identified (Table 3.1). This is consistent with other studies that find Lepidoptera to be the dominant family consumed by great tits (Betts, 1955; Royama, 1970). Through our DNA approach, we cannot be certain of the life stage of the consumed invertebrate prey. However,

many studies on tits highlight caterpillars as the primary food source in the spring (Betts, 1955; Naef-Daenzer, Naef-Daenzer and Nager, 2000; Wilkin, King and Sheldon, 2009). As such, it is likely that in our study, the moth genera that we identified were consumed in their caterpillar stage, which we could investigate further by looking at the moth genera life-histories, since a number may not have overlapping generations. The higher percentage of spider, shield bug, beetle and fly genera in the winter than the spring diet reflects the types of invertebrates that are more active, and whose life cycles mean they are available as prey, in the colder months (Aitchison, 1984; Eitzinger and Traugott, 2011). Parasitoid wasps (family: Hymenoptera) also appeared to be an important component of the diet, more so in the spring than the winter, with the second highest number of genera identified of any group (22 genera) and at least one genera was present in 42% of all samples. Hymenoptera have been identified in the diets of great tits previously (Betts, 1955; Velky, Kaňuch and Krištín, 2011) but detail on the groups within the family are lacking so our results provide new insight into the importance of the specific genera in this family.

Invertebrate populations can rise and fall from year to year due to climatic conditions such as temperature or rainfall (Bozinovic *et al.*, 2011; Barnett and Facey, 2016). The number of invertebrate genera consumed (richness) was higher in 2018 than in 2017. This may indicate that the abundance of preferred prey was lower in 2018 so great tits had to diversify their diet to include other genera. Alternatively, 2018 could have had more favourable weather conditions, leading to higher invertebrate abundance compared to 2017. We found that invertebrate composition differed with habitat type, likely due to variation in their host plant species between conifer and deciduous habitats. Despite this, neither invertebrate nor plant richness differed between habitats suggesting that great tits did not show stronger specialisation in one habitat than the other. This parallels the results of Shutt *et al.*, (2020) who found that dietary richness did not change with local tree composition. The authors suggest this was likely due to invertebrate species not being restricted to certain tree species, which may also be true for our study. Additionally, our habitat fragments where the great tits reside are fairly small (10 –

25 hectares; see Table S3.1) and it is likely that invertebrates can easily move between sites using vegetation between them.

We did not find a main effect of habitat, or an interaction between age and habitat, on plant composition. This may be due to the birds foraging around the edges of the habitat fragments, where the same plants overlap both habitat types. This is likely, given the small size of the fragments (see Table S3.1) and the patchy landscape around them. Conifer fragments were often not far away (≤5km) from patches of deciduous woodland and vice versa, and were mostly separated by large areas of farmland and hedgerows where the birds would have likely foraged. Additionally, although the primary tree species of each habitat are different, the understorey in both may be similar, leading to no observable difference in plant diet between the habitats. *Fagus* (Beech) was the most common genera consumed in both habitat types confirming previous studies stating the importance of beechmast for great tits in the winter (Perdeck, Visser and Van Balen, 2000; Chamberlain, Gosler and Glue, 2007). As the conifer fragments did not contain beech themselves, this supports the idea that great tits are foraging around the edge or traveling out of their habitat fragments to forage.

3.5.2 Variation in diet among life stages

Nestlings had a different composition of invertebrates in their diet than adults and first years. Great tits breed in their first year and by feeding on alternative prey, parents reduce food competition with their nestlings. We found that habitat influenced dietary composition between the three age classes and we saw a similar extent of dietary separation in both habitat types. It is possible that depending on the quality of their breeding habitat, great tit parents have to vary their foraging strategy to provide for both their own needs and those of their young. Alternatively, that we found a difference in diet between nestlings and adults and first years may be due to the fact that nestlings are being fed by two parents, which is then compared to single diets of the adults and first years.

Variation in diet between parents and offspring may be due to different nutrient requirements. Nestlings need nutrients for growth and development and first years and adults need nutrients for maintenance and reproduction (Munn and Dawson, 2003). In addition to deciding between finding food for themselves or for their young, parents face the challenge of provisioning their nestlings with the necessary nutrients for their development (Ramsay and Houston, 2003; Arnold *et al.*, 2007; Pagani-Núñez *et al.*, 2011). Indeed, we found that the dietary richness of nestlings was lower than both adults and first years, indicating that parents are feeding them a more specialised diet. A number of studies have found that spiders were preferentially given to nestling tits when they were between five and six days old (Betts, 1955; Royama, 1970; Naef-Daenzer, Naef-Daenzer and Nager, 2000; Arnold *et al.*, 2007) and our study showed that they are important on day 8 and 9 also (fourth most prevalent group in individual samples; Table 3.3). Evidence shows that spiders contain the amino acid taurine (Ramsay and Houston, 2003), which is important for the development and function of the central nervous system (Sturman, 1993). We found that the genus *Tipula* featured heavily in the diet of the nestlings on day 8 and 9 (present in 53% of samples, the largest amount of any single genus identified in the nestling diet), suggesting that these crane flies contain an essential nutrient for them. Töröck (1985) also found that *Tipula* featured in the nestling diet. Our results agree with other studies that found parent and offspring diets to be different (Cherel *et al.*, 2008; Young *et al.*, 2010). For example, in a number of seabirds, parents and their offspring have different isotope signatures of carbon-13 and nitrogen-15 (Young *et al.*, 2010).

We wondered if specialisation in parent diet may be reflected in offspring diet. For example, parents with a lower richness and a more specialised diet may also have offspring with low richness. We found this was not the case: richness of a single parent did not predict the richness of a single nestling. This result is supported by the idea mentioned above that if nestlings need certain nutrients for development, they may have a stable number of prey types, regardless of the specialisation of their parents. Alternatively, the lack of relationship may reflect the fact that the nestling diet consists of food provisioned by both parents, which we were

comparing to a single parent only. We found evidence for weak niche overlap between the parents' diet and that of their own offspring: dietary composition of parents was slightly more similar to their own offspring than to offspring from other nests. This suggests that parents may have their own signature composition of prey items that they consume and also feed to their chicks, or that the correlation emerges because of shared habitat by parents and offspring. Alternatively, the reason that we found only a weak overlap between parent and their own offspring diet may be because we included nests where we had data for only a single parent. Only including nests which have data for both parents in the analysis would be more informative in looking for between-nest differences. Investigating the diet of nestlings in combination with that of their parents provides insight into the factors influencing parental care and the challenging trade-offs faced by parents.

3.5.3 Study limitations

There are a number of limitations with our whole study. First, some prey types that were identified could have been consumed by the prey of the great tits, instead of by the great tits themselves (Sheppard *et al.*, 2005; Pompanon *et al.*, 2012; da Silva *et al.*, 2019). However, even if secondary predation did occur, our results are still likely to reflect that the great tits are feeding in the habitats and seasons where we identified their prey, and that the prey are present in the locations and times of year that we found them in. Additionally, the amount of secondary predation should be constant across our samples and therefore the separation observed between different groups may reflect differences in general. Second, we were unable to explore the temporal consistency of the patterns observed, an approach that is considered ideal when determining whether the patterns observed are likely to be of adaptive significance (Bolnick *et al.*, 2002). This lack of repeatability arose because the statistical method we used for investigating dietary composition did not facilitate random effects. Permutational multivariate analysis of variance (PERMANOVA) used to analyse multivariate data can incorporate random effects (Anderson, 2017) but this, and other distance-based approaches, calculate

dissimilarities between pairs of data and analyse the distances, thus they do not take into account the mean-variance relationship of multivariate data (Warton, Wright and Wang, 2012). For this reason, and because we were unable to get repeat measures for many individuals, we chose to use *mvabund*. Until *mvabund* can incorporate random effects, future work that seeks to measure dietary consistency over time will have to use a different method, such as Baysian approach (Shutt *et al.*, 2020). Third, the sampling period, particularly for winter, was fairly long so although samples were collected within the same season, the length of the period meant that diets could be different between the beginning and the end, which may have influenced the richness or composition. Finally, faecal samples from the great tits only contain food items eaten in the few hours prior to sample collection so is only a snapshot of the diet and does not reflect the considerable variation in prey abundance over time.

3.5.4 Conclusion

This study may be the first to characterise the diet of adult and nestling great tits using DNA metabarcoding and provides a deeper insight into their prey than previous work; certainly none have been published to date. We have shown dietary variation and specialisation between demographic groups and temporal and spatial environmental factors play an important role in revealing these diet differences. Being able to expand the diet to include alternative foods, or consume different prey items to others, allows individuals to reduce competition for food (Svanbäck and Persson, 2004; Svanbäck and Bolnick, 2005), including reducing conflict with offspring. The capacity to switch to alternative prey items is particularly beneficial if prey abundance declines either in the short term (e.g weather conditions) or over prolonged periods (e.g. destruction of habitats). Factors other than competition can also explain the variation in diet between demographic groups including adults having more foraging experience than first years and females having different nutrients requirements to males. It is important to examine the diet and identify the drivers of intraspecific dietary niche separation to enhance our knowledge of

how individuals fit into their species' niche, and how they adjust to changing environmental conditions.

3.6 Appendix B – Supplementary material for Chapter 3

Table S3.1. List of the 12 study sites in the Bandon Valley area, Co. Cork (Ireland), where birds were captured and samples were taken. We show the main habitat type of each fragment (mixed deciduous forest vs. coniferous plantation), the area (hectares), the number of nestboxes present, the coordinates in decimal degrees (DD) and the number of faecal samples from each site that were used in analysis.

The 12 study sites in the Bandon Valley

Name	**Habitat type**	**Area (ha)**	**Number of boxes**	**Coordinates (DD)**	**Num. samples**	
					Adults	**Single nestlings (Nests)**
Ballinphelic	Coniferous	18	36	51.840074, -8.628249	24	23 (7)
Castlebernard	Mixed	17	33	51.741821, -8.773443	40	24 (7)
Carrigeen	Coniferous	15	30	51.821298, -8.814267	6	0 (0)
Dunderrow	Mixed	14	28	51.719711, -8.604451	47	5 (2)
Dukes Wood	Mixed	16	31	51.787396, -8.755946	45	44 (12)
Farran	Coniferous	11	22	51.700448, -8.805728	2	5 (2)
Garretstown	Coniferous	25	51	51.654770, -8.616293	13	34 (10)
Inishannon	Mixed	10	20	51.763048, -8.662415	22	20 (8)
Kilbrittain	Mixed	25	49	51.671880, -8.683837	40	25 (12)
Lissarda	Coniferous	15	30	51.858086, -8.859128	10	16 (5)
Piercetown	Coniferous	15	30	51.788888, -8.456197	5	0 (0)
Shipool	Mixed	18	35	51.737620, -8.631437	10	15 (7)

Table S3.2. The explanatory variables and interactions included in the dietary composition models. The package *mvabund* was used to hold the matrix of presence/absence data as the response variable in a manyglm with a binomial family. See Table 3.4 for corresponding model results.

Composition (identity of genera present in each sample) as response variable.

Data	Model label	Diet	Main effects	Interactions	N
Adults and first years	a	Invertebrate (winter and spring)	Age Sex Habitat Season	Age × Season Sex × Season Age × Habitat Sex × Habitat	160
	b	Invertebrate 2017 (winter and spring)	Age Sex Habitat Season	None	113
	c	Invertebrate (spring only)	Age Sex Habitat Year	None	101
	d	Plant (winter)	Age Sex Habitat	Age × Habitat Sex × Habitat	105
Adults, first years and nestlings	e	Invertebrate	Age Habitat Year	Age × Habitat	181

Table S3.3. The explanatory variables in the dietary richness models. Random effects, model type, error structure and sample size are shown. See Table 3.5 for corresponding model results. Models including an interaction are also included in the model as a main effect.

Richness (number of genera present in each sample) as response variable

Data	Model label	Diet	Variables included		Model type (R package)	Error structure	N
			Explanatory	Random			
Adult and first years	f	Invertebrate (spring and winter)	Age × Habitat Age × Season Sex × Habitat Sex × Season	Site Bird ID	GLMM (lme4)	Poisson	167
	g	2017 only	Age Sex Habitat Season	Site Bird ID	GLMM (lme4)	Poisson	117
	h	Spring only	Age Sex Habitat Year	Site Bird ID	GLMM (lme4)	Poisson	101
	j	Plant (winter)	Age × Habitat Sex × Habitat	Site	GLMM (glmmTMB)	Conway-Maxwell Poisson	105
Adults, first years and nestlings	k	Invertebrate	Age × Habitat Year	Site	GLMM (MASS)	Negative binomial	181

Table S3.4. The invertebrate genera identified in adult and first year diets. The season each genus was found in, the raw number of samples in which each genera is present and as a percentage, is shown. N = 187.

Combined seasons

Genus	Group	Season found	No. samples overall	%
Operophtera	moths	spring	83	44%
Orthosia	moths	both	75	40%
Clubiona	sac spiders	both	45	24%
Amphipyra	moths	both	41	22%
Hydriomena	moths	both	40	21%
Pandemis	moths	spring	40	21%
Syrphus	hoverflies	both	40	21%
Anorthoa	moths	spring	35	19%
Elatobium	aphids	both	33	18%
Lozotaenia	moths	both	28	15%
Meliscaeva	hoverflies	both	27	14%
Psychoda	moth flies	both	27	14%
Melangyna	hoverflies	both	26	14%
Blastobasis	moths	both	25	13%
Anyphaena	spiders	both	24	13%
Rhynchaenus	beetles	both	24	13%
Agriopis	moths	spring	23	12%
Agrochola	moths	spring	22	12%
Eilema	moths	spring	22	12%
Neriene	spiders	both	22	12%
Acanthosoma	shield bugs	both	21	11%
Epinotia	moths	spring	21	11%
Neuroterus	gall wasps	both	20	11%
Tipula	crane flies	winter	18	10%
Agonopterix	moths	spring	17	9%
Scathophaga	true fly	spring	17	9%
Araneus	spiders	both	16	9%
Culicoides	biting midges	spring	16	9%
Thera	moths	spring	16	9%
Amaurobius	spiders	both	15	8%
Amphorophora	aphids	both	15	8%
Notocelia	moths	spring	15	8%
Ptycholoma	moths	spring	15	8%
Ditula	moths	both	14	7%
Archips	moths	spring	13	7%
Dryobotodes	moths	spring	13	7%
Metellina	spiders	both	13	7%
Phobocampe	parasitoid wasps	spring	13	7%

Aphrophora	spittlebugs	spring	12	6%
Capua	moths	both	12	6%
Dusona	parasitoid wasps	spring	12	6%
Cheilosia	hoverflies	spring	11	6%
Cosmia	moths	spring	11	6%
Enytus	parasitoid wasps	spring	11	6%
Glyptapanteles	parasitoid wasps	spring	11	6%
Sitobion	aphids	spring	11	6%
Aleiodes	parasitoid wasps	spring	10	5%
Campopleginae	parasitoid wasps	spring	10	5%
Mesapamea	moths	spring	10	5%
Petrophora	moths	spring	10	5%
Phlogophora	moths	both	10	5%
Bradysia	gnats	both	9	5%
Cotesia	parasitoid wasps	spring	9	5%
Empria	sawflies	spring	9	5%
Lithophane	moths	spring	9	5%
Aphidius	parasitoid wasps	both	8	4%
Colotois	moths	spring	8	4%
Cyclophora	moths	both	8	4%
Cyclosa	spiders	spring	8	4%
Deileptenia	moths	both	8	4%
Ectropis	moths	spring	8	4%
Helophilus	hoverflies	spring	8	4%
Herminia	moths	both	8	4%
Lonchoptera	true fly	winter	8	4%
Ochropleura	moths	winter	8	4%
Scoliopteryx	moths	spring	8	4%
Spilarctia	moths	both	8	4%
Acrobasis	moths	spring	7	4%
Bombus	bumblebees	spring	7	4%
Conistra	moths	spring	7	4%
Hypena	moths	spring	7	4%
Macrosiphum	aphids	both	7	4%
Nalassus	beetles	both	7	4%
Phaonia	true fly	winter	7	4%
Polia	moths	winter	7	4%
Baetis	mayflies	both	6	3%
Cinara	aphids	spring	6	3%
Euura	sawflies	spring	6	3%
Meteorus	parasitoid wasps	both	6	3%
Plectiscus	parasitoid wasps	winter	6	3%
Pterocomma	aphids	spring	6	3%
Quercusia	butterfly	spring	6	3%
Biston	moths	both	5	3%
Chrysotropia	aphids	both	5	3%

Gymnoscelis	moths	spring	5	3%
Hedya	moths	spring	5	3%
Lehmannia	slugs	spring	5	3%
Lepthyphantes	spiders	both	5	3%
Mesopolobus	true fly	winter	5	3%
Pygostolus	parasitoid wasps	spring	5	3%
Rhagium	beetles	spring	5	3%
Syndemis	moths	both	5	3%
Syrphoctonus	parasitoid wasps	spring	5	3%
Zeiraphera	moths	both	5	3%
Coleophora	moths	spring	4	2%
Diurnea	moths	winter	4	2%
Ephedrus	parasitoid wasps	spring	4	2%
Eriocrania	moths	spring	4	2%
Hemerobius	lacewings	both	4	2%
Melolontha	beetles	spring	4	2%
Noctua	moths	both	4	2%
Pammene	moths	spring	4	2%
Peristenus	parasitoid wasps	both	4	2%
Phyllonorycter	moths	winter	4	2%
Polydrusus	weevils	spring	4	2%
Protapanteles	parasitoid wasps	spring	4	2%
Sussaba	parasitoid wasps	spring	4	2%
Aglais	butterfly	spring	3	2%
Calliteara	moths	both	3	2%
Entomobrya	springtails	both	3	2%
Euproctis	moths	spring	3	2%
Ochropacha	moths	spring	3	2%
Ophion	parasitoid wasps	winter	3	2%
Pardosa	spiders	both	3	2%
Pterophorus	moths	spring	3	2%
Xestia	moths	winter	3	2%
Abrostola	moths	spring	2	1%
Acleris	moths	both	2	1%
Colostygia	moths	spring	2	1%
Diacrisia	moths	winter	2	1%
Earinus	parasitoid wasps	spring	2	1%
Eristalis	hoverflies	spring	2	1%
Hepialus	moths	both	2	1%
Lacanobia	moths	winter	2	1%
Spilosoma	moths	winter	2	1%
Syrphophilus	parasitoid wasps	spring	2	1%
Syrrhizus	parasitoid wasps	both	2	1%
Tetragnatha	spiders	spring	2	1%
Trochosa	spiders	winter	2	1%
Zele	parasitoid wasps	spring	2	1%

Athous	beetles	spring	1	1%
Celypha	moths	spring	1	1%
Chalarus	true fly	winter	1	1%
Coelichneumon	parasitoid wasps	winter	1	1%
Crepidodera	beetles	winter	1	1%
Dictyna	spiders	spring	1	1%
Drapetisca	spiders	winter	1	1%
Elachiptera	true fly	winter	1	1%
Epiphyas	moths	winter	1	1%
Eupithecia	moths	both	1	1%
Forficula	Earwigs	winter	1	1%
Mesoleuca	moths	spring	1	1%
Neon	spiders	winter	1	1%
Nomada	cuckoo bee	spring	1	1%
Pararge	butterfly	spring	1	1%
Phragmatobia	moths	winter	1	1%
Phratora	beetles	spring	1	1%
Rhopalosiphum	aphids	winter	1	1%

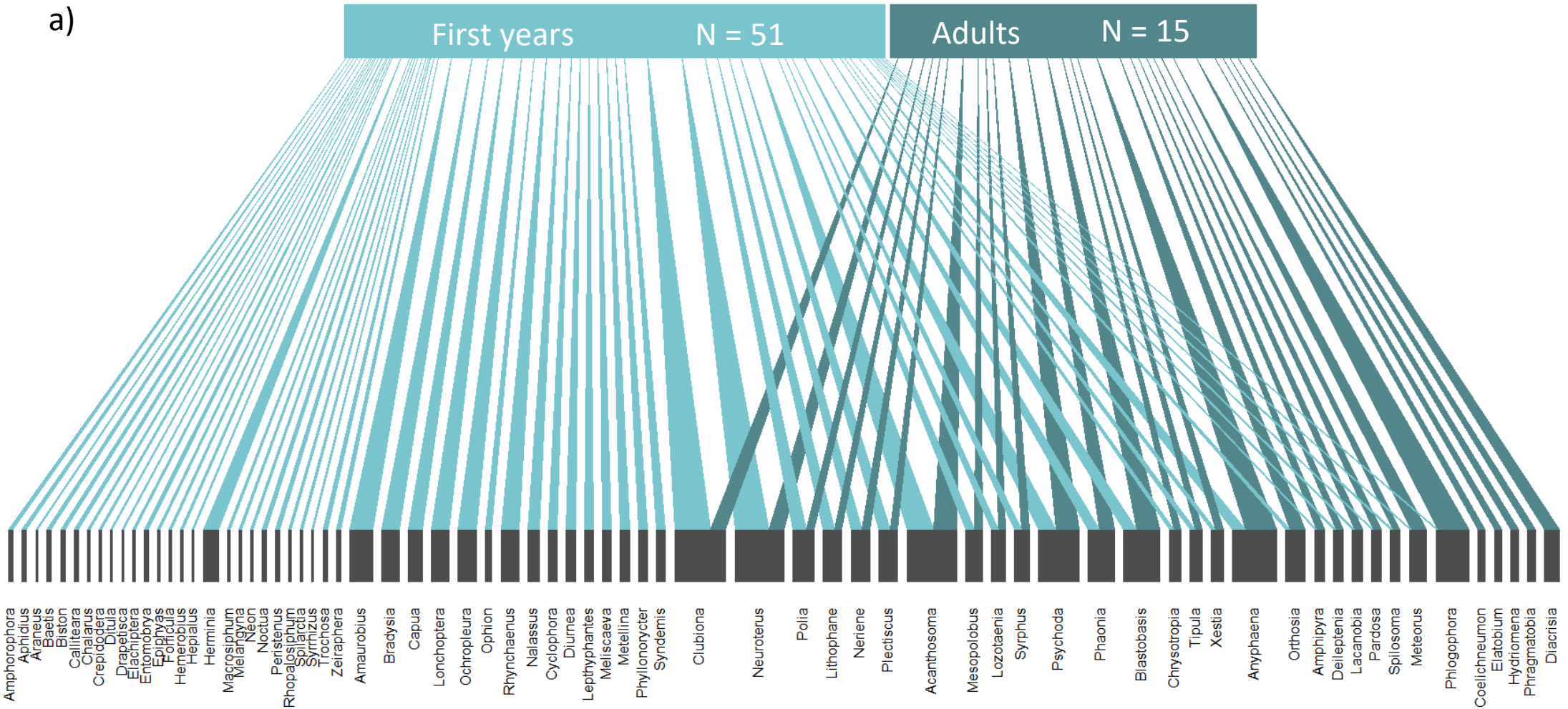
Table S3.5. The invertebrate genera present in the diet of individual nestlings and for each whole nest. The number of individual samples or nest that each genera was present in is shown, as well as the percentage. N = 192 nestlings and 80 nests. (Ordered according to percentage of number of individual samples that each genus is present in).

Individual nestlings and total for whole nest (add up all the genera present in each nest)					
Genus	Group	No. Individual samples present in	%	No. nests present in	%
Tipula	crane flies	101	52.60	54	67.50
Amphipyra	moths	97	50.52	49	61.25
Operophtera	moths	85	44.27	49	61.25
Orthosia	moths	62	32.29	37	46.25
Ptycholoma	moths	50	26.04	31	38.75
Colotois	moths	49	25.52	34	42.50
Helophilus	hoverflies	48	25.00	32	40.00
Lozotaenia	moths	46	23.96	28	35.00
Pandemis	moths	41	21.35	28	35.00
Cosmia	moths	39	20.31	28	35.00
Hydriomena	moths	37	19.27	22	27.50
Phlogophora	moths	37	19.27	30	37.50
Allophyes	moths	32	16.67	16	20.00
Bombus	bumblebees	31	16.15	22	27.50
Mesapamea	moths	27	14.06	18	22.50
Eristalis	hoverflies	25	13.02	16	20.00
Syrphus	hoverflies	23	11.98	13	16.25
Dryobotodes	moths	22	11.46	12	15.00
Ectropis	moths	22	11.46	15	18.75
Epirrita	moths	21	10.94	13	16.25
Scathophaga	flies	21	10.94	14	17.50
Scoliopteryx	moths	21	10.94	13	16.25
Agonopterix	moths	20	10.42	13	16.25
Anorthoa	moths	20	10.42	14	17.50
Culicoides	midges	19	9.90	9	11.25
Eilema	moths	19	9.90	15	18.75
Elatobium	aphids	19	9.90	12	15.00
Protapanteles	parasitoid wasps	19	9.90	13	16.25
Clubiona	spiders	18	9.38	14	17.50
Colocasia	moths	18	9.38	8	10.00
Amaurobius	spiders	17	8.85	11	13.75
Anyphaena	spiders	17	8.85	13	16.25
Lithosia	moths	17	8.85	9	11.25
Noctua	moths	17	8.85	12	15.00
Cotesia	parasitoid wasps	15	7.81	9	11.25

Acleris	moths	14	7.29	10	12.50
Brachypalpoides	hoverflies	12	6.25	6	7.50
Cyclosa	spiders	12	6.25	6	7.50
Eupsilia	moths	12	6.25	7	8.75
Tortricodes	moths	12	6.25	5	6.25
Autographa	moths	11	5.73	8	10.00
Euura	sawflies	11	5.73	7	8.75
Hemithea	moths	11	5.73	5	6.25
Hypena	moths	11	5.73	5	6.25
Apocheima	moths	10	5.21	6	7.50
Eupithecia	moths	10	5.21	8	10.00
Notocelia	moths	10	5.21	7	8.75
Udea	moths	10	5.21	8	10.00
Apeira	moths	9	4.69	6	7.50
Pseudoips	moths	9	4.69	7	8.75
Thera	moths	9	4.69	7	8.75
Aporophyla	moths	8	4.17	5	6.25
Archips	moths	8	4.17	6	7.50
Hedya	moths	8	4.17	5	6.25
Merodon	hoverflies	8	4.17	6	7.50
Opisthograptis	moths	8	4.17	5	6.25
Polia	moths	8	4.17	6	7.50
Pterocomma	aphids	8	4.17	5	6.25
Rhagium	beetles	8	4.17	7	8.75
Hepialus	moths	7	3.65	5	6.25
Poecilocampa	moths	7	3.65	7	8.75
Rhynchaenus	beetles	7	3.65	7	8.75
Agrochola	moths	6	3.13	6	7.50
Anaplectoides	moths	6	3.13	3	3.75
Calliteara	moths	6	3.13	5	6.25
Celypha	moths	6	3.13	6	7.50
Epinotia	moths	6	3.13	4	5.00
Geometra	moths	6	3.13	3	3.75
Meliscaeva	hoverflies	6	3.13	5	6.25
Mormo	moths	6	3.13	4	5.00
Nalassus	beetles	6	3.13	5	6.25
Spilarctia	moths	6	3.13	6	7.50
Chortodes	moths	5	2.60	3	3.75
Dyseriocrania	moths	5	2.60	5	6.25
Notodonta	moths	5	2.60	4	5.00
Abrostola	moths	4	2.08	3	3.75
Agriopis	moths	4	2.08	4	5.00
Blastobasis	moths	4	2.08	4	5.00
Calliphora	flies	4	2.08	2	2.50
Deileptenia	moths	4	2.08	3	3.75
Diacrisia	moths	4	2.08	3	3.75

Nomada	cuckoo bees	4	2.08	4	5.00
Patania	moths	4	2.08	2	2.50
Pisaura	spiders	4	2.08	3	3.75
Simulium	flies	4	2.08	3	3.75
Abia	sawflies	3	1.56	3	3.75
Aphelia	moth	3	1.56	2	2.50
Araneus	spiders	3	1.56	3	3.75
Biston	moths	3	1.56	3	3.75
Cyclophora	moths	3	1.56	3	3.75
Deroceras	slugs	3	1.56	3	3.75
Diachrysia	moths	3	1.56	2	2.50
Metopolophium	aphids	3	1.56	2	2.50
Pararge	butterflies	3	1.56	3	3.75
Sitobion	aphids	3	1.56	3	3.75
Xanthorhoe	moths	3	1.56	3	3.75
Acronicta	moths	2	1.04	2	2.50
Alcis	moths	2	1.04	1	1.25
Apamea	moths	2	1.04	2	2.50
Cinara	aphids	2	1.04	1	1.25
Ennomos	moths	2	1.04	2	2.50
Erannis	moths	2	1.04	1	1.25
Lithophane	moths	2	1.04	2	2.50
Meteorus	parasitoid wasps	2	1.04	2	2.50
Paradarisa	moths	2	1.04	2	2.50
Phobocampe	parasitoid wasps	2	1.04	2	2.50
Phryxe	flies	2	1.04	2	2.50
Psychoda	moth flies	2	1.04	2	2.50
Ambigolimax	slugs	1	0.52	1	1.25
Apis	bees	1	0.52	1	1.25
Athous	beetles	1	0.52	1	1.25
Bibio	flies	1	0.52	1	1.25
Dusona	parasitoid wasps	1	0.52	1	1.25
Empoasca	leafhoppers	1	0.52	1	1.25
Forficula	earwigs	1	0.52	1	1.25
Megaselia	flies	1	0.52	1	1.25
Mesoleuca	moths	1	0.52	1	1.25
Naenia	moths	1	0.52	1	1.25
Quercusia	butterflies	1	0.52	1	1.25
Scoparia	moths	1	0.52	1	1.25
Serromyia	flies	1	0.52	1	1.25
Vespula	wasps	1	0.52	1	1.25
Xyela	sawflies	1	0.52	1	1.25

a)


First years N = 51
Adults N = 15
Amphorophora
Aphidius
Araneus
Baetis
Biston
Calliteara
Chalarus
Crepidodera
Dytiula
Drapetisca
Elachiptera
Entomobrya
Epiphyas
Forcipula
Hemerobius
Hepialus
Herminia
Macrosiphum
Melangyna
Neon
Noctua
Peristenus
Rhopalosiphum
Spilarctia
Syrmizus
Trochosa
Zeiraphera
Amaurobius
Bradysia
Capua
Lonchoptera
Ochropleura
Ophion
Rhynchaenus
Nalassus
Cyclophora
Diurnea
Lepthyphantes
Meliscaeva
Metellina
Phyllonorycter
Syndemis
Clubiona
Neuroterus
Polia
Lithophane
Neriene
Plectiscus
Acanthosoma
Mesopolobus
Lozotaenia
Syrphus
Psychoda
Phaonia
Blastobasis
Chrysotropia
Tipula
Xestia
Anyphaena
Orthosia
Amphipyra
Deileptenia
Lacanobia
Pardosa
Spilosoma
Meteorus
Phlogophora
Coelichneumon
Elatobium
Hydriomena
Phragmatobia
Diacrisia

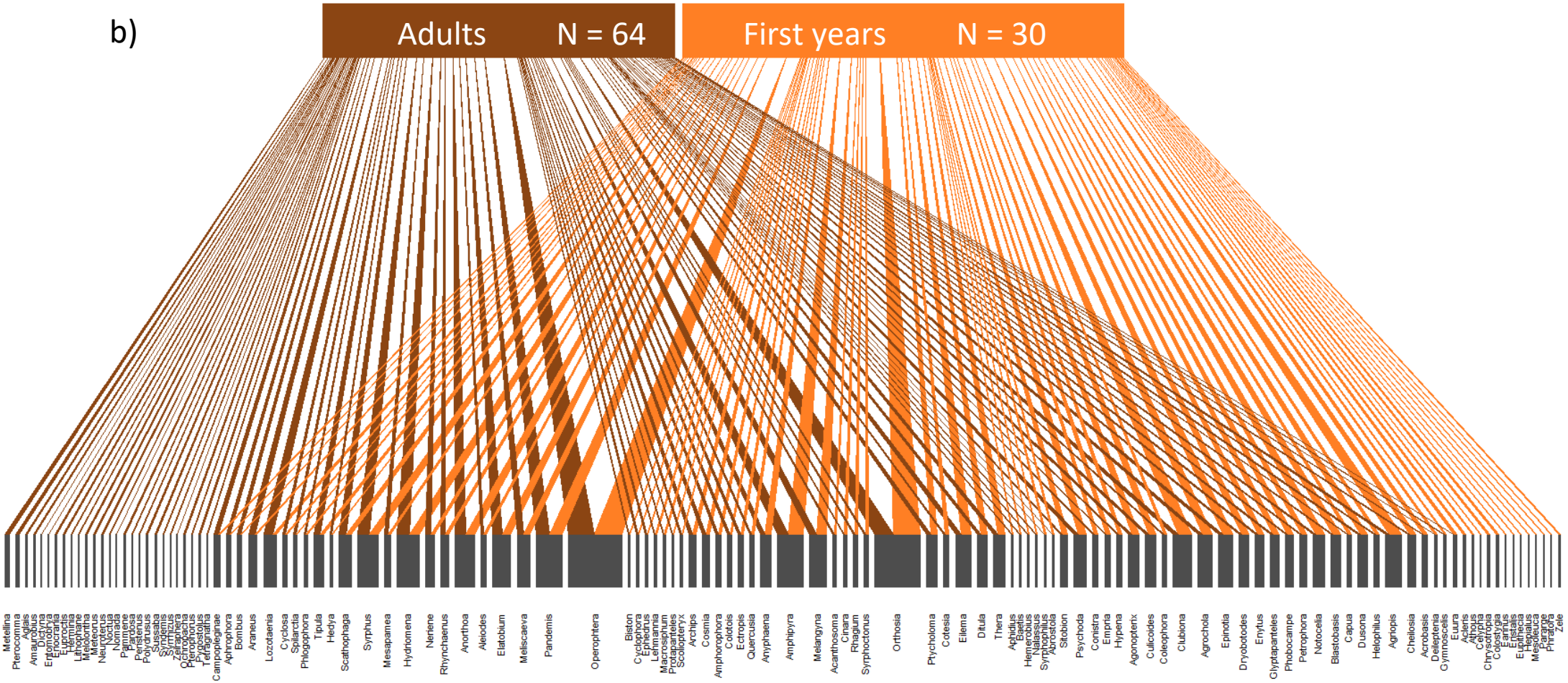
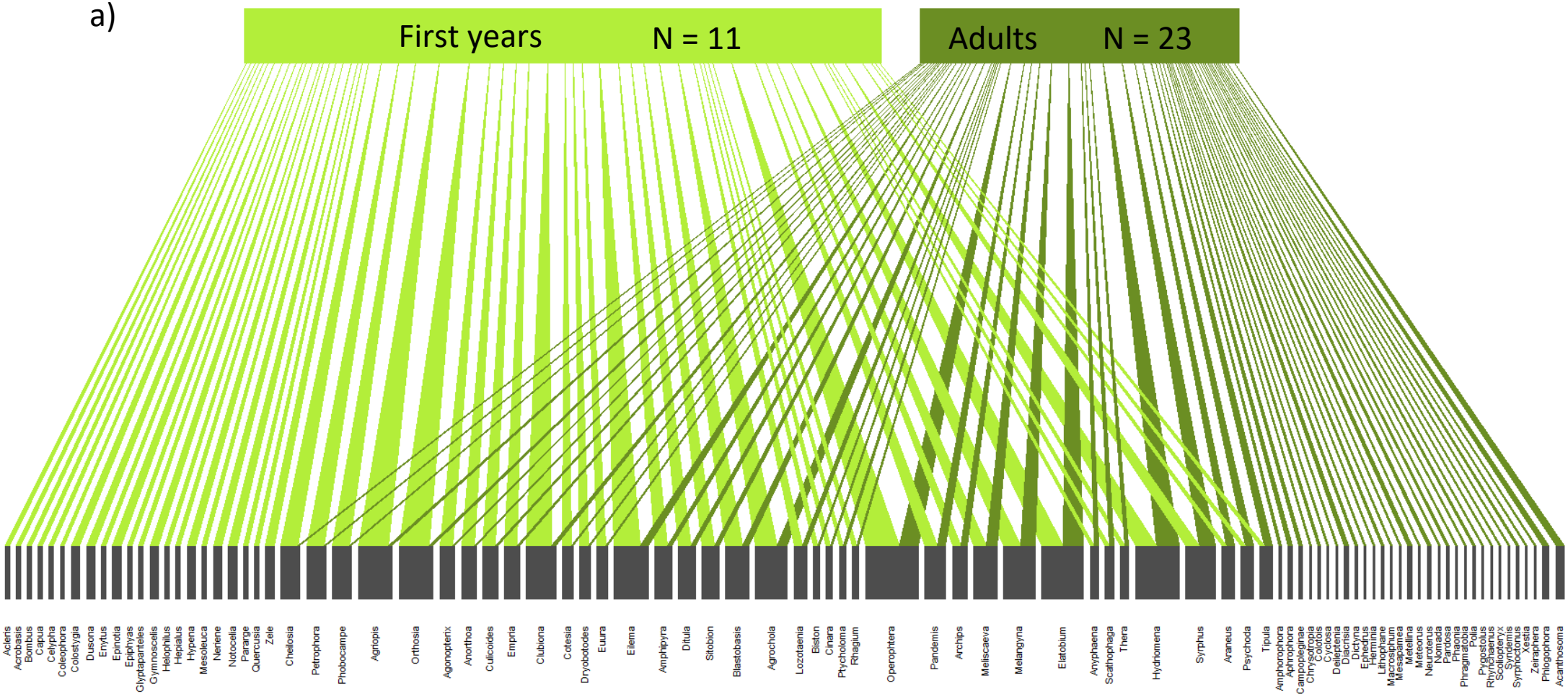


Figure S3.1. The invertebrate genera consumed by first years and adults for a) winter and b) spring. Sample sizes are given on each upper bar. Data do not contain any duplicate samples from the same individual. The birds that consumed a genus are linked by interacting lines and the width of the lines represents the proportion of birds from each age group that consumed the genus. The width of the lower bars is proportional to the sum of the interactions involving that genus. So genera that were involved in more interactions (ie. were present in the diet of more birds) have a wider bar. All bipartite plots of this type were created using the *bipartite* package (v2.14) in R.

a)


First years N = 11
Adults N = 23
Acleris
Acrobasis
Bombus
Capua
Celypha
Coleophora
Colostygia
Dusona
Enytus
Epinotia
Epiphyas
Glyptapanteles
Gymnoscelis
Helophilus
Hepialus
Hypena
Mesoleuca
Nerlene
Notocelia
Pararge
Quercusia
Zele
Cheilosia
Petrophora
Phobocampe
Agriopis
Orthosia
Agonopterix
Anorthoa
Culicoides
Empria
Clubiona
Cotesia
Dryobotodes
Euura
Eilema
Amphipyra
Ditula
Sitobion
Blastobasis
Agrochola
Lozotaenia
Biston
Cinara
Ptycholoma
Rhagium
Operophtera
Pandemis
Archips
Meliscaeva
Melangyna
Elatobium
Anyphaena
Scathophaga
Thera
Hydriomena
Syrphus
Araneus
Psychoda
Tipula
Amphorophora
Aphrophora
Campoplegmae
Chrysotropia
Colotois
Cyclosa
Deileptenia
Diacrisia
Dictyna
Ephedrus
Heminia
Lithosiane
Macrosiphum
Mesapamea
Metellina
Meteorus
Neuroterus
Nomada
Pardosa
Phaonia
Phragmatobia
Rolla
Pygostolus
Rhynchaenus
Scolopteryx
Syndemis
Symphoctonus
Xestia
Zeraphera
Phlogophora
Acanthosoma

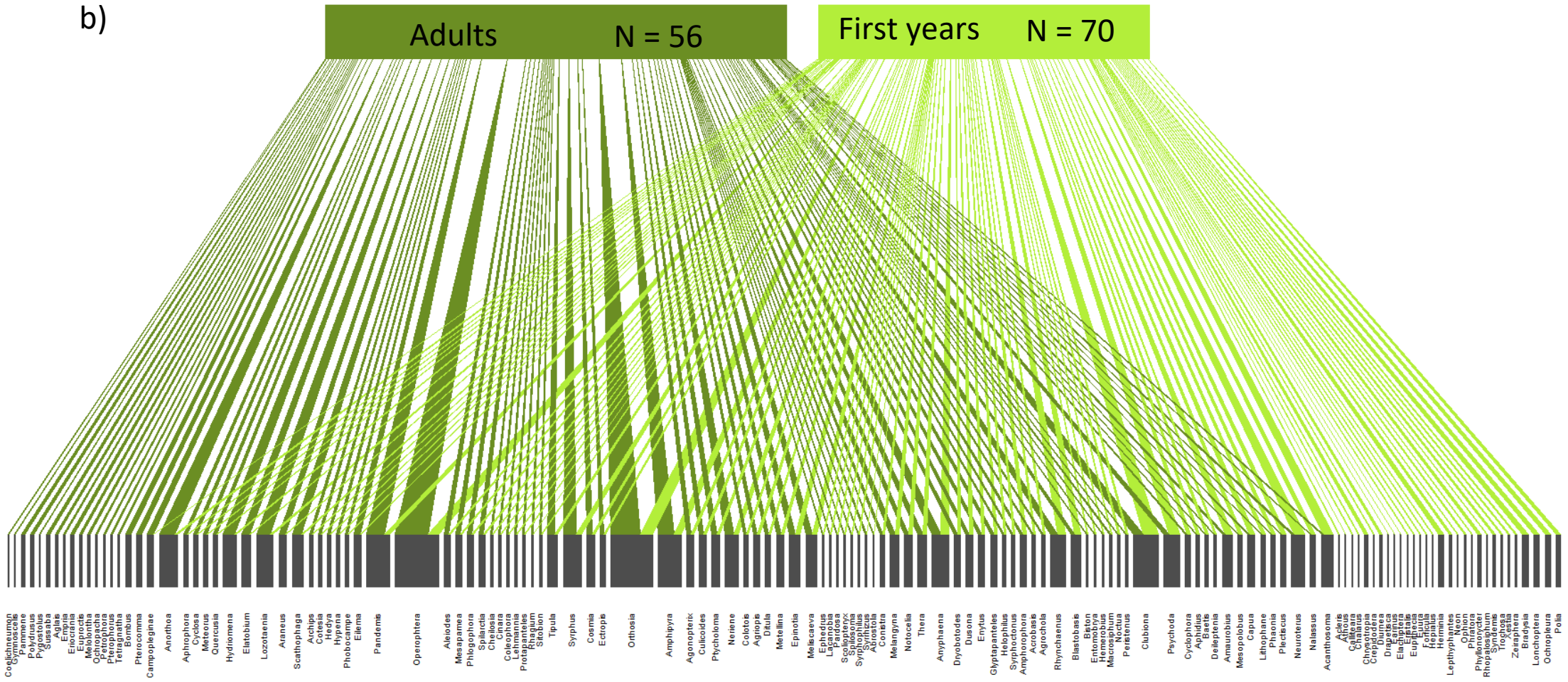
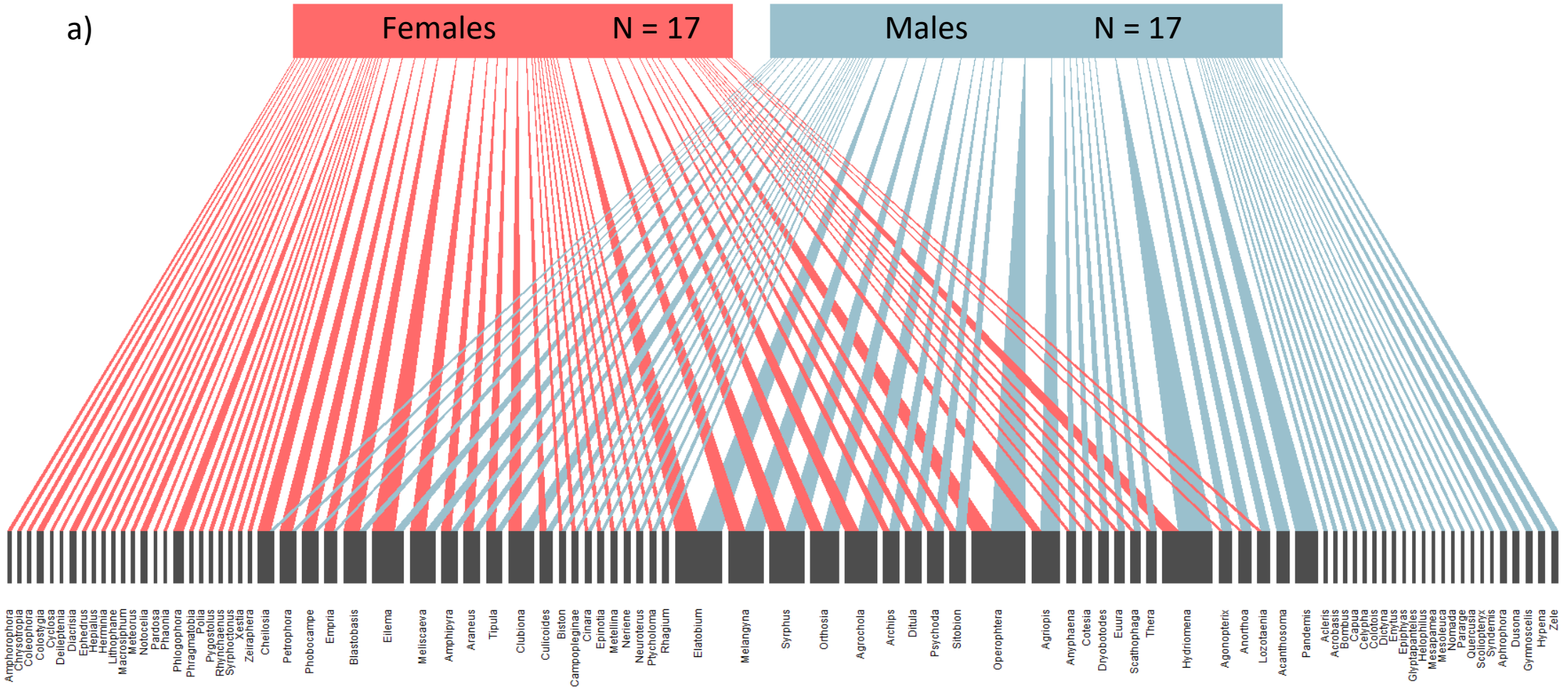


Figure S3.2. The invertebrate genera consumed by first years and adults for a) conifer habitats and b) deciduous habitat. Data do not contain any duplicate samples from the same individual. See Figure S3.1 for further details of the plot.


a)
Females N = 17
Males N = 17
Amphorophora
Chrysotropia
Coleophora
Colostygia
Cyclosa
Deileptenia
Diacrisia
Ephedrus
Hepialus
Herminia
Lithophane
Macrosiphum
Meteorus
Notocelia
Pardosa
Phaonia
Phlogophora
Phragmatobia
Polia
Pygostolus
Rhynchaenus
Syrphoctonus
Xestia
Zeiraphera
Cheilosia
Petrophora
Phobocampe
Empria
Blastobasis
Eilema
Meliscaeva
Amphipyra
Araneus
Tipula
Clubiona
Culicoides
Biston
Campopleginae
Cinara
Epinotia
Metellina
Nerlene
Neuroterus
Ptycholoma
Rhagium
Elatobium
Melangyna
Syrphus
Orthosia
Agrochola
Archips
Ditula
Psychoda
Sitobion
Operophtera
Agriopis
Amyphaena
Cotesia
Dryobotodes
Euura
Scathophaga
Thera
Hydriomena
Agonopterix
Anorthoa
Lozotaenia
Acanthosoma
Pandemis
Acleris
Acrobasis
Bombus
Capua
Celypha
Colotois
Dictyna
Enytus
Epiphyas
Glyptapanteles
Heliophilus
Mesapamea
Mesoleuca
Nomada
Panarge
Quercusia
Scoliopteryx
Syndemis
Aphrophora
Dusona
Gymnoscelis
Hypena
Zele

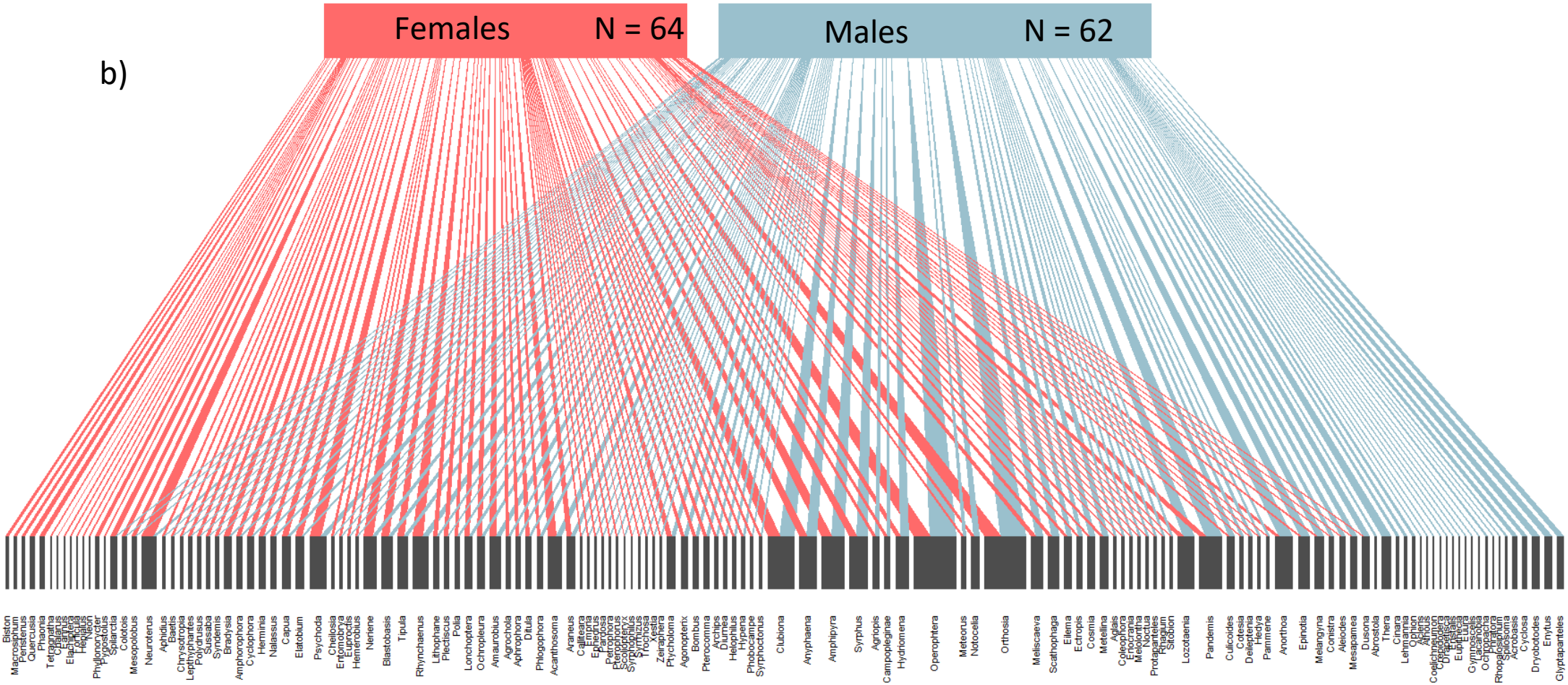


Figure S3.3. The invertebrate genera consumed by males and females for a) conifer habitats and b) deciduous habitat. Data do not contain any duplicate samples from the same individual. See Figure S3.1 for further details of the plot.

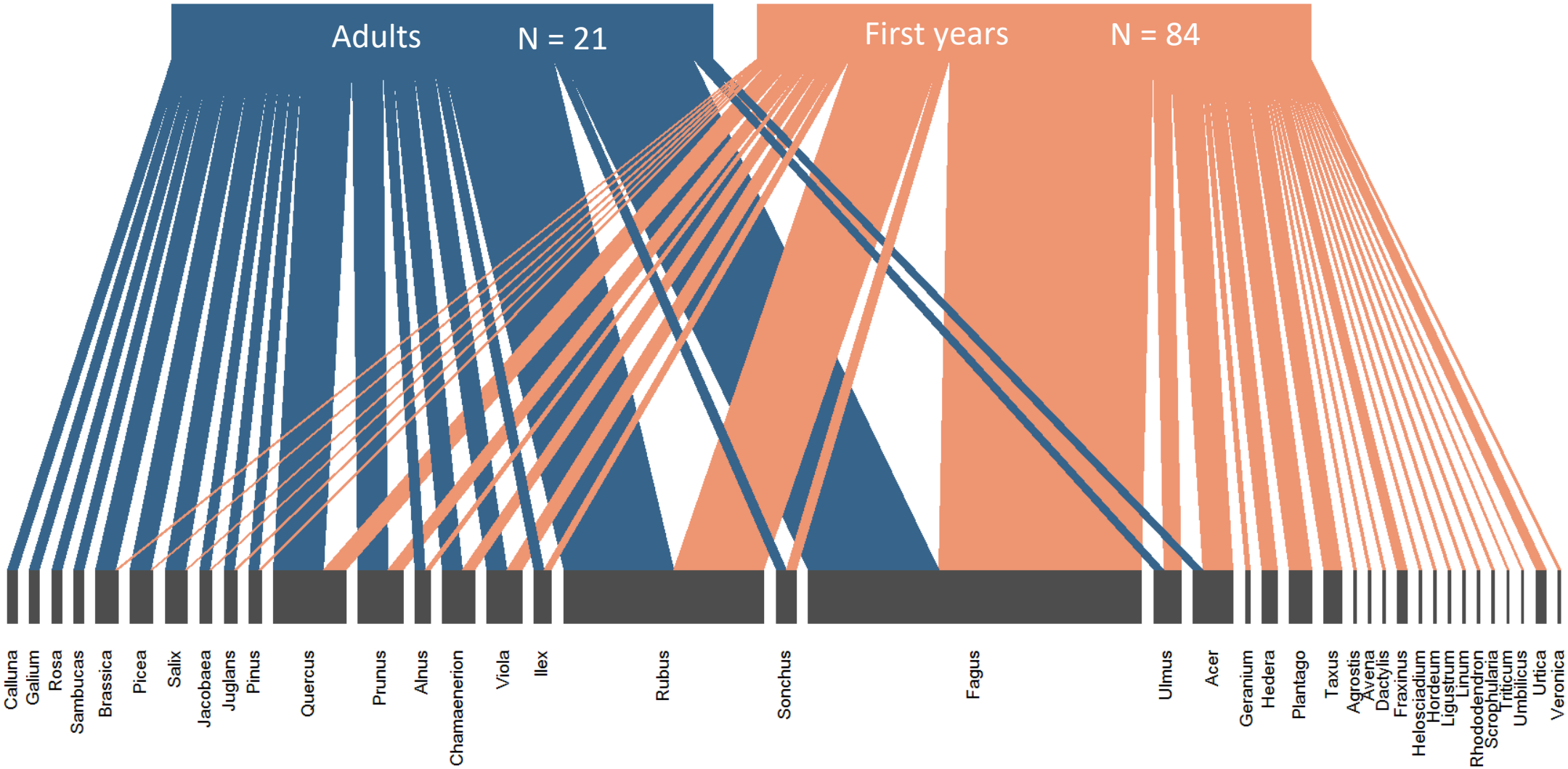
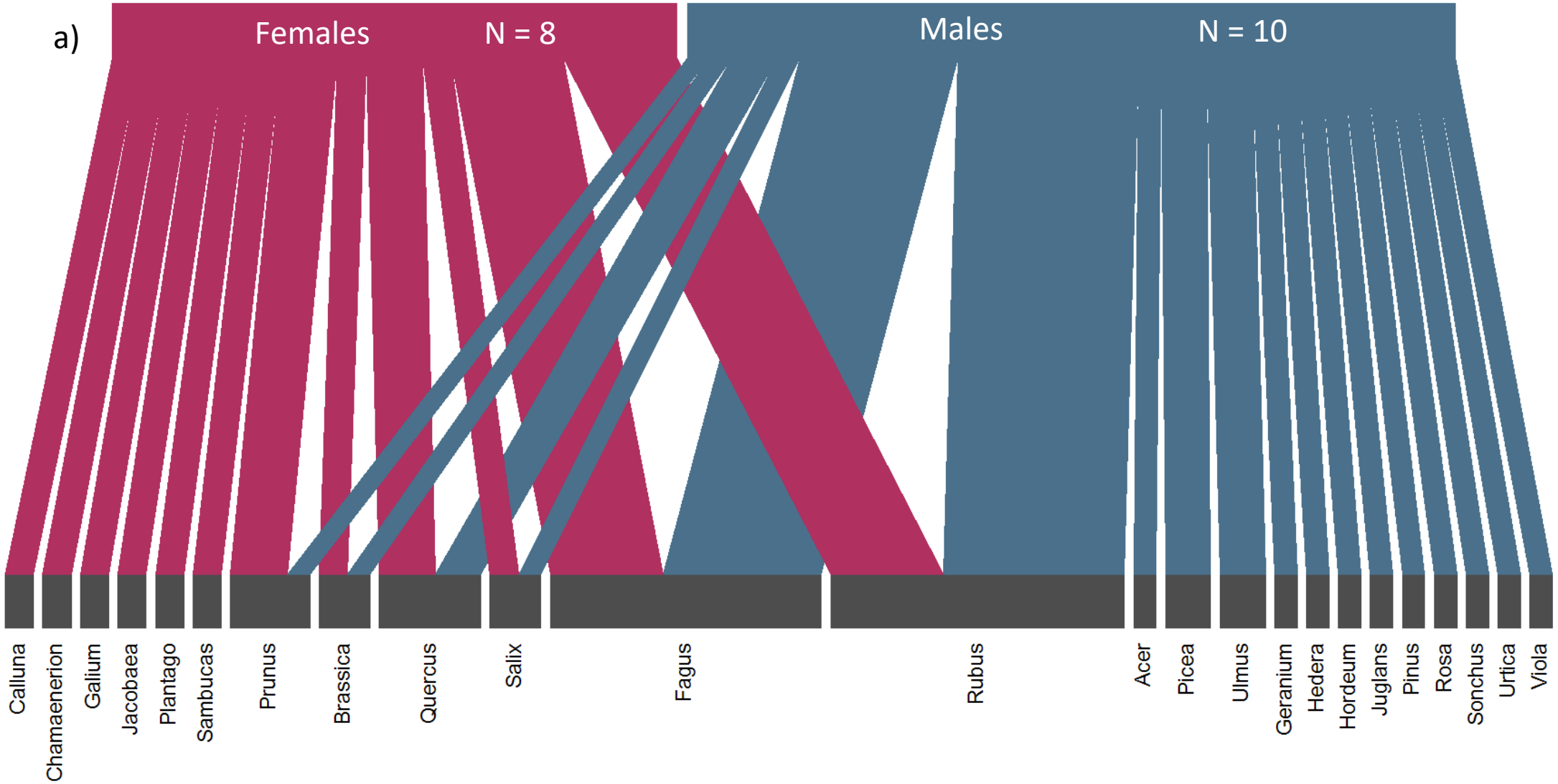


Figure S3.4. The plant genera consumed by adults and first years. Data do not contain any duplicate samples from the same individual. See Figure S3.1 for further details of the plot.


a)
Females
N = 8
Males
N = 10
Calluna
Chamaenerion
Galium
Jacobaea
Plantago
Sambucas
Prunus
Brassica
Quercus
Salix
Fagus
Rubus
Acer
Picea
Ulmus
Geranium
Hedera
Hordeum
Juglans
Pinus
Rosa
Sonchus
Urtica
Viola

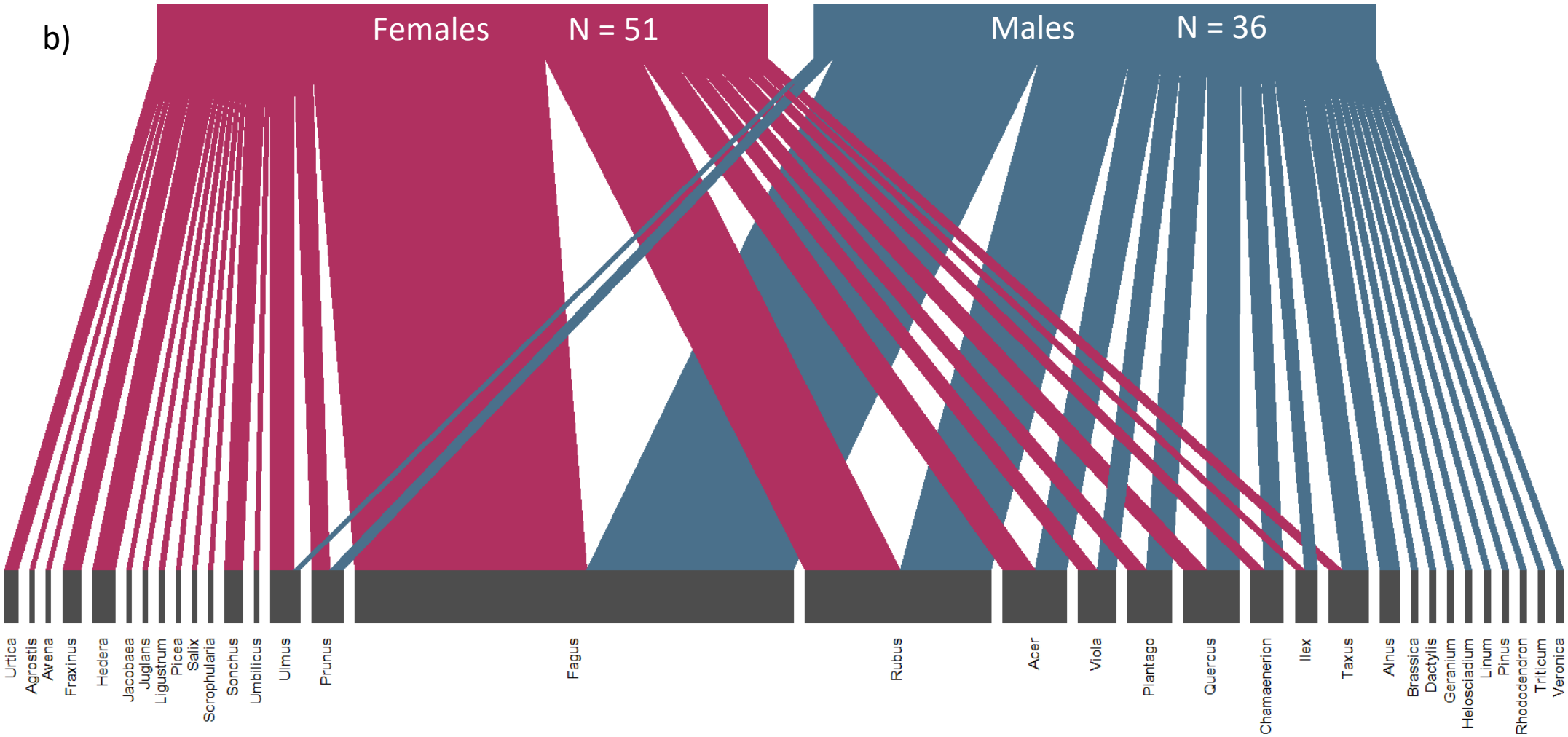
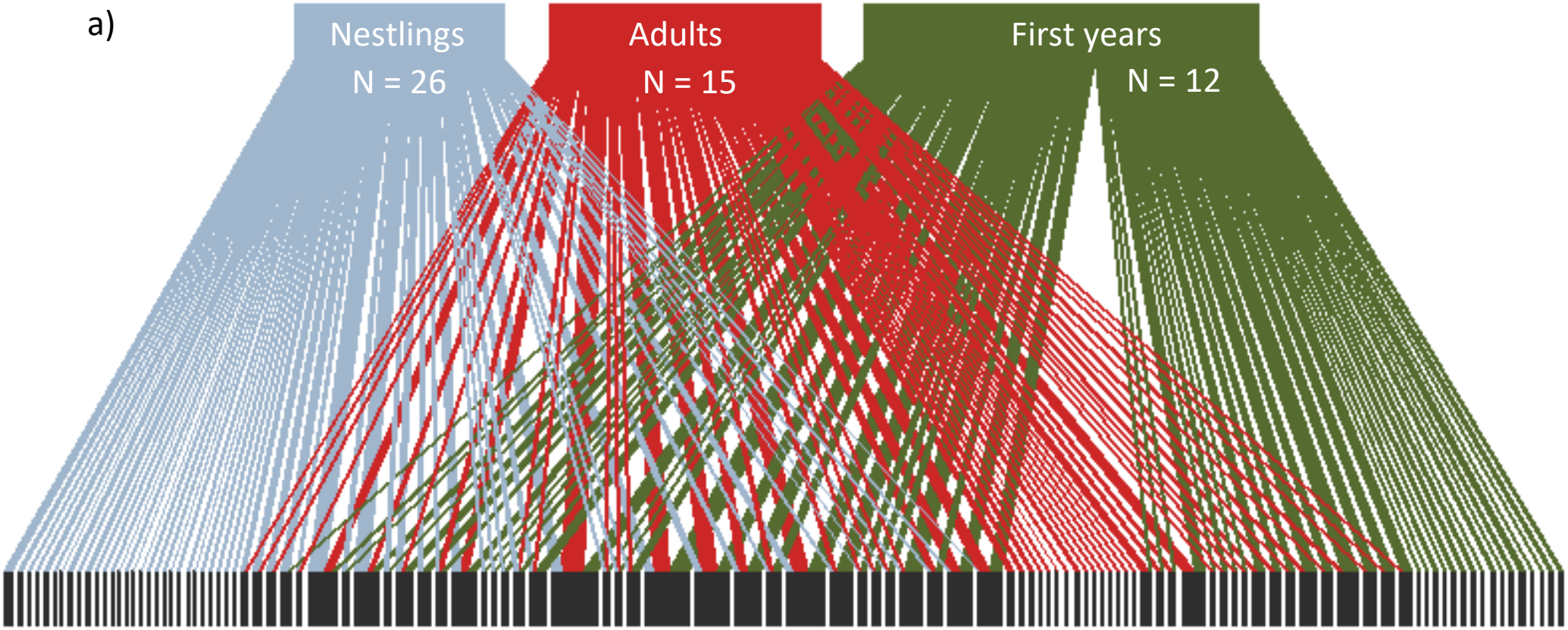


Figure S3.5. The plant genera consumed by males and females for a) conifer habitats and b) deciduous habitats. Data do not contain any duplicate samples from the same individual. See Figure S3.1 for further details of the plot.


a)
Nestlings
N = 26
Adults
N = 15
First years
N = 12

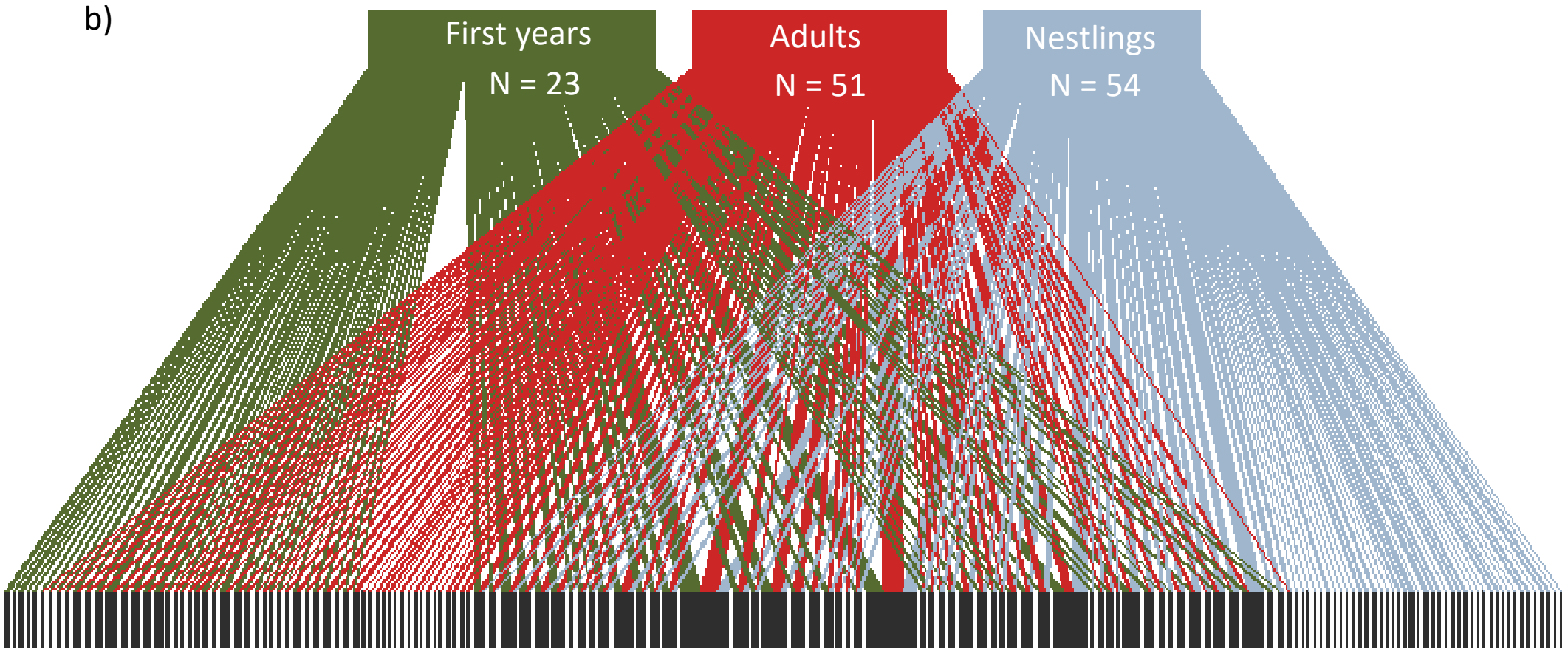


Figure S3.6. The degree of overlap in the diets of adults (red), first years (green) and nestlings (blue) in the spring for a) conifer and b) deciduous habitats. Each black bar is a genus and genera names have been removed to improve clarity of the plots. See Figure S3.1 for further details of plot creation.

3.7 Bibliography

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Chapter 4

Inhibitory control in the wild is associated with the diet of adult and nestling great tits



A nest box, 2 day old and 15 day old nestlings

Author contributions: Jenny R. Coomes and John L. Quinn designed the study, JRC and Gabrielle L. Davidson collected the field data. JRC analysed the data. JRC wrote the study with help from JLQ, GLD, Michael S. Reichert and Ipek G. Kulahci.

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4.1 Abstract

Inhibitory control is an executive function that plays an important role in decision making. It is the ability to stop performing a dominant or impulsive behaviour, in favour of a more beneficial or appropriate behaviour. However, the ecological relevance of this cognitive mechanism is poorly understood but it is expected to be important when choosing which foods to consume and which to avoid. Moreover, in altricial species, inhibitory control could also play a role in how parents choose which foods to provision their young. To test this hypothesis, we investigated whether individual differences in inhibitory control in wild great tits were associated with their own diet, the diet of their offspring and their provisioning rates. Diet was assessed using DNA metabarcoding to identify the taxa that were present in faecal samples, and the macronutrient content of each taxonomic family was calculated from invertebrate specimens. Our results show an association between adult inhibitory control and their own dietary composition (identity of taxa), for males but not females at the level of the genus. However, the opposite was the case for nestling diet: female but not male inhibitory control was associated with nestling dietary composition at genus level. One possible explanation for this contrast between the sexes is that, because females invest more in the brood than males, they may only be able to afford to discriminate between prey types for their nestlings' diet and not whilst self-feeding. Parents with poor inhibitory control provisioned their nestlings at a higher rate, providing support for lower selectivity of prey than birds with high inhibitory control. There was no effect of inhibitory control on dietary richness (number of taxa present) of adult birds or their nestlings, and no correlation between inhibitory control and the macronutrient content of the taxonomic families consumed. Our study is the first to investigate possible links between inhibitory control and the diet of adults and their nestlings, and suggests cognitive differences between the sexes is linked to parental care, reflecting different preferences and needs that arise due to parent-offspring conflict.

4.2 Introduction

It is vital for animals to be successful foragers and a variety of cognitive processes underpin the food choices animals make and their success in acquiring it. Animals must be flexible when making foraging decisions such as when, where and on what to forage, so they can avoid predators or exploit new food sources when preferred prey is not available. These decisions are particularly challenging for altricial species where parents are faced with a choice between feeding their offspring or feeding themselves (Davoren and Burger, 1999; Markman *et al.*, 2004; Wischnewski *et al.*, 2019). Furthermore, the decisions made by parents may differ between the sexes due to nutritional needs and variation in investment in the offspring (Kokko and Jennions, 2012; Liker *et al.*, 2015). We hypothesised that inhibitory control is a relevant cognitive mechanism underlying these foraging and provisioning decisions. Studies that explicitly investigate the role of inhibitory control in foraging behaviour in wild animals are lacking.

Inhibitory control is an executive function (i.e. a cognitive process for the monitoring and control of thoughts and actions; Pecora *et al.*, 2017) that involves the suppression of a dominant (prepotent) behaviour in favour of a more beneficial or appropriate behaviour (Diamond, 2013). Inhibitory control is likely to be important when animals are making decisions between different food types. For example, animals make decisions to avoid certain foods because of their unpalatability (Takahashi and Kaji, 2001), toxicity (Skelhorn and Rowe, 2010) and appearance (Stoddard, 2012). Furthermore, they may avoid foods if the return is not worth the effort invested, i.e. the energy or time costs to obtain and process the prey is greater than the benefit of consuming it (Emlen, 1966; MacArthur and Pianka, 1966). In addition, animals may choose between food types depending on the foods' nutritional benefit. Many studies have shown that animals are able to balance their macronutrient (carbohydrate, lipid and protein) intake from prey (Simpson and Raubenheimer, 1993; Behmer, 2009; Coogan *et al.*, 2014), which enhances their fitness (Raubenheimer and Simpson, 1997; Lihoreau *et al.*, 2016). We might expect that animals with good inhibitory control will be more efficient at

avoiding unprofitable foods, consuming higher quality foods and regulating their macronutrients, than individuals with poor inhibitory control, but this has not been tested. Results are contradictory from the few studies that do investigate an association between inhibitory control and diet (Stevens *et al.*, 2005; Stevens, Hallinan and Hauser, 2005; Amici, Aureli and Call, 2008; MacLean *et al.*, 2014; van Horik *et al.*, 2018). A comparative study found that primate species with increased inhibitory control had greater dietary breadth (MacLean *et al.*, 2014) but an individual level study on pheasants found that this relationship was negative (van Horik *et al.*, 2018). Whether these discrepancies are due to the method used to quantify diet (i.e. generalised diet from the literature or food preferences instead of the wild diet) is unknown. More studies that accurately quantify individual diet in the wild alongside individual differences in inhibitory control, are needed to determine the generality of these processes.

In addition to investigating the importance of inhibitory control when deciding on prey to consume, inhibitory control might also be important for the trade-off parents face between self-feeding and provisioning their offspring (Weimerskirch and Cherel, 1998; Weimerskirch *et al.*, 2003). This trade-off might differ between the sexes due to variation in how they value their own survival over that of their offspring (Wittenberger, 1982), which may occur due to differing levels of investment by each sex in the brood (Kokko and Jennions, 2012). Additionally, inhibitory control may be important for the decision between quality and quantity of prey delivered to nestlings. Grieco, (2002) found that blue tit parents showed continuous adjustment in prey selectivity whilst provisioning their offspring and because inhibitory control may influence how selective parents are when choosing prey, inhibitory control may underlie this finding. If individuals with high inhibitory control prioritise prey quality over quantity and show greater selectivity of prey, they will have an increased search time and therefore a reduced provisioning rate. How parental inhibitory control is associated with provisioning rate has not been investigated and will further our understanding of how cognition is associated with the trade-offs involved in parental care.

This study examines the diet of adult and nestling great tits and explores links with inhibitory control. The great tit is a common garden passerine and a model species in ecology (Cole, Cram and Quinn, 2011; Morand-Ferron *et al.*, 2011; Aplin *et al.*, 2015), making it ideal for studying the association between inhibitory control and diet. Great tits readily breed in nest boxes in the wild where provisioning behaviour can be observed and cognitive tasks can be deployed. They do not have a crop so cannot store excess food in their beaks meaning they cannot forage simultaneously for themselves and for their nestlings. Therefore, they make constant decisions between provisioning and self-feeding and we expected that inhibitory control would aid in making such decisions. Although some studies attempt to measure the diet of great tits at nests using video recording, it is often difficult to identify smaller prey items, or to distinguish between closely related taxa that may vary dramatically in their ecology or abundance. Additionally, this method does not allow observation of what the adults themselves are eating. Therefore, we used DNA metabarcoding – a high throughput sequencing method that facilitates non-invasive quantification of diet from faeces with taxonomically high resolution (Shokralla *et al.*, 2012; Taberlet, Coissac, Hajibabaei, *et al.*, 2012; Taberlet, Coissac, Pompanon, *et al.*, 2012; Yu *et al.*, 2012) – to analyse both adult and neonatal diets.

Inhibitory control was estimated using a modified version of the well-established detour task. In the task, subjects must inhibit their response to move straight for a reward behind a transparent barrier and must instead move around the barrier to acquire the reward. While there are other ways of testing inhibitory control that may tap into distinct facets of this cognitive mechanism (e.g. delayed gratification: Beran, Rossettie and Parrish, 2016), our detour task was designed to be able to test adults in the wild and to target the same individuals for whom we had dietary data. Moreover, our wild detour task has been validated in our system as a measure of impulse control (Davidson *et al.* 2021, Pre-print). We used a version of this task that was modified for use at nest boxes, where trials coincided with parents returning to their box to provision their nestlings (Davidson *et al.* 2021, Pre-print). The authors showed that the task is temporally repeatable across years, and contextually repeatable against the captive version of the task. Additionally, there is no evidence

that performance on the wild task is sensitive to extraneous variables, for example, persistence, motivation, personality and body size, that are unrelated to inhibitory control (Davidson *et al.* 2021, Pre-print).

This study explored links between parental inhibitory control and diet of parents and nestlings, and investigated whether a link between inhibitory control and nestling diet had knock on effects for provisioning rate and offspring condition. The following two primary questions were addressed: 1) is adult inhibitory control correlated with their own dietary composition (identity of taxa present) and dietary richness (number of taxa present), and 2) is parental inhibitory control correlated with nestling dietary composition and dietary richness. Here we predicted that birds with different inhibitory control abilities would have, and would feed their nestlings, different compositions of prey. We also predicted that birds with poor inhibitory control would both consume and provision their nestlings with a greater number of taxa (high dietary richness) (van Horik *et al.*, 2018) because they would not be able to inhibit their response to eat or collect every prey type they come across, as opposed to showing control by targeting high quality prey. As diet varies between the sexes (Chapter 3), and there is some evidence that cognition might vary with sex (Jones, Braithwaite and Healy, 2003; Carazo *et al.*, 2014), we tested if the association between inhibitory control and diet varied between the sexes. Furthermore, we thought that any effect of inhibitory control on own or nestling diet could vary between the sexes due to differences in energetic constraints and parental care trade-offs (Kokko and Jennions, 2012). Finally, if there was a relationship between inhibitory control and diet, we predicted birds with good inhibitory control would consume and provision prey with a higher nutritional value than birds with poor inhibitory control, because they have a greater ability to inhibit choosing unprofitable prey.

Our secondary two questions investigated the knock on effects of a relationship between parental inhibitory control and nestling diet: 3) is provisioning rate linked to nestling diet or to parental inhibitory control, and 4) is nestling mass linked to nestling diet or to parental inhibitory control. Question 3) explored the role of inhibitory control on provisioning quantity versus quality of prey and we predicted

that parents providing a more diverse and less discriminatory diet, those with poor inhibitory control, would provision more frequently. Finally, as nestling diet is linked to their mass (Bańbura *et al.*, 2004; García-Navas and Sanz, 2011) and heavier nestlings have increased fledging success and survival (Naef-Daenzer and Keller, 1999; Naef-Daenzer, Widmer and Nuber, 2001), question 4) explored if the association between inhibitory control and nestling diet had consequences for nestling mass. Here we predicted that if parents with good inhibitory control provisioned their nestlings with better quality prey, their nestlings would be in better condition and would weigh more.

4.3 Methods

This study was conducted under licences from the Health Products Regulatory Authority (Project licence: AE19130/P017, Individual licence to JCoomes: AE19130/I250), the National Parks and Wildlife Service (Project licences: 004/2017, 001/2018, C02/2018; Individual licences to JCoomes: 70/2017, 11/2018) and the British Trust for Ornithology (individual ringing licences for JCoomes (C6597), Sam Bayley, Ivan de la Hera Fernandez). The research project received ethical approval from the Animal Welfare Body at University College Cork and was in accordance with the ASAB (Association for the Study of Animal Behaviour) Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

4.3.1 Diet data

We collected faecal samples (total N = 137; males = 76, females = 61) from adult birds in May and June in 2017 and 2018 by trapping the parents at the nest (when the chicks were 9-12 days old), at 12 field sites from two habitat types (mixed deciduous and coniferous woodland) in County Cork, Ireland. Birds were aged and sexed according to plumage characteristics (Svensson 1984), were fitted with a metal British Trust for Ornithology (BTO) ring, a unique colour ring for identification and a passive integrated transponder (PIT) tag (IB Technology Aylesbury, UK). With the addition of this tag, receivers that use RFID (radio-frequency identification)

technology could be placed on the nest box to record the identity of a bird that entered the box. Prior to being ringed, birds were placed individually into clean bird bags, inside each of which was a coffee filter to absorb liquid urea, and given time to defecate. Birds were held until they defecated (not exceeding 30 mins). We collected faecal samples from nestlings (N = 211) in May 2017 and from May - June 2018 by removing nestlings from the nest when they were eight or nine days old and transferring them singly to a plastic pot where they were likely to defecate. Nestling mass was taken at this time. All samples were transported to Cardiff University where DNA analysis took place from September 2018 to March 2019. Lab work consisted of DNA extraction, PCR to establish presence of invertebrate DNA using COI primers, PCR to add unique identifying tags to the samples and next-generation sequencing. We followed a bioinformatics pipeline developed by Lorna Drake (Drake, 2020) to obtain the final diet data of presence/absence of each taxa. See Chapter 3 for full details. We performed the analyses at the level of the genus and at the level of the family. We were primarily interested in the diet at genus level but we also investigated the diet at family level for two reasons. First, we only had nutrient values for family level (and above) so we wanted to confirm effects of inhibitory control on the diet at family level. Second, taxa at the family level are more likely to be consumed by a greater number of individuals than those at the genus level and, as we had limited sample sizes of birds with inhibitory control and diet data, we wanted to confirm our results were not being driven by a small number of individuals. Comparing the family to the genus level analysis would allow us to do this. Of 436 identified sequences (see Chapter 3), 61 were identified to a taxonomic rank above genus and below family. We excluded faecal samples where no DNA was detected (likely due to low biomass).

4.3.2 Provisioning rate

To record provisioning rate at the nest box, a wire structure with a wooden perch was fastened to the outside of the box and a video camera was attached to the side to view the approaching parent (Figure 4.1). The camera was connected to a 12v

battery and a DVR device. The wire perch was fastened when the nestlings were nine days old, to ensure habituation of the parents to the structure. Videos were recorded when the nestlings were 16 or 17 days old, for two hours in the morning (0600 – 1200). Provisioning rate data for the same time point as nestling diet data was not sufficient to undertake analysis and was not available in both years. We used the programme MotionMeerkat (Weinstein, 2015) to detect motion events of parents entering the nest and then reviewed the image stills produced by the programme to identify provisioning events. Provisioning rate was recorded as the total number of visits within the two hour period for each individual parent. For frequency distributions of the provisioning rates used in analysis, see Figure S4.1.

Figure 4.1. The wire perch attached to a nest box with the miniature camera on the left hand side to film the parents coming into the nest box to provisioning their nestlings. The camera was attached to a DVR recorder and a 12v battery. The set-up was placed on the nest box a few days prior to filming to allow birds to habituate. It was placed on day 3 post-hatching in 2017 to record videos at earlier time points (data not used in this study) and on day 15 post-hatching in 2018.

4.3.3 Inhibitory control measured in the wild

We measured performance on a detour task as a measure of inhibitory control at the nest box from 25th May to 25th June 2017, and from 26th May to 15th June 2018. The modified detour task consisted of a plastic barrier placed in front of the nest box entrance, which birds had to detour underneath in order to enter the nest box (Figure 4.2). There were three phases to the experiment: habituation, training and test (Figure 4.2). During habituation, an opaque rectangular piece of plastic film (0.1cm x 10cm x 5cm) was attached to the top rim of the box pointing upwards and a wooden perch was attached to the base of the box with metal wire to provide the birds with something to land on before entering the nest. The woodcrete front to the nest box was replaced with one that also had a PIT-tag receiver mounted on the back ("RFID logger for Schwegler 1B": naturecounters.com), which recorded the PIT-tag identity of a bird that entered the nest box. To pass the habituation phase, individuals had to enter the nest box at least three times before moving on to the training phase. During the training phase, the opaque rectangle of plastic was repositioned so it overhung the nest-box entrance, the purpose of which was to ensure that birds could perform the motor action of going underneath the barrier to enter the nest. Birds had to enter the box without touching the barrier at least three times (and once in 2018) before moving on to the test phase. During the test phase, the plastic barrier was made transparent and a bird had to make at least five attempts to enter the nest box in order to complete the experiment. An attempt was scored as a fail if the bird collided with the barrier whilst flying towards the nest entrance or jumped into the barrier from the perch at the bottom of the box. An attempt was scored as a success if the bird flew under the barrier straight into the box or landed on the perch and jumped into the box without touching the barrier. The three phases (habituation, training and test) were presented at the nest box for approximately one hour each on consecutive days during 2017. In 2018, the habituation phase was set on the box from day 8 or 9 (immediately after faecal sampling of nestlings) until the start of training. Video footage of the phases was reviewed on the same day as testing to determine if each bird had passed. If both parents did not pass a phase after two days, the experiment was abandoned at that

nest box to limit disturbance. A detour score was calculated for each bird as the proportion of successes out of the number of attempts made across all days of testing, with the number of attempts capped at ten. A higher score represents higher inhibitory control. This assay was designed and the data collected by G. Davidson, with support from JC and other group members. For full details, see Davidson *et al.* (2021, Pre-print). For frequency distributions of the detour scores used in analysis, see Figure S4.2.

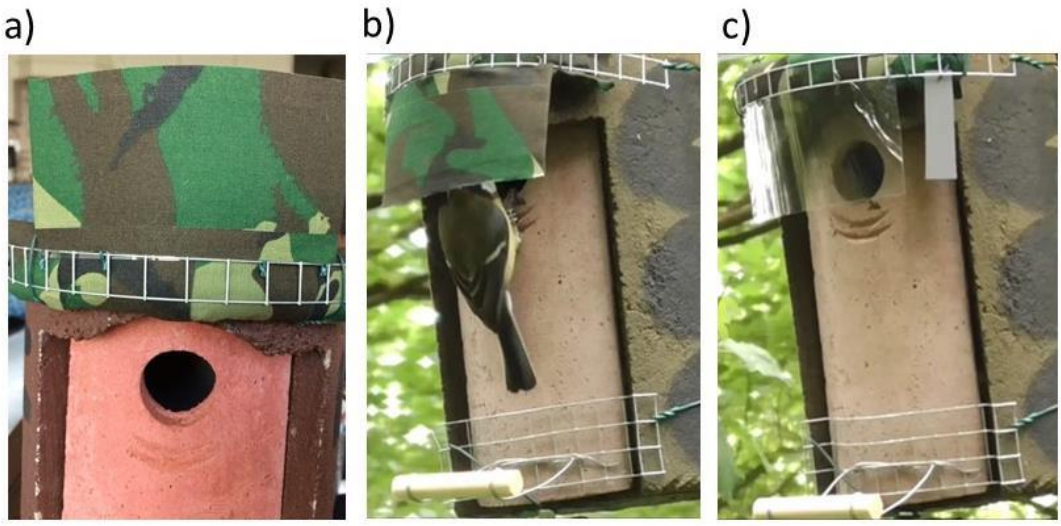


Figure 4.2. The three experimental phases of the detour task at the nest box: a) habituation – to make sure birds were accustomed to the addition of the apparatus on the box, b) training – birds had to perform the motor action of detouring underneath the barrier (covered in camouflage tape) and c) test – the tape is removed from the barrier so it is transparent and birds must inhibit flying straight into the nest box and instead detour underneath. Photos b) and c) also show the wooden perch attached to the base of the nest box for the birds to land on and then hop up underneath the barrier to the nest box hole. Photos taken by G. Davidson.

4.3.4 Nutrient analysis

To test the relationship between inhibitory control and nutritional content of prey in the diet, we correlated detour score with the percentage mass of macronutrients (carbohydrate, protein and lipid) of the taxonomic families identified. Mean percentage of total mass for the macronutrients was calculated for specimens from as many taxonomic families identified in the diet of adults and nestlings as possible, following methods in Cuff *et al.*, (2021) with adjustments for the small size of specimens (Cuff, 2020). Macronutrient data is unpublished and was collected by Jordan Cuff from Cardiff University. Specimens were soaked in a chloroform-methanol solution to remove lipids and the remaining tissue solubilised for protein and carbohydrate analysis. Colorimetric assays were used to determine macronutrient contents (Cuff, 2020; Cuff *et al.*, 2021). Percentage of total macronutrient mass was used in the analysis e.g. % carbohydrate, % protein and % lipid making up the whole for each taxonomic family. The number of specimens used per family varied based on availability of samples (range: 1-54). We did not use the raw nutrient content values of specimens because they are meaningless unless the mass of the invertebrate is known and because of the very small size of many of the invertebrates, mass readings were inaccurate. Additionally and more importantly, we do not have any data on the mass of invertebrates fed to the nestlings. In cases where data was not available at family level, we used data for superfamily or order instead.

4.3.5 Statistical analysis

Questions 1 and 2

All analyses were performed using R (v3.6.1) (R Core Team, 2019). To investigate dietary composition throughout this study we used the package *mvabund* v4.1.3 (Wang *et al.*, 2012) to run a manyglm with a binomial family and a 'cloglog' link function. This package allows us to use the matrix of presence/absence of taxonomic identity as the response variable. We used the *anova* function to obtain

summary statistics with the default Likelihood Ratio test and we added a montecarlo (parametric bootstrap) resampling method to calculate P values, as recommended in Wang *et al.*, (2012) for presence/absence data. Because terms are added to the model sequentially, detour score was written in the model last, after the other explanatory variables that we wanted to control for (see below). We were therefore testing for the effect of detour score on diet, given that the other variables were already in the model. For further details of *mvabund* see Chapter 3. We also ran univariate comparisons for each model, using '*p.uni=adjusted*', to assess whether any effects were being driven by certain genera.

To investigate our first question of whether adult inhibitory control was correlated with their own diet, we established the number of birds that we had diet and inhibitory control measures for in the same year (N = 38 of 30 nests; males = 22, females = 16). We avoided comparing diet data and inhibitory control measures across years because both diet and cognition are likely to depend on age (Thornton and Lukas, 2012; Griffin and Guez, 2014; Jones *et al.*, 2020). For dietary composition, our response variable was adult diet and our explanatory variables were age (first year: <1 year or adult: >1 year), sex, year (2017 or 2018) and detour score (continuous between 0 and 1), as well as the interaction detour score × sex. Habitat (deciduous or coniferous) was not sufficiently balanced to include as an explanatory variable due to all the birds in 2018 being from deciduous sites. In addition to this, to interpret the interaction between detour score and sex, we subsetted the data into females and males and looked for an effect of detour score on dietary composition (see Table 4.1).

To investigate our second question of whether adult inhibitory control was correlated with nestling diet, we used nests for which we had both nestling diet data and inhibitory control for at least one parent (total N = 37; N = 27 for both parents). For dietary composition, we could not include nest ID as a random effect because random effects are not possible in a manyglm, so our response variable was the total combined diet of all the nestlings in a nest, to avoid having repeats of the same nest (see Dunn *et al.*, 2018). For this, if a taxon was present in the diet of any nestling in the nest, it was considered present, and otherwise it was considered

absent. Our explanatory variables were year, the number of samples (individual nestlings) that contributed to the nestling diet data, detour score of father and detour score of mother (see Table 4.2). The removal of one outlier nest (a female detour score of zero) ensured non-collinearity between the parent detour scores (N = 36).

We used surface plots and bipartite plots to visualise how detour score was associated with dietary composition. The surface plots were created using the 'metaMDS' and 'ordisurf' functions in the *vegan* package (v2.5-6) (Oksanen *et al.,* 2020). The Jaccard index was used to calculate the distances between samples and the further two datapoints are from each other after this calculation, the more different their diets are. Lines on the surface plots that are mostly parallel indicate a linear relationship, whereas loops and circles indicate no relationship. The bipartite plots were created using the *bipartite* package (v2.14) (Dormann, Gruber and Fründ, 2008). For bipartite graphs where the taxa are grouped by common name (e.g. Figure 4.3), the mean detour score of the birds that consumed (or their nestlings consumed) at least one genus of that group are displayed on the lower bars.

For questions 1 and 2 we also investigated dietary richness (number of taxa consumed). To investigate adult dietary richness (question 1), we ran a generalised linear mixed model (GLMM) with a negative binomial error distribution on the genus level diet data and a GLMM with a Poisson error distribution for the family level, with number of taxa consumed by the adult (for genera and family levels separately) as our response variable. The explanatory variables were detour score, age, sex and year (Table 4.1). The model would not converge if we included the interaction detour score × sex. For nestling dietary richness (question 2), we ran a negative binomial GLMM for genus and a Conway-Maxwell Poisson GLMM for family, with the number of taxa consumed by all nestlings in a nest as the response. The explanatory variables were male detour score, female detour score, year and number of faecal samples obtained per nest (Table 4.2). Site was included in both the adult and nestling dietary richness models as a random effect. We checked model fit and tested the assumptions of the GLMMs using the *DHARMa* package (v 0.2.6) (Hartig, 2019) and chose the error structure that provided the best model fit.

Nutrition analysis

We examined if adult inhibitory control was related to the nutritional content of the diet of both adults and nestlings by investigating if the percentage of carbohydrate, protein or lipid in each family was correlated with the detour score of the birds that consumed each family. We ran separate Spearman's rank correlations between the macronutrient percentages of carbohydrate, protein and lipid in each family (or superfamily or order), and the mean detour score of the birds that had consumed, or had provisioned their nestlings with, that family. We calculated mean detour score separately for males and females.

Questions 3 and 4: provisioning rate and nestling mass

Since we found an association between the detour score of at least one parent and nestling diet composition, we investigated if this relationship had knock-on effects for provisioning rate (question 3) and nestling mass (question 4). There were two analyses for question 3 which investigated if i) parental detour score was linked to provisioning rate (model 3.1) and ii) if provisioning rate was linked to nestling dietary composition (model 3.2). Model 3.1 was a negative binomial GLMM that had provisioning rate of individual parent as the response, and detour score, brood size, year and sex as explanatory variables. Lay date could not be added as an explanatory variable as the model would not converge. Nest ID was added as a random effect. Model 3.2 was a manyglm that had total nestling diet composition at genus level as the response variable and included year, number of faecal samples obtained per nest and total provisioning rate for both parents controlled for brood size, in that order, as explanatory variables (see Table 4.3).

There were two analyses for question 4 which investigated if i) parental detour score was linked to nestling mass (model 4.1) and ii) if nestling mass was linked to nestling dietary composition (model 4.2). Model 4.1 was a general linear model (GLM) with a Gaussian error distribution that had mean nestling mass of the nest as the response variable and female detour score, male detour score, brood size, lay date and year as explanatory variables. Model 4.2 was a manyglm that had total nestling diet composition at genus level as the response variable and included year,

number of faecal samples obtained per nest and mean nestling mass, in that order, as explanatory variables (see Table 4.3). Provisioning rate and nestling mass were correlated and so could not go in the same model, meaning models 3.2 and 4.2 were done separately.

To examine if the number of genera consumed by the nestlings was related to the rate at which they were provisioned or their mass, models 3.1 and 4.1 had the addition of total nest richness as an explanatory variable. Because we did not have specific predictions for analyses 3.1 and 4.1 we used the *dredge* function from the *MuMIn* package (Barton, 2019), and an information-theoretic approach in combination with model averaging (Grueber *et al.*, 2011) to generate the model(s) with the most support generated from a global model. The information-theoretic approach compares all possible combinations of models simultaneously and we calculated the amount of support for each model using Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson, 2002). Models with a ΔAICc <2 were retained as the 'top' models that included the most important explanatory variables. We report the full averaged weighted parameter estimates across all models in the top set because this method takes into account that some variables are not present in all models.

4.4 Results

4.4.1 Adult diet

The correlation between adult detour score and adult dietary composition differed between the sexes at the level of the genus but not at the level of the family (Detour × Sex: Table 4.1; Figure 4.3). This result was not driven by any particular taxa and did not change when genera only present in single samples (singletons) were removed (no singletons: Genus: Likelihood ratio test (LRT) = 100.50, P = 0.006; Family: LRT = 31.89, P = 0.30). When examining the interaction at genus level, the detour scores of males correlated with their diet composition, but we did not find an effect for females (Table 4.1; Figure 4.3), though we note the low sample sizes, particularly for females (N = 16). True flies (*Scathophaga*), spittlebugs (*Aphrophora*), shield bugs (*Acanthosoma*), gnats (*Culicoides* and *Bradysia*) and crane flies (*Tipula*) were detected in males with low (<0.49) detour scores, i.e. with relatively poor inhibitory control. Sawflies (*Empria*), lacewings (*Chrysotropia* and *Hemerobius*) and bees (*Bombus* - only one bird) were detected in the diet of males with high (>0.8) detour scores i.e. with relatively good inhibitory control (Figure 4.3a). More hoverfly and parasitoid wasp genera were detected in males with low detour scores than high detour scores.

Of the birds we had diet data for, more males than females had detour scores below 0.5 (Figure S4.2) and the mean detour score for males was lower than the females (0.52 compared to 0.74). Only two females, out of the 16 for which we had diet data, had a detour score of 0.5 or lower (≥50% success). When looking at both sexes, there was a main effect of detour score on adult dietary composition at the family level only (Table 4.1; Figures 4.4 and S4.3) and this result was not driven by any particular taxa and was not robust to the removal of singletons (Family, no singletons: LRT = 55.99, P = 0.11). At the family level, butterflies (*Lycaenidae* and *Nymphalidae*) were present in the diet of birds with a mean detour score of 0.7, and ladybirds were present with a mean score of 1 (although only one individual) i.e. with relatively good inhibitory control (Figure 4.4). There was a main effect of sex

and year on dietary composition for both genus and family level and an effect of age for family but not genus (Table 4.1).

There was no correlation between detour score and invertebrate richness (number of taxa consumed) at the genus or family level (Table 4.1). There was no effect of age or year on dietary richness at either genus or family level and a slight effect ($p = 0.05$) of sex at family level only (Table 4.1). There was no correlation between the mean detour score of males or females that consumed each taxonomic family and the percentage of carbohydrate, protein or lipid in the family (Table S4.1).

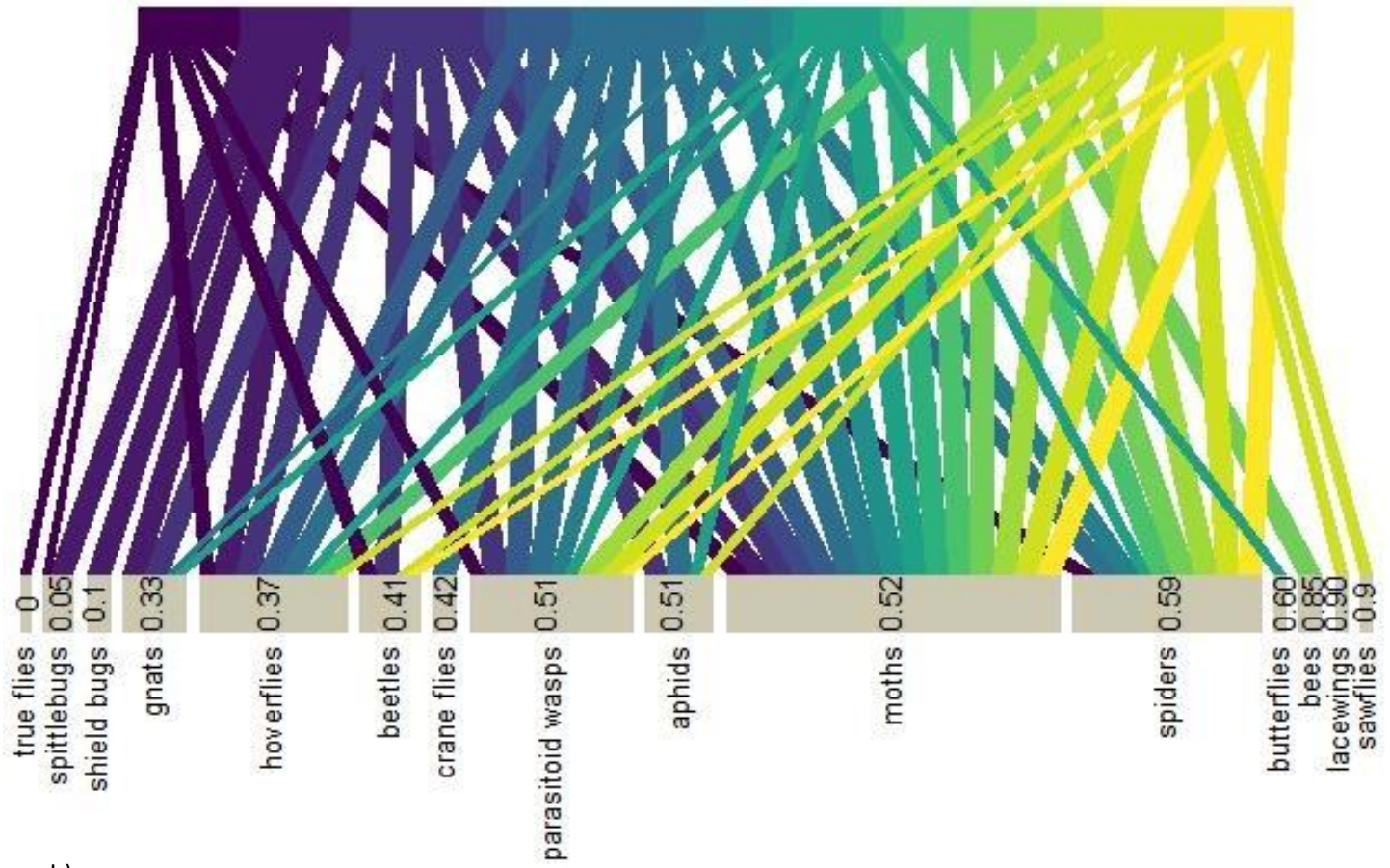
Table 4.1. Model summaries for invertebrate composition and invertebrate richness in the diet of adults (Question 1). N = 38; 18 in 2017 and 20 in 2018. Females: N = 16, Males: N = 22. The likelihood ratio test (LRT) indicates deviance. The standard error (SE) and the 95% confidence intervals (CI) are shown for the richness models.

Taxonomic level of data	**Composition**			**Richness**				
	Explanatory variable	LRT	P value	Explanatory variable	Estimate	SE	95% CI	P value
Genus	Age	111.8	0.199	Intercept	2.26	0.36	1.55; 2.97	**<0.001**
	Sex	162.1	**0.002**	Detour score	-0.18	0.45	-1.06; 0.70	0.69
	Year	210.0	**0.001**	Age	0.16	0.17	-0.17; 0.49	0.35
	Detour score	163.0	0.117	Sex	<0.001	0.20	-0.39; 0.39	1.00
	Detour × Sex	100.5	**0.005**	Year	-0.07	0.35	-0.76; 0.62	0.85
	Males only							
	Age	70.24	0.662					
	Year	150.51	**0.001**					
	Detour score	157.48	**0.003**					
	Females only							
	Age	99.39	**0.022**					
	Year	106.97	**0.016**					
	Detour score	115.95	0.392					
Family	Age	68.02	**0.026**	Intercept	2.34	0.27	1.81; 2.87	**<0.001**
	Sex	77.72	**0.016**	Detour score	-0.36	0.35	-1.05; 0.33	0.30
	Year	81.29	**0.004**	Age	0.07	0.13	-0.18; 0.32	0.58
	Detour score	99.31	**0.019**	Sex	-0.29	0.15	-0.58; 0.00	**0.05**
	Detour × Sex	31.90	0.333	Year	-0.23	0.28	-0.78; 0.32	0.40

a)

Low detour score

High detour score



b)

Low detour score

High detour score

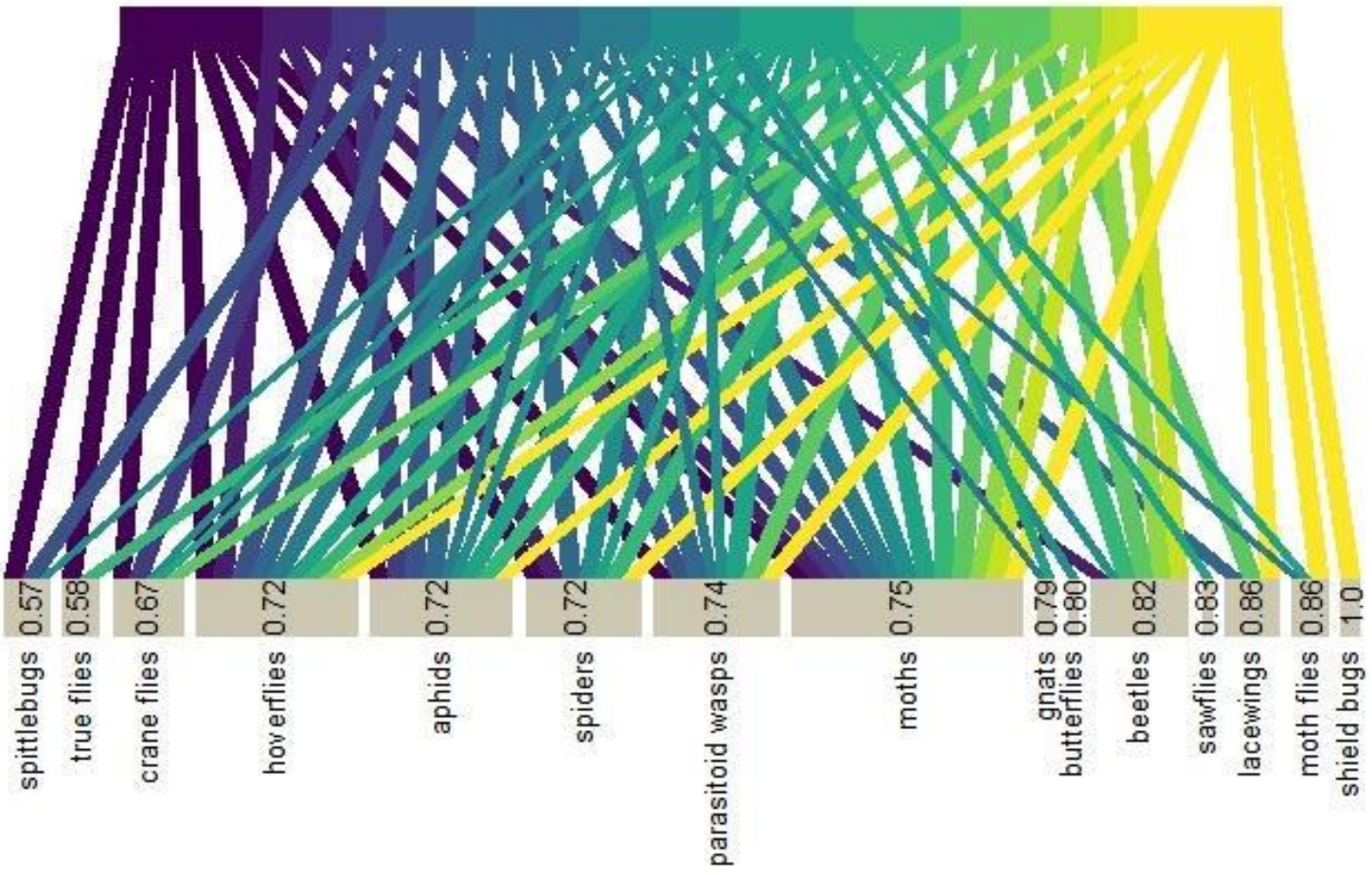


Figure 4.3. The invertebrate diet of a) males (N = 22) and b) females (N = 16) at the level of the genus with respect to their detour score. The colour from dark to light (purple to yellow) represents the continuous detour score from low (0) to high (1). A high detour score is high inhibitory control. See Figure S4.2a for the distribution of detour scores. Data from both years (2017 and 2018) is shown. The genera are grouped by common name and some groups contain genera from different taxonomic families. Lines connect the detour score of birds that consumed at least one genus from each group. The width of the interacting lines represents the proportion of birds of each detour score that consumed at least one genus from that group. The width of the lower bars is proportional to the sum of the interactions involving that group: groups that were involved in more interactions (ie. were present in the diet of more birds) have a wider bar. The mean detour score of all the birds that consumed at least one genus in the dietary group is shown on the lower bars.

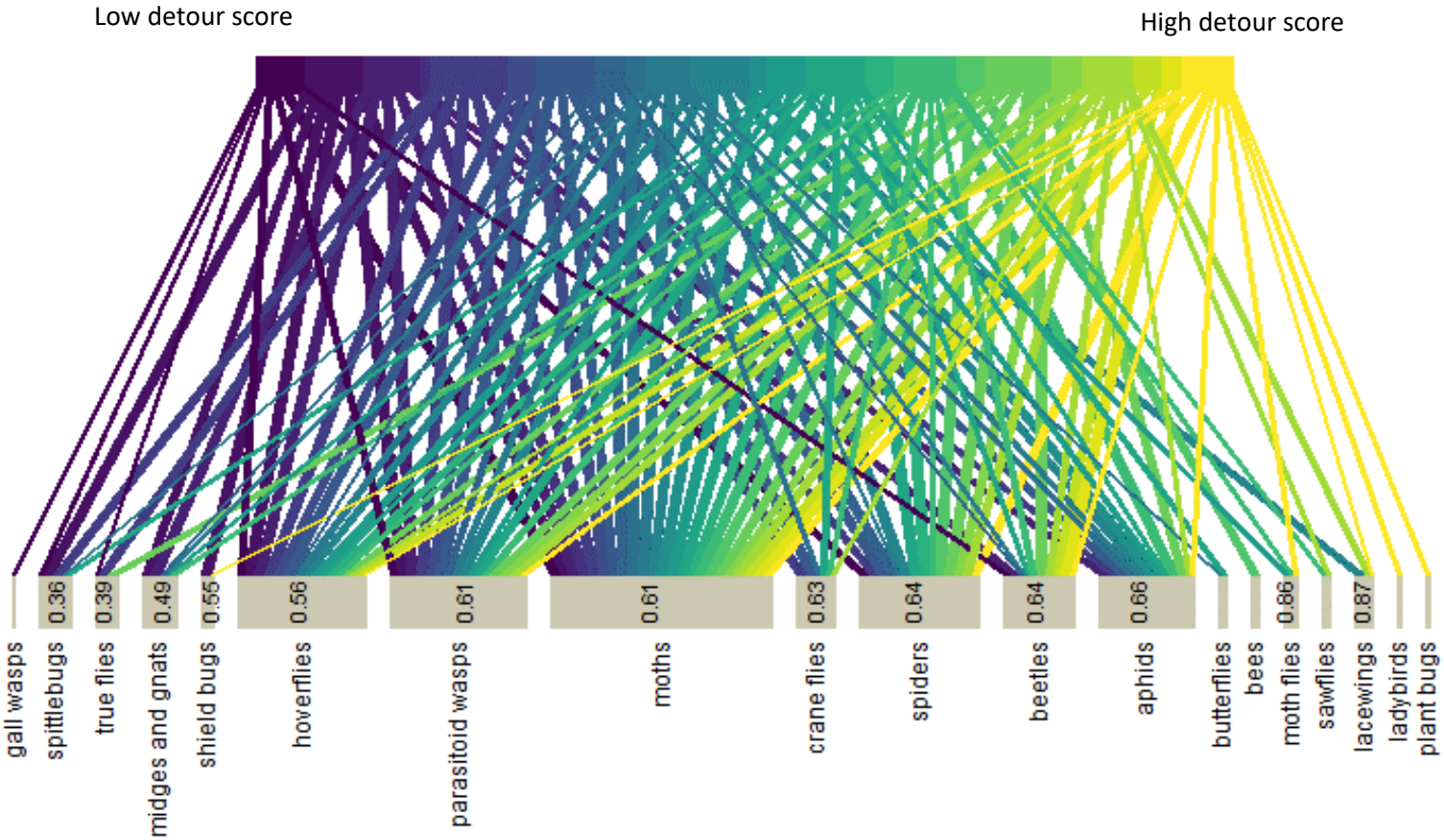


Figure 4.4. The invertebrate diet of adults of both sexes at the level of the family, grouped by common name, with respect to their detour score (high detour score indicates high inhibitory control). See Figure 4.3 for detail on the construction of the bipartite plot. The mean detour score of all the birds that consumed at least one family in the dietary group is shown on the lower bars.

4.4.2 Nestling diet

Female detour score was correlated with the invertebrate composition of her nestlings, at genus and family level (Table 4.2; Figures 4.5a, 4.6 and S4.4) and this result did not change with the removal of singletons (No singletons: Genus: LRT = 168.2, *P* = 0.003; Family: LRT = 63.17, *P* = 0.027) and was not driven by any particular taxa. Visualisation using a surface plot indicates that there is a linear relationship in how the diet changes with increasing detour score (Figure 4.5a). Male detour score was not correlated with nestling dietary composition at the level of the genus or family (Table 4.2; Figure 4.5b) and this result did not change with the removal of singletons (No singletons: Genus: LRT = 129.0, *P* = 0.11; Family: LRT = 50.37, *P* = 0.21). The range of mean female detour scores for the prey groups was narrow (0.55 – 0.87; Figure 4.6) showing that many prey groups were found in nests with a wide range of female detour scores. Parasitoid wasps (*Cotesia*, *Phobocambe* and *Protapanteles*), wasps (*Vespula* – only one individual) and moth flies (*Psychoda*) were detected in the nests of females with a mean detour score below 0.6 (i.e relatively low inhibitory control) (Figure 4.6). Flies (*Bibio*, *Calliphora*, *Phyrxe* and *Scathophaga*), sawflies (*Abia* and *Euura*) and slugs (*Deroceras*) were detected in the nests of females with a mean detour score above 0.8 (Figure 4.6) (i.e. relatively high inhibitory control). There was no correlation between mean parental detour score and the percentage of carbohydrate, protein or lipid in the family consumed by their nestlings (Table S4.1).

There was no correlation between male or female detour score and total nest richness at the genus or family level (Table 4.2). There was a significant effect of number of faecal samples obtained per nest on total nest dietary composition and richness (Table 4.2). The more faecal samples that were analysed within a nest, the more taxa were identified. There was an effect of year on nestling composition but not richness (Table 4.2).

The higher the detour score of the parent, the less they provisioned their nestlings within a two hour period (Table 4.3, model 3.1; Figure S4.5). Nests with a lower richness (consumed fewer genera) had a higher provisioning rate (Table 4.3, model

3.1; Figure S4.5). There was no effect of brood size, year or sex on provisioning rate (Table 4.3, model 3.1).

There was no effect of parental detour score, total nest richness, brood size or year on nestling mass (Table 4.3, model 4.1). There was a significant effect of lay date; the later the eggs were laid, the heavier the nestlings were at day 8/9 (Table 4.3, model 4.1). There was no effect of provisioning rate or nestling mass on nestling dietary composition (Table 4.3, model 3.2, 4.2).

Table 4.2. Model summaries for the effect of parental detour score on nestling dietary composition and dietary richness (Question 2). N = 36; 19 in 2017 and 17 in 2018 (one outlier was removed from 2017). The likelihood ratio test (LRT) indicates deviance. The standard error (SE) and the 95% confidence intervals (CI) are shown for the richness models.

Taxonomic level of data	**Composition**			**Richness**				
	Explanatory variable	LRT	P value	Explanatory variable	Estimate	SE	95% CI	P value
Genus	Year	204.6	**0.001**	Intercept	1.48	0.31	0.87; 2.09	**<0.001**
	Sample N*	217.1	**0.001**	Male detour	-0.17	0.18	-0.52; 0.18	0.34
	Male detour	160.9	0.105	Female detour	-0.10	0.31	-0.71; 0.51	0.74
	Female detour	225.5	**0.001**	Year	0.12	0.12	-0.12; 0.36	0.34
				Sample N*	0.47	0.07	0.33; 0.61	**<0.001**
Family	Year	73.94	**0.001**	Intercept	0.96	0.29	0.39; 1.53	**<0.001**
	Sample N*	102.47	**0.001**	Male detour	-0.04	0.17	-0.37; 0.29	0.83
	Male detour	54.04	0.362	Female detour	0.07	0.30	-0.52; 0.66	0.80
	Female detour	89.06	**0.004**	Year	0.01	0.11	-0.21; 0.23	0.90
				Sample N*	0.40	0.07	0.26; 0.54	**<0.001**

Note: *The number of faecal samples obtained per nest

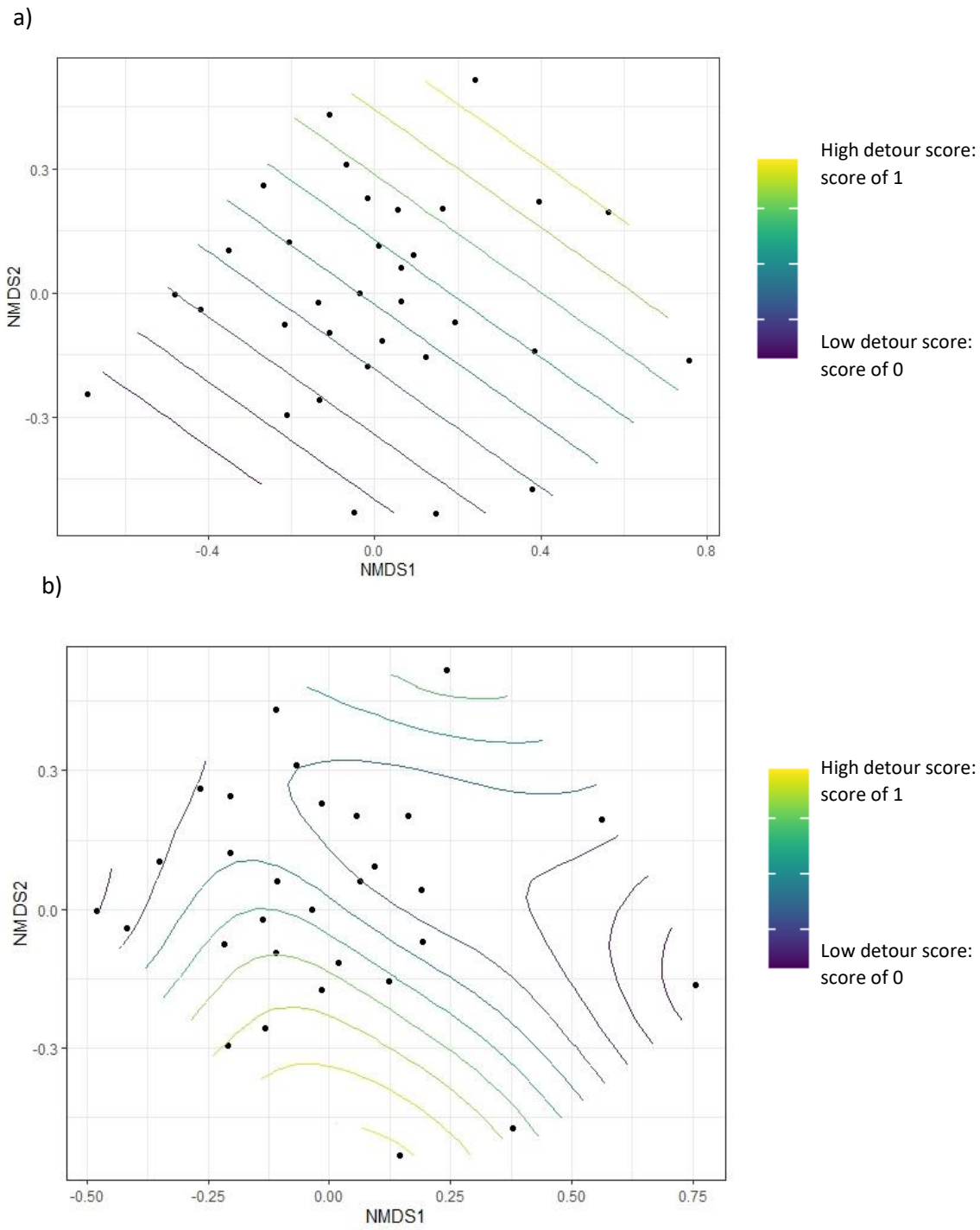


Figure 4.5. The invertebrate diet of nestlings, at the genus level, with respect to the detour score of a) their mother (N = 33), and b) their father (N = 30). The colour from dark to light (purple to yellow) represents the continuous detour score from low (0) to high (1). A high detour score is high inhibitory control. See Figure S4.2b for the distribution of detour scores. Data is from 2017 and 2018. One outlier nest was removed to ensure the parent detour scores from the same nest were not correlated. The diet data for each nests is combined for all nestlings and is

condensed from a matrix to two values using non-metric multidimensional scaling. Each point on the graph is a nest. The Jaccard index was used to calculate the distance between nests. For the female detour score, there is a linear trend from low detour score to high but this is not the case for the male score.

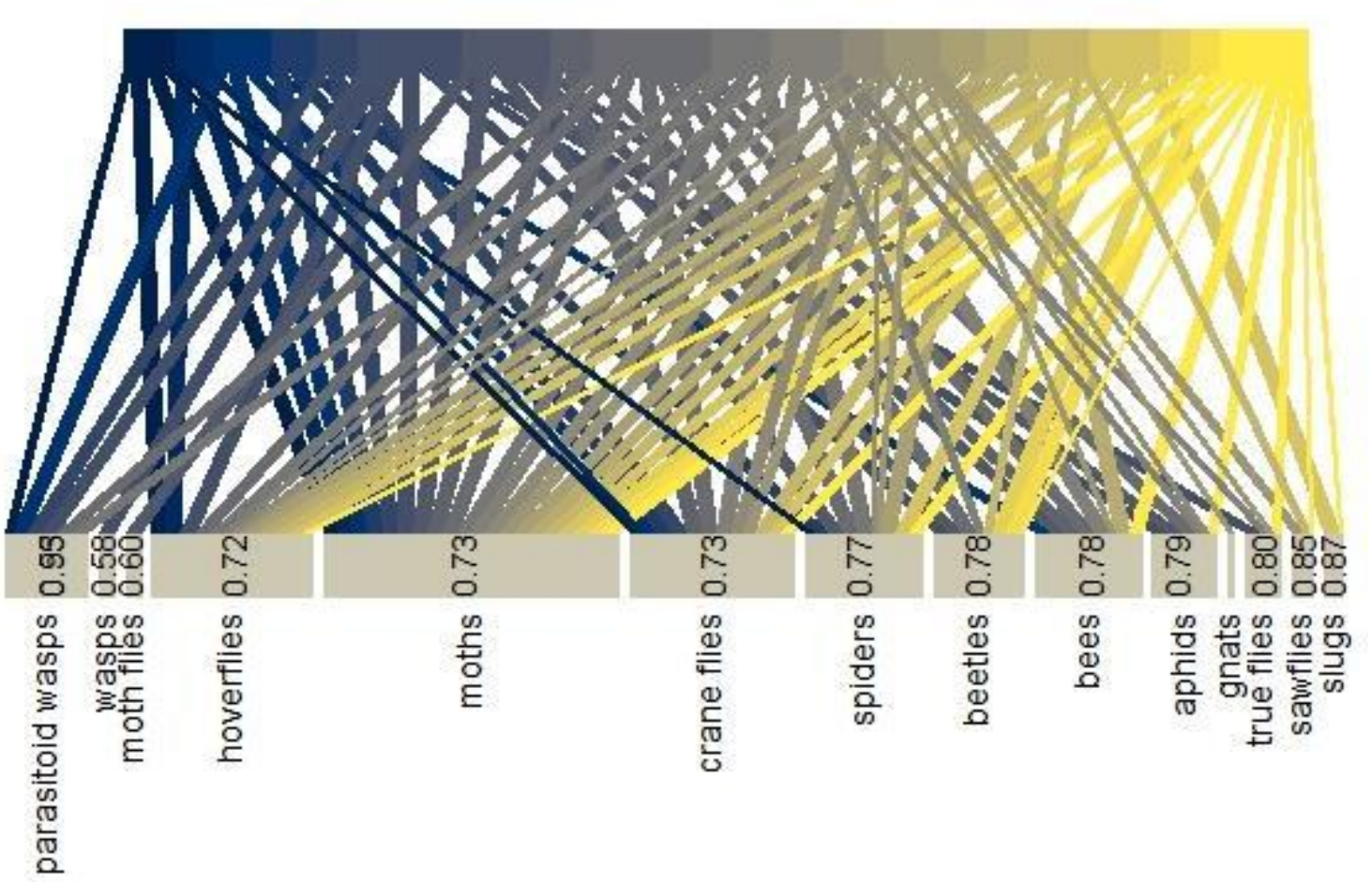


Figure 4.6. The invertebrate diet of nestlings, at the genus level, with respect to the detour score of their mother (N = 34 females). Detour scores of the females are on the upper bar, from low (blue) to high (yellow). A high detour score indicates high inhibitory control. See Figure S4.2b for the distribution of detour scores. The genera are grouped by common name and some groups contain genera from different taxonomic families. Lines link the detour score of mother to her nestlings that consumed at least one genera from that group. The width of the lines represents the proportion of birds from each detour score whose nestlings consumed at least one genera in that group. The width of the lower bars is proportional to the sum of the interactions involving that group. So groups that were involved in more interactions (ie. were present in the diet of more nests) have a wider bar. The mean detour score of all the females whose nests consumed at least one genus in the dietary group is shown on the lower bars.

Table 4.3. GLMM model summaries for the effect of detour score and richness on provisioning rate (model 3.1) and nestling mass (model 4.1), and the manyglm model summaries for the effect of provisioning rate (model 3.2) and nestling mass on nestling dietary composition (model 4.2). The richness models show the full average of all the top models within two AICc of the best model. The relative importance (averaged weight: sum of Akaike weights) for each parameter is shown. The reference level of categorical variables is next to it in brackets. Variables that were not in the top set of models and therefore did not appear in the model average are represented by dashes (-). SE is the standard error and LRT is the likelihood ratio test.

Model	Response variable	Explanatory variable	Estimate	SE	95% confidence interval	Averaged weight	P value
3.1	Provisioning rate	Intercept	3.72	0.31	3.11; 4.33		**<0.001**
(N = 41)		Detour score	-0.54	0.24	-1.01; -0.07	1.0	**0.028**
		Total nest richness	-0.04	0.02	-0.08; 0.0	1.0	**0.022**
		Brood size	0.02	0.04	-0.06; 0.10	0.23	0.718
		Sex	-	-	-	-	-
		Year (2017)	0.04	0.12	-0.20; 0.28	0.23	0.716
4.1	Nestling mass	Intercept	0.40	2.32	-4.15; 4.95		0.87
(N = 27)		Male detour score	-	-	-	-	-
		Female detour score	0.32	0.77	-1.19; 1.83	0.27	0.68
		Total nest richness	-	-	-	-	-
		Brood size	-0.04	0.14	-0.31; 0.23	0.21	0.74
		Lay date	0.18	0.03	0.12; 0.24	1.0	**<0.001**
		Year (2017)	-	-	-	-	-
Model	**Response variable**	**Explanatory variable**	**LRT**	**P value**			
3.2	Nestling dietary composition	Year	173.3	**0.001**			
(N = 36)		Sample N*	169.4	**0.001**			
		Provisioning rate**	129.0	0.212			
4.2	Nestling dietary composition	Year	245.3	**0.001**			
(N = 36)		Sample N*	228.4	**0.001**			
		Nestling mass	118.4	0.718			

Note: *The number of faecal samples obtained per nest. **Provisioning rate was controlled for brood size by calculating rate divided by the number of chicks in the nest.

4.5 Discussion

Little is known about the role of inhibitory control on foraging behaviour and diet in the wild. Here we investigated how performance on a detour task at the nest box, as a measure of inhibitory control, is associated with the diet of adults and their dependent offspring. We found that inhibitory control was correlated with adult dietary composition of genera, but only in males. In contrast, female, but not male, inhibitory control was correlated with the dietary composition of her offspring (note that nestling diet consists of food fed by both parents). Parents with high inhibitory control provisioned their nest less frequently, and nests of parents with a low provisioning rate had a higher total richness, yet there was no direct association between parental inhibitory control and nestling dietary richness (see Figure S4.5). The significance of these results for the understanding of cognition and parental care is discussed below. Our results lay important groundwork for evaluating how at least one measure of inhibitory control may be related to parental and nestling diet in the context of prey features, nutritional content, reproductive investment and food availability.

4.5.1 Effects of inhibitory control on the diet of adults and nestlings

Our results show that inhibitory control of adults is associated with the composition of invertebrates they consumed, in males only at the genus level and in both sexes at the family level. Spittlebugs, true flies, shield bugs and gnats were consumed mostly by males with poor inhibitory control, and lacewings, sawflies, bees and butterflies were consumed mostly by males with high inhibitory control, and this was also the case for both sexes at the family level. While we can only speculate as to why these taxa were more likely to be present in the diet of birds with high inhibitory control, we suggest that the visual and palatable features of prey may influence how strongly birds respond negatively or positively to confronting or consuming them, and therefore the degree to which impulses (either to avoid or consume) must be inhibited. In the case of visual features, conspicuous and

brightly-coloured insects consumed by great tits, including bees, some butterflies (though we note some butterflies are cryptic), ladybirds and butterfly caterpillars, suggests males consumed these prey items because they inhibited startle responses to conspicuous warning signals on otherwise palatable insects. Such signals include eyespots (Kodandaramaiah, 2011) and the classic high-contrast yellow and black patterning (Plowright and Owen, 1980). In support of the interpretation that inhibitory control functions to overcome prepotent responses to visual signals, males with poor inhibitory control were more likely to consume genera that do not have warning colouration (e.g. spittlebugs and shield bugs).

Another possible explanation for our result is that inhibitory control may be linked with the palatability of prey items in the diet. We predicted that animals with poor inhibitory control might be less efficient at avoiding unpalatable foods and our results show some support for this. More parasitoid wasp genera, many of which may possess a venomous sting (Moreau and Asgari, 2015), were present in males with low inhibitory control than high, and at least one genus we identified that was consumed by males with low inhibitory control were *Phratora* beetles which produce defensive secretions to deter predators (Denno, Larsson and Olmstead, 1990). Nevertheless, our dietary analysis lacks the ability to differentiate between life-stages which can impact on the degree of palatability or toxicity (Arenas, Walter and Stevens, 2015; Medina, Wallenius and Head, 2020) and conspicuousness (e.g. caterpillar vs butterfly). For instance, some butterfly species and their caterpillars sequester chemicals from their host plants and are toxic to predators (Trigo *et al.*, 1996; Nishida, 2002) whereas others do not. Analysing the diet data at the species level would allow investigation of an association between inhibitory control and the palatability of prey species. The role of inhibitory control on startle responses and avoidance behaviour would be an intriguing further study to confirm these suggested mechanisms.

We predicted that inhibitory control of parents would be associated with the prey they provision their nestlings, due to variation in their abilities to inhibit responses to certain foods and instead choose others. In support of our prediction, our results showed that inhibitory control of females was associated with the dietary

composition of their nestlings at the genus and family level, but we did not find the same for males. We found no link between parental inhibitory control and nestling richness, either because parents provision specific prey to their nestlings for development (Ramsay and Houston, 2003; Pagani-Nunez *et al.,* 2011), regardless of their inhibitory control ability, or because richness is a combination of food fed to nestlings by both parents. There are two possible mechanisms for the link between female inhibitory control and nestling dietary composition. First, the association may occur during the searching stage. It is possible that females with poor inhibitory control are less selective in the prey they provision their young, for instance by provisioning nestlings with potentially harmful prey. Nestlings of females with low inhibitory control were more likely to have parasitoid wasps in their diet, a taxonomic group where many species possess a venomous sting (Moreau and Asgari, 2015). Despite our result that female inhibitory control correlated with nestling diet, we do not know for certain which prey were fed by the female, and which by the male, so the link between female inhibitory control and diet might be spurious or could be indirect. For instance, instead of being directly more selective when choosing prey, high inhibitory control females could be using other cues to decide what to provision the nestlings, and be more responsive to these cues than females with low inhibitory control. Cues such as begging calls or drawing on knowledge of what they previously provisioned nestlings could be used to decide what to search for next. Additionally, there is evidence that parents adjust their care effort according to that of their partner (Barta *et al.*, 2002; Harrison *et al.*, 2009) so females with high inhibitory control could be better at responding to what the males are feeding the nestlings than females with poor inhibitory control. Though difficult to collect in high resolution, video footage of the prey brought to the nest by each parent would aid in resolving the question of whether female inhibitory control is directly or indirectly related to nestling diet.

Second, the association between inhibitory control and nestling diet may occur if females trade-off self-feeding with finding food for nestlings (Weimerskirch *et al.*, 1997; Wischnewski *et al.*, 2019). Our results showed that female inhibitory control was associated with their nestlings' diet but not their own diet, and male inhibitory

control was associated with their own diet but not nestling diet. This may be because females have higher brood investment than males (Kokko and Jennions, 2012). It is possible that because of their increased investment in the brood, females cannot afford to be discriminatory (at the level of the genus) when finding food for themselves. Females may apply their inhibitory control when finding food for their nestlings but may not do so when self-feeding, perhaps because of constraints on resource acquisition. To test if females are prioritising provisioning nestlings over self-feeding, we would need information on quality and palatability of the dietary items discovered, and could then examine if high inhibitory control females provisioned high quality, profitable food to their young and consumed poor quality prey themselves. Males on the other hand may invest less in the brood in the early stages (Kokko and Jennions, 2012), so our results may reflect that, for males, inhibitory control is more important when self-feeding than when provisioning nestlings at this age. Males do provision the nestlings but our results suggest they are not being discriminatory over what prey they bring to the nest (assuming that the prey they bring is readily available) and are instead using their energy reserves to apply inhibitory control when self-feeding. Males may invest more in other parental care behaviours such as nest defence (Regelmann and Curio, 1986).

Our results suggest that the potential trade-off between greater cognitive investment in self-feeding or provisioning nestlings (assuming nestling diet reflects female inhibitory control) is only revealed at the genus level, since despite finding no association between female inhibitory control and adult diet at genus level, we did find an association at the family level. We note this association at the family level was not robust to the removal of singletons so is likely driven by rare taxa. That the trade-off is only revealed at the genus level indicates the importance of obtaining detailed dietary measures using molecular approaches rather than categorising the diet into imprecise, generalised groups such as seeds, fruit or caterpillars (MacLean *et al.*, 2014).

There may be two reasons why we have found an effect of female inhibitory control on nestling diet at the family level but not at the genus level. First, the birds are

likely to be choosing prey items based on morphology and prey in the same genera are more likely to be similar in their morphology than prey from across the family. Second, there are fewer OTUs in family level analyses compared to those at the genus level, which might be insufficient to give significant differences between behavioural cohorts. While we cannot account for changes in parental care over the breeding season (Curio, 1987) or the small sample size for females, we nevertheless demonstrate, for the first time, a link between cognition and dietary composition in a natural context. Our study adds to the small body of work on how cognitive abilities may influence sex differences in parental care (Wetzel, 2017).

4.5.2 Nutrient content

Given that our results showed associations between inhibitory control and diet, we explored whether there were any consequences of this for the macronutrient content consumed by adults or nestlings. We did not find a correlation between inhibitory control and the carbohydrate, lipid or protein content in the taxonomic families eaten by males or females, or provisioned to young. There may be a number of reasons for this. First, it is optimal for animals to balance their intake of all three macronutrients (Raubenheimer and Simpson, 1997; Simpson *et al.*, 2004), and animals can compensate, within days, for the nutrients they are lacking (Raubenheimer and Jones, 2006). A principle component analysis, or similar, could be used to investigate whether birds with high inhibitory control were better at balancing all three macronutrients in their diet, or the nestling diet, which we did not have sufficient power to do here. Second, the proportion of prey items in the diet is likely to have an effect on the macronutrient content that the birds consume so our presence/absence data may not have been sufficient to see a relationship. Third, we may have simply captured variation in how individuals forage which leads to them being more likely to capture certain types of prey depending on their inhibitory control. Alternatively, if there is a functional difference for the association between inhibitory control and diet of adults and nestlings, perhaps our measures of nutrient content were too crude to detect correlations. Finally, we may have

needed to consider micronutrient content of prey, such as amino acids, which play an important role in cognitive development (Bhatnagar and Taneja, 2001; Swaminathan, Edward and Kurpad, 2013) and to consider the faecal sampling period, as taurine in particular is known to influence spatial learning in nestlings at a critical developmental window (Arnold *et al.*, 2007). Empirical studies are needed to investigate if inhibitory control is associated with an increased ability to balance nutrient intake in animals, through the ability to inhibit choosing certain prey over others, or if inhibitory control is linked to diet composition through the micronutrient content of prey.

4.5.3 Provisioning rate and nestling mass

Parents with poor inhibitory control provisioned their nestlings at a higher rate, suggesting that they are less selective in their prey choices and are only provisioning what they directly come across, leading to shorter searching times and a higher number of visits to the nest. In contrast, high inhibitory control parents are more selective, are spending more time searching for their preferred prey, and are not returning to the nest until they find it, leading to low provisioning rates. Being less selective could mean that low inhibitory control birds are provisioning really abundant prey that they find close to the nest. There is evidence that tit parents adjust their selectivity in the size and type of prey provisioned to offspring (Grieco, 2001; García-Navas and Sanz, 2011; Wiebe and Slagsvold, 2015) and individual variation in this selective ability may be explained by similar variation in inhibitory control, a hypothesis that can be tested in the future. Our study joins the one other study we know of that has looked at parent cognition related to provisioning rate, which found that latency to solve a task was negatively correlated to provisioning rate (Wetzel, 2017). Our study found that the nests of parents with a higher provisioning rate, consumed a lower number of genera. This may suggest that parents with high provisioning rate do not travel very far from the nest and may not come across a large diversity of prey, leading to lower dietary richness in nestlings, and the converse for low provisioning rate parents (assuming that diversity is

correlated with distance travelled). Alternatively, it could be the case that if there is a very abundant prey type, the great tits capitalise on it so only a single/few taxa are provisioned to nestlings and provisioning rate is high because it takes a short amount of time to gather. We note that provisioning rate was measured on day 16 and nestling diet was measured on day 8 because we did not have sufficient data for provisioning rate on day 8. If individuals were not consistent in provisioning rate from day 8 to day 16 then our correlation between dietary richness and provisioning rate may not be accurate. Despite the correlations we found with provisioning rate, we did not find a direct link between parental inhibitory control and nestling dietary richness (Figure S4.5). This may be an artefact of two weak relationships, indeed the effect sizes were not very large and the confidence intervals for the correlation between richness and provisioning rate overlapped zero (see Table 4.3). Alternatively, inhibitory control and richness may be independent traits that are not correlated with each other, or there may be no causal link between inhibitory control and richness and therefore no causal link with provisioning rate.

Whilst we found an association between provisioning rate and inhibitory control and nestling richness, female inhibitory control was not related to mean mass of her nestlings, and nestlings with different diets did not vary in mass. Our study is the first to investigate a link between inhibitory control and nestling condition on day 8-9 and our result draws comparison with two other cognitive studies that found that nestling mass did not differ between great tit pairs that solved and did not solve a task (Cole *et al.*, 2012; Cauchard *et al.*, 2017). A number of reasons may explain this result. First, day 8 may be too early to detect a difference in mass between nests of parents with high and low inhibitory control. Nestling weight at fledging (around 17-20 days) is a strong indicator of fledging success (Naef-Daenzer, Widmer and Nuber, 2001) so differences in diet may translate into differences in weight at this later stage. Second, an effect of inhibitory control on nestling diet could have fitness consequences for nestlings that are unrelated to mass, for instance, micronutrients that are critical for brain development or development of other functions (Bhatnagar and Taneja, 2001; Swaminathan, Edward and Kurpad, 2013). Third,

perhaps investigating the relative abundance of taxa in the diet, rather than presence/absence would provide some link with nestling mass. For instance, a study on blue tits showed that nestling mass was positively associated with the proportion of noctuid caterpillars relative to tortricids in the diet (García-Navas and Sanz, 2011), though here the size of these different prey groups could be the most important factor determining nestling mass and would be a possible avenue to pursue in our study. Finally, variation in diet linked to inhibitory control may benefit other aspects of reproductive success such as clutch size or fledging success. In the studies mentioned above, nests with at least one solving parent fledged more young than nests with non-solving parents (Cauchard *et al.*, 2017) and solvers produced larger clutches, which the authors suggest was due to solvers being more efficient at exploiting their environment (Cole *et al.*, 2012).

4.5.4 Conclusion

Our study has investigated how a cognitive mechanism, inhibitory control, is associated with the diet in the wild of adults and nestlings. We provide a more fine-scale approach than previous studies by using molecular approaches to determine food choice, which allows a more detailed understanding of potential drivers of individual diet variation, though we note that the direction of causation between inhibitory control and diet is unknown. Our study has investigated how parent cognition is associated with the dietary composition of their young and our results show some suggestive correlational relationships between inhibitory control, diet and provisioning rate that can be empirically tested in future research. Our results suggest a role for inhibitory control in foraging, and for driving sex differences in parental care, and raise the possibility that this may be explained by potential trade-offs between self-feeding and provisioning nestlings.

4.6 Appendix C – Supplementary material for Chapter 4

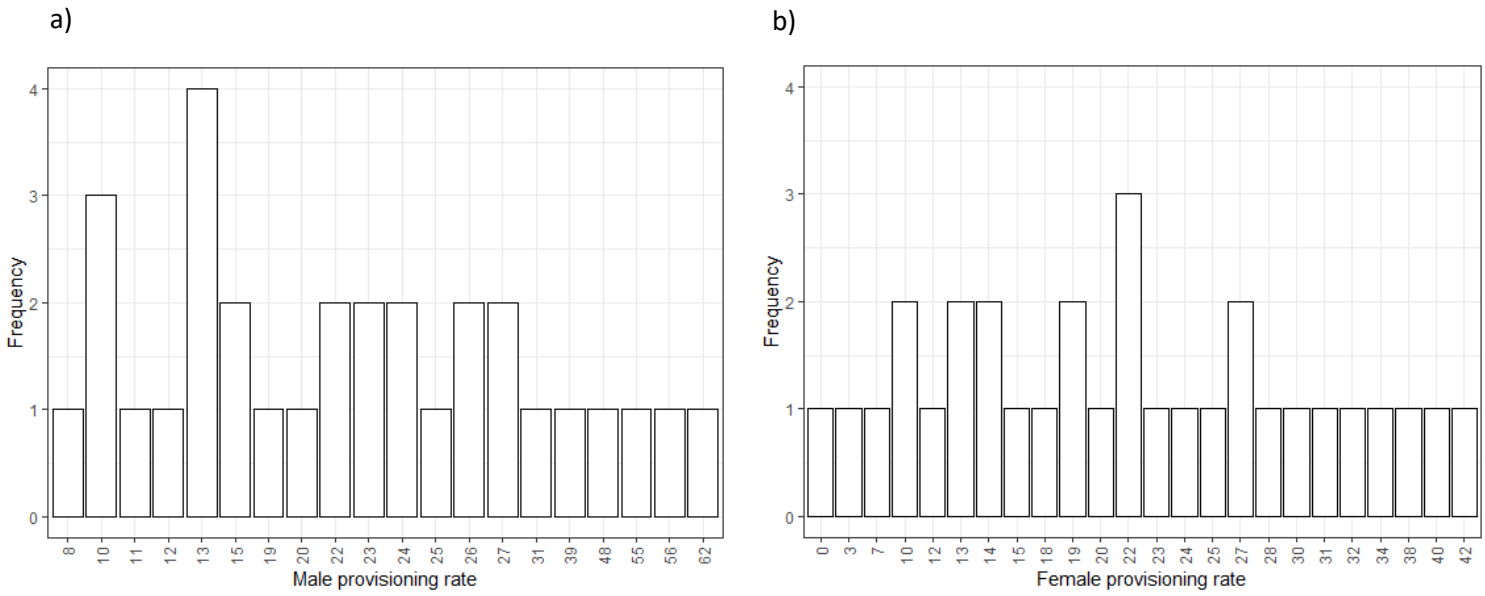


Figure S4.1. Frequency distribution of provisioning rates (number of items in 2hrs) for a) males (N = 31) and b) females (N = 31). Mean±SE: Male: 23.9±2.57; Female: 21.1±1.88.

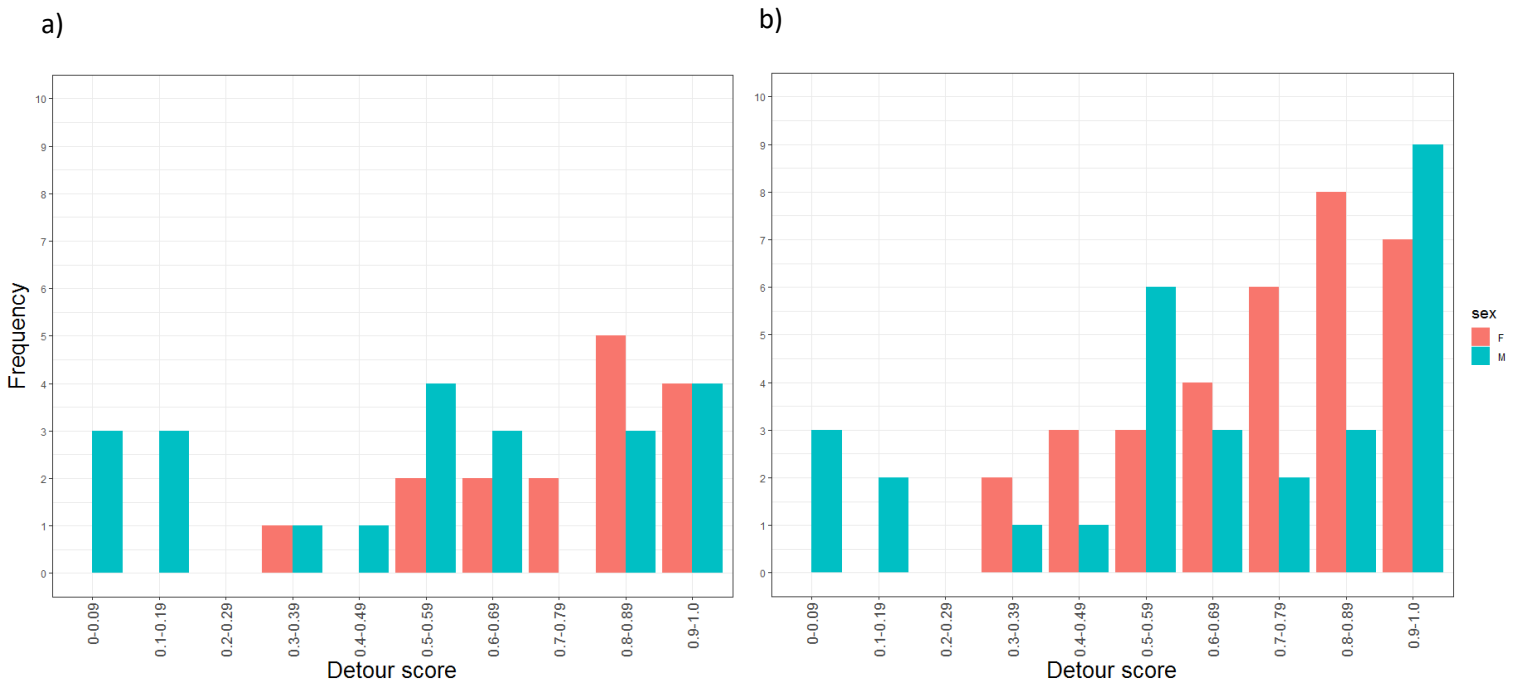


Figure S4.2. Frequency distribution of detour scores for males and females, for which we have a) own diet data (Male: N = 22, Female: N = 16), and b) for which we have nestling data (Male: N = 30, Female: N = 33). Mean±SE: male detour, adult diet: 0.52±0.07; female detour, adult diet: 0.75±0.04; male detour, nest diet: 0.62±0.06; female detour, nest diet: 0.73±0.04. One outlier nest was removed and following this removal, male and female detour scores were not correlated.

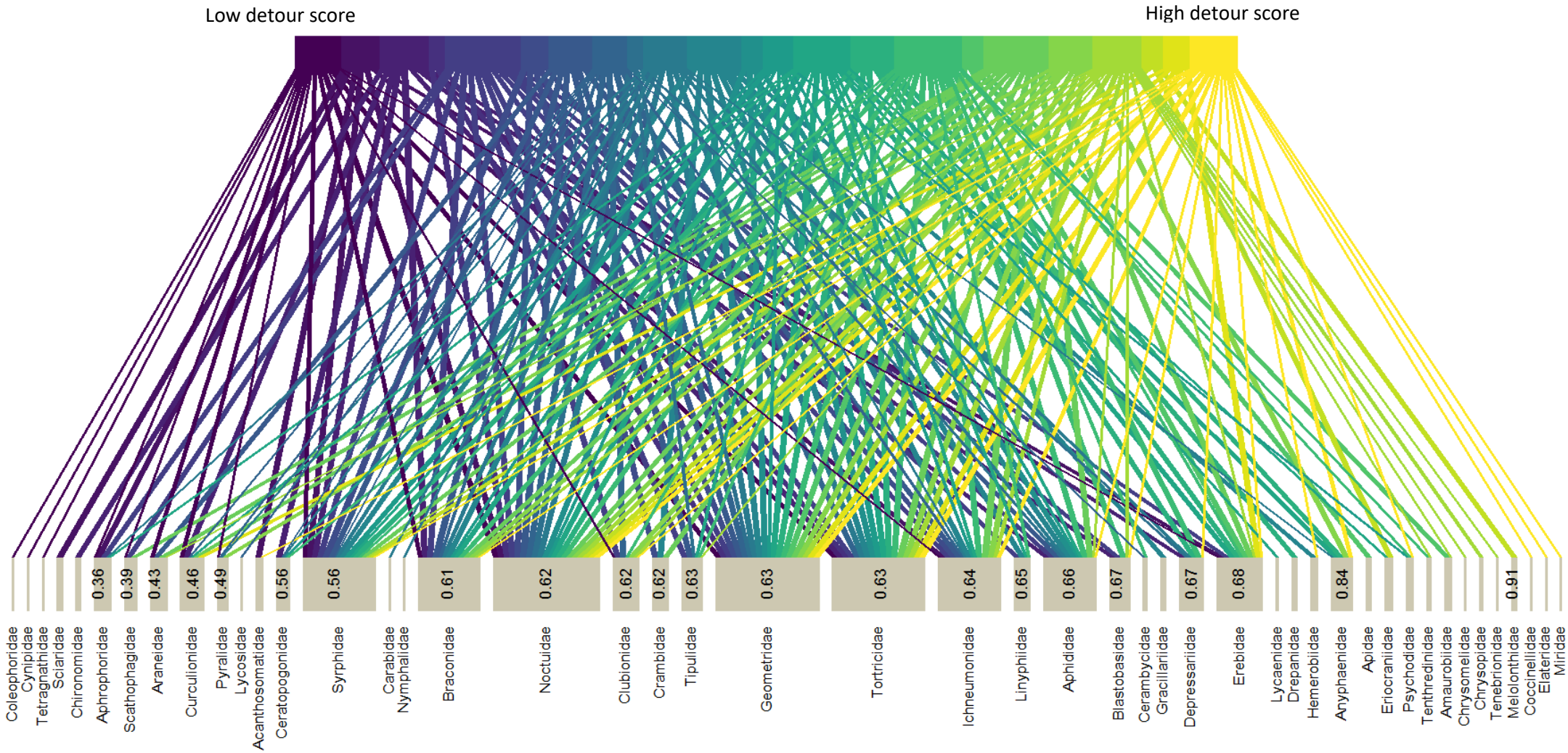


Figure S4.3. The invertebrate diet of adults of both sexes at the level of the family, with respect to their detour score. N = 38 from 23 unique scores and there are nine scores which are represented by more than one bird. The birds that consumed at least one genus from each family are linked by interacting lines. The width of the lines represents the proportion of birds from each detour score that consumed a prey item from that family. The width of the lower bars is proportional to the sum of the interactions involving that

family. So families that were involved in more interactions (ie. were present in the diet of more birds) have a wider bar. The mean detour score of all the birds that consumed a prey item from that family is shown on each family bar.

Table S4.1. Spearman's Rank correlation results between adult inhibitory control and diet of adults and nestlings. Rho (ρ) is the Spearman's rank correlation coefficient indicating the strength of the correlation between the mean detour score of the birds that consumed each family and the macronutrient percentage (carbohydrate, protein or lipid) for each family. Mean detour scores were calculated for males and females separately. If nutrient content for the family was not available, data on superfamily or order was used (N: family = 19, superfamily = 4, order = 34).

Diet Data	Mean detour scores	Macronutrient	S statistic	Rho (ρ)	P value
Adults	Females (N = 16)	Carbohydrate	1233.1	0.30	0.17
		Protein	1993.5	-0.13	0.58
		Lipid	1643.9	0.07	0.75
	Males (N = 22)	Carbohydrate	2749.9	0.06	0.77
		Protein	2246.8	0.23	0.25
		Lipid	3127.2	-0.07	0.74
Nestlings	Females (N = 34)	Carbohydrate	2208.0	0.04	0.85
		Protein	1786.0	0.22	0.29
		Lipid	2469.3	-0.07	0.73
	Males (N = 31)	Carbohydrate	1492.6	0.16	0.48
		Protein	1646.3	0.07	0.76
		Lipid	2074.9	-0.17	0.45

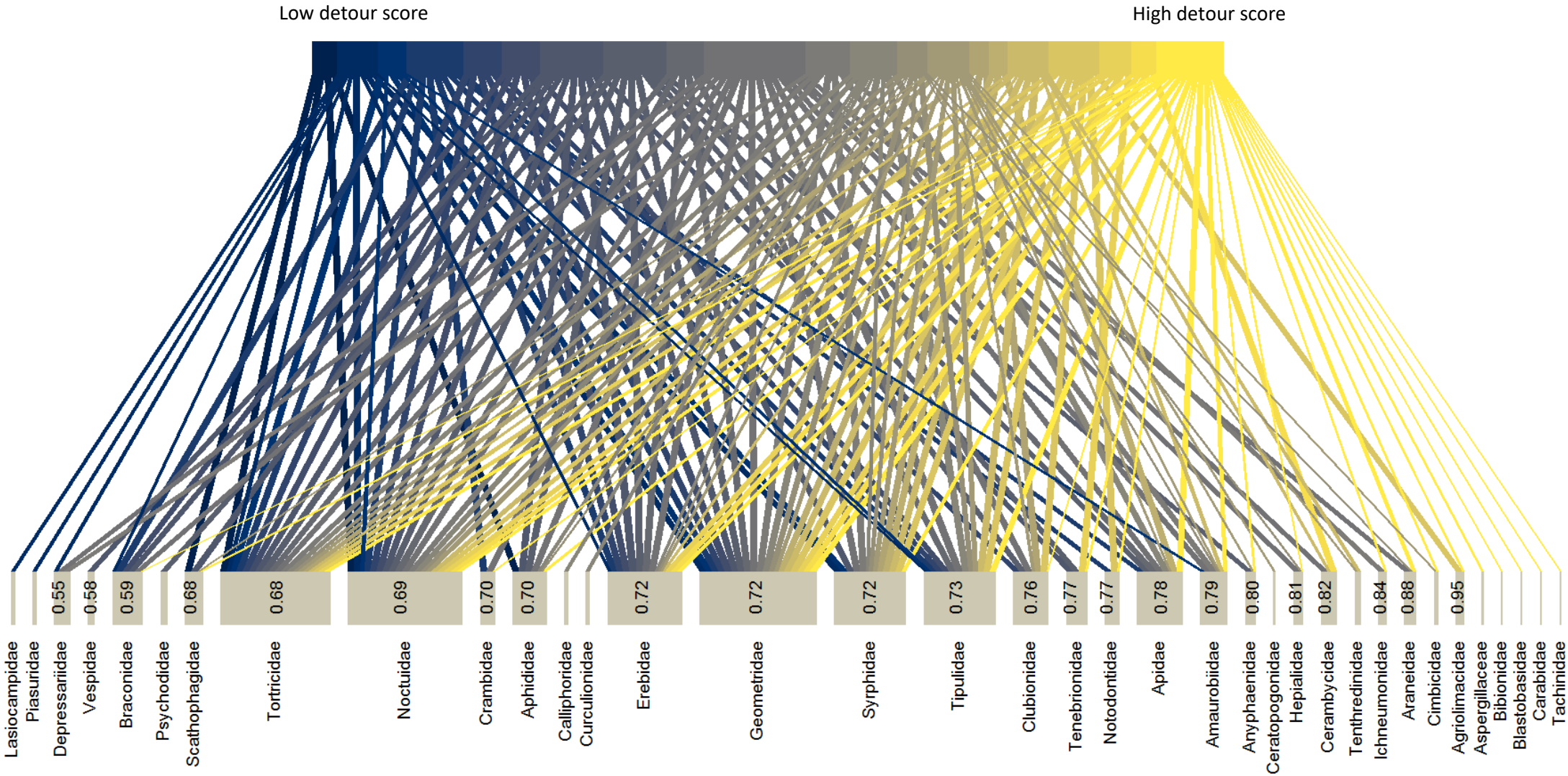


Figure S4.4. Nestling diet at the family level with respect to female parent detour score. N = 34 females. See Figure 4.3 for details of plot creation.

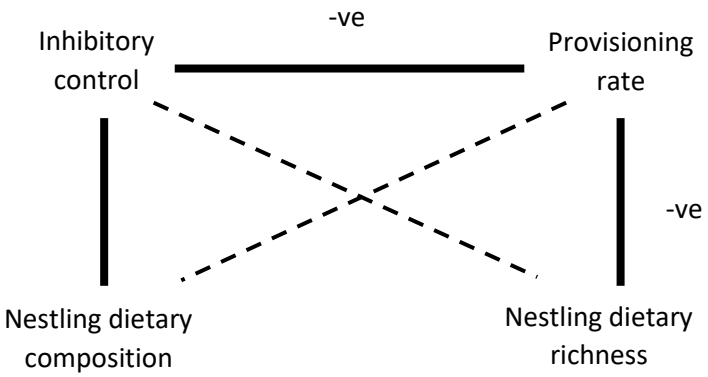


Figure S4.5. Illustration of the relationship between parental inhibitory control, provisioning rate, nestling dietary composition (identity of genera) and dietary richness (number of genera). Thick black lines indicate significant relationships between the variables and dotted lines indicate non-significant relationships. The relationships between inhibitory control and provisioning rate, and between provisioning rate and richness were negative. The relationship between inhibitory control and composition cannot be given a direction since composition is not a numerical value.

4.7 Bibliography

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Chapter 5

Innovative problem solving, inhibitory control and exploration behaviour are associated with the winter diet of great tits

Great tits, Co. Cork

James O'Neill

Author contributions: Jenny R. Coomes and John L. Quinn designed the study, JRC and Gabrielle L. Davidson collected the field and aviary data. JRC analysed the data with help from Camille A. Troisi. JRC wrote the study with help from JLQ and Michael S. Reichert.

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5.1 Abstract

Cognition and personality are expected to contribute to individual diet variation, both because traits associated with these concepts differ consistently among individuals and because they strongly influence foraging behaviour, yet studies of the role of these factors on dietary variation are lacking. We used DNA metabarcoding to establish the winter diet of great tits and investigated whether individuals of different cognitive abilities and personalities showed differences in diet. We used three measures of cognition; innovative problem-solving, inhibitory control and discrimination learning, and exploration behaviour, a behavioural trait that is closely associated with personality. We looked at both the composition (identity) and richness (number) of invertebrate and plant genera present in the winter diet. Our results showed that problem solving, inhibitory control and exploration behaviour were associated with dietary composition. More non-solvers than solvers consumed oak, possibly because non-solvers are more likely to be dominant and have access to the best territories of oak woodland. Additionally, more non-solvers than solvers consumed peanuts, a monopolisable resource, suggesting that because non-solvers are more competitive, they exclude conspecifics from feeding, who then have to find alternative resources and are more likely to become solvers. Both of these findings are consistent with the 'necessity drives innovation' hypothesis, which predicts that individuals that are poor competitors for food should be more innovative. Inhibitory control was associated with plant dietary composition. Plants with soft seeds (e.g. oats and ash) were eaten by more birds with high inhibitory control and plants with tough seeds (e.g. walnut) were consumed more by birds with low inhibitory control. We speculate that this could be linked to the ability of individuals with high inhibitory control to avoid tough seeds that are potentially unprofitable, and preferentially select soft seeds, which may have implications for net rates of energy gain. Exploration behaviour was associated with invertebrate dietary composition but not richness, which may be explained by fast explorers traveling further than slow explorers, so they come across different invertebrate prey, but because fast birds explore their environment less thoroughly, they do not consume a greater number of invertebrate genera, compared to slow explorers. There was no association between discrimination learning and dietary composition and none of the behavioural traits

we measured were associated with dietary richness of plants or invertebrates. Our results suggest that many of the kinds of cognitive and behavioural assays that are often hypothesised to influence ecology are linked to some but not all aspects of the diet. Whether these effects are general and have implications for nutrition, foraging success and fitness remain to be determined.

5.2 Introduction

To survive, animals must be successful foragers and a number of factors can influence foraging success. Cognition and personality are two behavioural concepts that are important for foraging (Janmaat, Byrne and Zuberbühler, 2006; Raine and Chittka, 2008; Kurvers *et al.*, 2010; Rosati, 2017). Individual differences in cognition and personality are likely to give rise to individual differences in diet through variation in the resources available to individuals as a result of their cognitive abilities or behavioural tendencies (Dall *et al.*, 2012; Rosati, 2017). Individual variation in diet has consequences for how individuals cope with changes in resource abundance (Terraube *et al.*, 2011). For instance, dietary generalists are not as likely to be affected by changes in resource abundance as specialist species (Terraube *et al.*, 2011). Despite their importance for foraging, there is a lack of literature examining links between the diet and individual differences in cognition and personality.

Individuals differ in how they process and use information from their environment and researchers have long been interested in this individual variation in cognition (Thornton and Lukas, 2012; Boogert *et al.*, 2018). Foraging requires individuals to make decisions about when, where and on what to feed, and a variety of cognitive factors have been studied in the context of foraging. First, spatial learning and memory is important for animals when remembering the location of profitable food patches (Pravosudov and Clayton, 2002; Winter and Stich, 2005; Janmaat, Byrne and Zuberbühler, 2006). For example, bumble-bee colonies that learnt locations the slowest collected 40% less nectar than those that learnt the fastest (Raine and Chittka, 2008). Additionally, classic examples of foraging associated with memory come from species that cache, where individuals can remember not only the location but also the contents of their hidden food (Kamil and Balda, 1985; Clayton and Dickinson, 1999). Second, associative learning of a novel stimulus in the presence of food has been demonstrated in many taxa (Sison and Gerlai, 2010; Bonaparte, Riffle-Yokoi and Burley, 2011; Boogert *et al.*, 2011), and is likely to be ecologically important as it can allow animals to anticipate future events (Lind, 2018) and discriminate among different classes of cues (Howery *et al.*, 2000). Third, tool use is an example of a composite cognitive trait that is likely underpinned by a variety of

cognitive mechanisms and allows access to food that would otherwise not be available (Goodall, 1964; Boesch and Boesch, 1983; Bluff *et al.*, 2010).

Compared to the wealth of studies on cognitive factors linked to foraging success in general, relatively little work has been done on how cognitive factors are linked to diet (i.e. the identity, composition and variety of different foods eaten by an individual). First, inhibitory control is required by individuals to stop performing a counter-productive, dominant behaviour in favour of a behaviour that is more beneficial or appropriate (Diamond, 2013) and is important for making optimal choices among different foraging options (Stevens *et al.*, 2005; Stevens, Hallinan and Hauser, 2005; Rosati, 2017). There are a number of different facets of inhibitory control, for example, delayed gratification where an immediate reward is disregarded in favour of a future reward (Dufour *et al.*, 2012; Miller *et al.*, 2019), or motor inhibition that requires an individual to inhibit a physical response to a food reward that is only accessible by diverting around a barrier (Bray, Maclean and Hare, 2014; Kabadayi *et al.*, 2017). Few studies have linked any facet of inhibitory control with the diet and results are mixed (Stevens *et al.*, 2005; MacLean *et al.*, 2014; van Horik *et al.*, 2018). For example, one study showed that primate species with increased inhibitory control had a greater dietary breadth, but the diet information was imprecise as the authors used broad food categories from the literature known to be consumed by each species (MacLean *et al.*, 2014). Another comparative study found that common marmosets waited longer for a larger reward than cotton-top tamarins, a result that is attributable to the feeding ecology of the species (Stevens, Hallinan and Hauser, 2005). Neither of these interspecific studies looked at individual differences in diet. A study that did look within a single species found that common pheasants with high inhibitory control had a narrower dietary breadth, but diet preference rather than a measure of the natural diet was used, as the pheasants were presented with a choice of items and the number chosen was recorded (van Horik *et al.*, 2018). If high inhibitory control prevents individuals from selecting certain foods, they may also have a different dietary composition, as well as showing variation in dietary diversity, compared to individuals with poor inhibitory control.

Second, innovation is thought to be necessary for exploiting new food sources (Fisher and Hinde, 1949; Ennion, 1962; Kawai, 1965; Weinrich, Schilling and Belt, 1992) and innovators of many species have been characterised as consuming a wider diversity of prey items than non-innovators (Navarrete *et al.*, 2016). Innovation is a composite trait, underpinned by a variety of cognitive functions, including problem-solving, which is most commonly measured by animals having to retrieve food from extractive 'puzzle' devices (Webster and Lefebvre, 2001; Griffin and Guez, 2014). In addition to these cognitive functions, innovative individuals may have greater motor diversity (Manrique, Völter and Call, 2013; Griffin, Diquelou and Perea, 2014), and competitive ability (Laland and Reader, 1999b). Animals that are more competitive can easily monopolise resources so less competitive individuals must find new ways to extract food, or apply known foraging techniques to new food sources (Cole and Quinn, 2012). Innovators are therefore predicted to be the less competitive animals who innovate through necessity, as proposed by the 'necessity drives innovation' hypothesis (Reader and Laland, 2001; Morand-Ferron *et al.*, 2011 but see also Boogert *et al.*, 2008).

Consistent differences in behaviour across time and contexts exist in all taxa (Sih *et al.*, 2004; Groothuis and Carere, 2005) and there are a number of ways that this so-called 'personality' may lead to diet differences between individuals. Furthermore, if temporally consistent, diet choice itself can be part of personality. First, animals with different personalities can occupy distinct habitat types that hold different resources (Boon, Réale and Boutin, 2008; Griffen, Toscano and Gatto, 2012). Second, personality can lead to individuals associating more or less strongly with conspecifics, thus increasing or limiting foraging opportunities (Michelena *et al.*, 2009; González-Bernal, Brown and Shine, 2014). Additionally, dietary differences between personality types may occur if they have different roles in foraging groups (producer-scrounger systems: Kurvers *et al.*, 2010, scramble competition: David, Cézilly and Giraldeau, 2011, dominance: Hansen and Closs, 2005). Third, risk-taking behaviour when in the presence of a predator or when approaching unknown prey is a personality trait (van Oers *et al.*, 2004; Réale *et al.*, 2007), and there is evidence that bold, risk-prone birds are more willing to choose aposematic prey (Exnerová *et al.*, 2010). Finally, personality has been shown to influence metabolic rate, meaning

individuals may require different food resources to sustain body growth and maintenance (Careau *et al.*, 2008). Exploration behaviour is a behavioural trait closely associated with the 'fast-slow exploration' personality axis (Groothuis and Carere, 2005) and is especially likely to be linked to dietary differences. For instance, more exploratory individuals have wider home ranges (Schirmer *et al.*, 2019) and travel further to find food (van Overveld and Matthysen, 2010), so they may be more likely to come across a greater diversity of prey items than less exploratory individuals. Additionally, if there is variation in how individuals explore their environment, there will be variation in how much time individuals spend searching in a specific location and variation in the type of prey encountered (Troxell-Smith and Mella, 2017). Basic descriptions linking diet to cognitive and personality traits are scarce in the literature, particularly in the non-breeding season when foraging is especially challenging. Investigating the association between individual variation in diet, cognition and personality allows us to understand more about how individual variation in behavioural traits contributes to the use of resources and success in different environments.

One of the major challenges in examining the diet of animals in the natural environment is that, in most species, food is consumed out of sight. In the breeding season, this can be partially addressed by using cameras at fixed locations (e.g. nest boxes) but this is only likely to reveal the prey fed to offspring and provide no insight into the diet of adults. Moreover, assessing diet in the non-breeding season may be even more challenging if animals travel in large groups and do not regularly come back to the same location. Current methods of diet analysis can be destructive (the animal has to be killed), difficult to implement (identification of food items requires specialist knowledge) or achieve poor taxonomic resolution (e.g. stable isotope analysis). DNA metabarcoding can overcome these challenges by using environmental samples, such as faeces, which are taken non-invasively. DNA metabarcoding taxonomically identifies multiple items in an individual's diet by high-throughput sequencing (Shokralla *et al.*, 2012; Taberlet *et al.*, 2012; Yu *et al.*, 2012), often down to the species level (Taberlet *et al.*, 2012). DNA metabarcoding is a useful technique for achieving high resolution diet data, making it ideal for answering questions on individual differences in diet.

Our aim was to investigate how exploration behaviour and three measures of cognition correlate with the composition and number of taxa in the diet. Both of these dietary metrics are important. The number of genera consumed reflects the breadth of resources used by the birds and this measure of dietary diversity can be compared with other studies that have investigated dietary breadth (Overington *et al.*, 2011; Reader, Hager and Laland, 2011). Dietary composition provides a measure of the community of invertebrate prey, which is likely to reflect systematic differences in the locations and types of prey the birds are feeding on. We used great tits (*Parus major*), a common passerine in woodland habitats and a model species for studies on individual variation in cognition (Cole, Cram and Quinn, 2011; Amy, van Oers and Naguib, 2012; Morand-Ferron *et al.*, 2015) and personality (Verbeek, Drent and Wiepkema, 1994; Marchetti and Drent, 2000; Dingemanse *et al.*, 2012). Great tits habituate readily to captivity, allowing personality traits and cognitive performance to be measured easily. They are assumed to be generalist foragers but recent work has found evidence for specialisation at the individual level (Pagani-Núñez *et al.*, 2016) and within breeding pairs (Pagani-Núñez, Valls and Senar, 2015). Environmental factors such as season influence the diet (Pagani-Núñez *et al.*, 2016, Chapter 3), and are important to consider when investigating the mechanisms of dietary differences. Many studies have looked at the diet of great tits in the breeding season (Betts, 1955; Naef-Daenzer and Keller, 1999; Naef-Daenzer, Naef-Daenzer and Nager, 2000) but diet in the winter is also important when there is a lower availability of invertebrate prey than in the summer, and unpredictable, sometimes harsh, weather conditions can make it challenging to find sufficient food to fulfil energy requirements. We used DNA metabarcoding to examine the diet of individual great tits in winter and asked whether dietary richness and composition were associated with exploration behaviour, discrimination learning, innovative problem-solving performance and inhibitory control.

5.3 Methods

Great tits (N = 252) were captured at 12 field sites in County Cork, Ireland and were aged and sexed according to standard protocols (O'Connor, 1985). Birds were fitted with a metal British Trust for Ornithology ring and a unique colour ring for identification. Of the 252 birds caught, 136 produced a faecal sample and 49 were taken into captivity. Innovative problem-solving, detour-reaching (inhibitory control) and exploration behaviour were measured from January to March 2018 in captivity, and discrimination learning was measured in the wild from November 2017 to March 2018.

This study was conducted under licences from the Health Products Regulatory Authority (Project licence: AE19130/P017, Individual licence to JCoomes: AE19130/I250), the National Parks and Wildlife Service (Project licences: 004/2017, 001/2018, C02/2018; Individual licence to JCoomes: 70/2017, 11/2018) and the British Trust for Ornithology (individual ringing licences for JCoomes (C6597), Sam Bayley, Ivan de la Hera Fernandez). The research project received ethical approval from the Animal Welfare Body at University College Cork, and was in accordance with the ASAB (Association for the Study of Animal Behaviour) Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

5.3.1 Diet data

We collected faecal samples (N = 136) between November 2017 and February 2018. Prior to ringing, birds were placed individually into clean bird bags, each of which contained a coffee filter for absorption of liquid urea, and given time to defecate. Faeces were removed from the bag via a sterilised plastic rod and were placed into a 1ml tube filled with ethanol. They were stored in a -20°C freezer before being transferred to a -80°C freezer at the end of the season. The samples were transported to Cardiff University where DNA analysis took place from September 2018 to March 2019. Lab work consisted of DNA extraction, PCR to establish presence of invertebrate and plant DNA using COI and ITS2 primers respectively, PCR to add unique identifying tags to the samples and finally next-generation

sequencing. We followed a bioinformatics pipeline developed by Lorna Drake (Drake, 2020) to obtain the final diet data (presence/absence) and ran all analysis at the level of the genus. See Chapter 3 for full details of dietary analysis. In Chapter 3 peanuts (*Arachis*) and sunflower seeds (*Helianthus*) were removed from the plant analysis because these were the food types provided to the birds during trapping, and we were only interested in examining the wild diet. At least one sunflower seed and one peanut feeder were present at all field sites for the trapping period and we assumed all birds would have access to both these food types. For the analysis in the current chapter, we included these two genera because we hypothesised that cognition, and innovation in particular, might be linked to the consumption of the supplemented food. The peanuts were contained in a wire feeder so could be monopolised by a few highly competitive individuals, whereas the sunflower seeds could be taken away whole to be eaten out of view of conspecifics and were therefore less subject to competition (Hogstad, 1988; Cole and Quinn, 2012).

5.3.2 Exploration behaviour, inhibitory control and innovative problem-solving assays

After being ringed in the field, great tits were brought into the aviary at University College Cork (maximum travel time = 45 mins) where they were held for a maximum of three weeks (N = 49). The birds that participated in the aviary assays came from nine field sites (four mixed deciduous and five coniferous) and were kept in individual cages (62 x 50 x 60cm, H x W x D). When the birds were not participating in experiments, they were fed with *ad-libitum* sunflower seeds, peanuts and water with added vitamin drops (AviMix®). Mealworms (*Tenebrio molitor*) were provided three times a day and waxworms (*Galleria mellonella*) were provided as experimental rewards.

On their first full day in the aviary, birds participated in an open field 'exploration of a novel environment' assay (N = 49) in which they had two minutes to explore a novel room. This data was collected by J. Coomes and G. Davidson and full details are provided in Chapter 2. The number of 'hops' and 'flights' the birds made on on five artificial trees was counted (by observation only) and totalled to give an

'exploration score' (Verbeek, Drent and Wiepkema, 1994; Dingemanse *et al.*, 2002). Birds with the highest scores were named fast explorers and birds with the lowest scores slow explorers. For a trait to be classed as 'personality' it should be repeatable. In this study, birds were only assayed once for exploration behaviour but we have shown this trait to be repeatable in our population (O'Shea, Serrano-Davies and Quinn, 2017), as it is in a number of others (Dingemanse *et al.*, 2012), and this approach allowed us to minimise the number of 'procedures' that the birds in captivity were exposed to. Thus, we refer to exploration behaviour as a personality trait.

On the following day, birds were assayed for inhibitory control using a detour-reaching task in their individual cages, following the methods described in MacLean *et al.,* (2014). Birds were required to retrieve a waxworm from within a transparent cylinder without pecking directly at the cylinder. First, birds were habituated to the apparatus, second they were trained to perform the motor skill of reaching around to the side of the cylinder and finally were tested on their ability to avoid pecking straight through the cylinder to the food inside. Prior to testing, birds were deprived of food, but not water, for one hour. We measured success/failure on a per-trial basis repeated ten times (N = 42). This data was collected by G. Davidson and full details are provided in Chapter 2.

On their last night in the aviary, great tits were given an innovative problem-solving device in their individual cages (Figure S5.1). They could solve the task from an hour before lights-off and then for another hour in the morning before being released back to the wild at the location of capture. Birds were given seeds, peanuts and water *ad-libitum* whilst they had the device in their cage. The device was a vertical transparent tube (16cm x 5cm, H x W) that was open at both ends, had three possible ways of solving and was baited with two waxworms. One waxworm was placed on a metal disc suspended in the centre of the tube on a thin wooden dowel and the second waxworm was tied to a piece of string that hung down in the centre of the tube. The three methods of solving were provided so that the motor ability of the birds would not confound their ability to solve. Birds could either, 1) push aside a flap on the front of the device to reach through a hole and claim a

waxworm, 2) pull out the wooden dowel to make the metal disc fall out through the bottom of the cylinder and the waxworm with it, or 3) pull up the string from the top of the device and take the waxworm from the end. A 'free' waxworm was provided in a tray at the bottom of the tube as a measure of motivation to feed. In the morning we recorded the bird's success as 'solve' (by any of the three methods) or 'not solve' (N = 32). Those that solved the task we named solvers and those that did not solve we named non-solvers. This data was collected by J. Coomes.

5.3.3 Discrimination learning in the wild

We measured discrimination learning in the wild at six field sites (one coniferous and five mixed deciduous) in the Bandon Valley, County Cork. The experiment operated in three sites (Ballinphellic, Innishannon and Kilbrittain) from the 16th of November 2017 to the 22nd of January 2018 and in three other sites (Castle Bernard, Dunderrow and Duke's Wood) from the 23rd of January to the 29th of March 2018. First, we attached passive integrated transponder (PIT) tags (IB Technology Aylesbury, UK) to the legs of all great tits ever caught at our field sites, which were regularly surveyed to ensure the majority of the population was tagged. Next, we installed a linear array of five automated 'selective' sunflower seed feeders (Firth *et al.*, 2015), each separated by 1m, to measure small-scale spatial learning of the birds. The feeders had a single transparent door at the base and a receiver platform in front of the door for the birds to land on. The PIT tags used RFID (radio-frequency identification) technology to trigger the transparent door (maas.ie) to 'lock' or 'unlock' depending on the identity of the bird that landed on the receiver platform. The circuit boards (Stickman Technologies Inc., Southampton, UK) that controlled the feeders were programmed to allow specific individual great tits access to the seeds at certain times, in different steps of the experiment. The feeders recorded the individual ID and time of visit for every PIT-tagged bird that arrived to feed. Feeders were active during daylight hours and were switched off at night to preserve battery life. We visited each site every 3-4 days to refill the feeders, change the batteries and to check that all feeders were fully operational.

The experiment itself involved three phases. In the first habituation phase, the feeder doors were fixed open for ten days, allowing all birds in the area to access the food and become familiar with the feeders. In the second phase (12-13 days), the feeder doors only unlocked for PIT-tagged birds that landed on the receiver platform. PIT-tagged birds had to push the transparent door open to retrieve a seed. In the third phase, the circuit boards controlling the feeder doors were programmed to allow each PIT-tagged great tit access to only one of the five feeders. We assigned roughly the same number of great tits to each feeder from a list of individuals that had been captured in the area, and we did not assign birds to their preferred feeder, defined as the feeder most frequently visited during the second phase. If a bird landed on the receiver platform of a feeder that it was not assigned to, the feeder door would remain locked and would not allow the bird to access the seeds. In this instance, the feeder would still record the identity of the PIT-tagged bird. We assumed that each visit to a feeder was an attempt to feed, and we counted each visit to an incorrect feeder as an error (Reichert *et al.*, 2020). We considered consecutive detections of the same bird to the same feeder within one second of each other to be a single visit. It would not have been possible for a bird to leave the feeder and come back within this time so likely represents an RFID read failure or a slight change in position of the bird on the feeder (Evans, Jones and Morand-Ferron, 2018). Birds were considered to have learned as soon as they had visited their correct feeder 80% of the time on 20 consecutive visits, with the requirement that the first visit in that window be correct. We calculated learning speed as the number of visits made until the bird reached this criterion and therefore the higher the number the slower the learning speed (Reichert *et al.*, 2020).

5.3.4 Statistical analysis

Winter diet data was matched to the birds that we had cognitive and personality measures for (for sample sizes see Table 5.1). See Table 5.2 for a breakdown of the number of samples available for each behavioural trait and the number in which invertebrate and plant DNA was identified. Any category of cognition/personality

data, which had less than 15 birds when matched to the diet data was not analysed (see Table 5.1).

Table 5.1. Sample sizes for birds that we had data for each behavioural trait and also had diet data for plants or invertebrates. Any categories with less than 15 were not analysed. The sample size varied between plants and invertebrates for a single behavioural trait if some faecal samples did not test positive for plant or invertebrate DNA. Also shown are the error distributions for each GLMM run on dietary richness with the behavioural traits as explanatory variables.

Behavioural trait	**Plants**		**Invertebrates**	
	N	Error distribution	N	Error distribution
Problem solving	26	Negative binomial	16	Negative binomial
Inhibitory control	29	Poisson	20	Negative binomial
Exploration behaviour	35	Poisson	23	Negative binomial
Learning	19*	Poisson	14	NA

Note: *For the learning-plant richness model, three outliers (learning scores higher than 100) were removed leaving N = 16.

Table 5.2. Total number of birds for whom we measured each behavioural trait, the number of faecal samples that were available from these birds and the number of these samples in which we identified invertebrate and plant DNA.

Behavioural trait	**Number of birds measured for behavioural trait**	**Total samples available from these birds**	**Number of samples in which DNA was identified**	
			Invertebrate	*Plant*
Problem-solving performance	32	27	16	26
Exploration behaviour	49	37	23	35
Detour-reaching performance	42	31	20	29
Learning	51	20	14	19

Faecal samples were tested for plant and invertebrate DNA using different primers (see Diet Data section above) and the final data for analysis was a matrix of great tit ID × genera, with a 1 indicating presence of a genus in a faecal sample and 0 indicating absence. We excluded faecal samples where no DNA was detected for any taxa (likely due to their small size). If plant DNA was not detected in a sample whilst invertebrate DNA was, we could be fairly confident that the lack of plant DNA was not an error in the lab process, because of the presence of invertebrate DNA, though we note that errors are still possible. Therefore, we concluded with reasonable certainty that there was not enough/any plant DNA in the sample to be detected. So, we assigned zeros to all plant taxa for a bird in this scenario, and vice versa for cases when invertebrate DNA was not detected whilst plant DNA was. If DNA was detected in a sample but it was not successfully sequenced (most commonly because the PCR to attach unique identifying tags was not successful), we indicated this with NAs in our data. We removed bird IDs from the data if we assigned NAs to both plant and invertebrate genera.

We used R (v3.6.1; R Core Team, 2019) to investigate the influence of our behavioural traits on both dietary composition (identity of genera) and dietary richness (number of genera), of plants and invertebrates, in the winter diet. Due to unequal sample sizes, we analysed the plant and invertebrate taxa separately. To investigate dietary composition we used the package *mvabund* v4.1.3 (Wang *et al.*, 2012). The 'manyglm' function was used to create multivariate generalised linear models with a binomial family and a 'cloglog' link function for each behavioural trait separately. The response variable was the matrix of presence/absence of each genus and the behavioural traits were included as explanatory variables. Additionally we added age (first year: <1 year, or adult: >1 year), sex (male or female) and habitat (coniferous or mixed deciduous) as additional explanatory factors that we wanted to control for. There was one exception to this: age, sex and habitat could not be included in the model for learning with the plant data due to unbalanced sample sizes for these three variables.

We used the 'anova' function to obtain summary statistics with the default Likelihood Ratio test (LRT) and we added a montecarlo (parametric bootstrap)

resampling method to calculate P values, as recommended in Wang *et al.,* (2012) for presence/absence data. Because terms are added to the multivariate models sequentially, our behavioural traits were written in the model last, after the other explanatory variables that we wanted to control for. We were therefore testing for the effect of cognition or personality on diet, given that the other variables were already in the model. For further details of *mvabund* see Chapter 3. We also ran univariate comparisons for each model, using '*p.uni=adjusted*', to assess whether any effects were being driven by certain genera. The composition of the diet was visualised in two ways. First, with NMDS (nonmetric multidimensional scaling) plots using the 'metaMDS' function in the *vegan* (v 2.5-6) package (Oksanen *et al.* 2019). The plots display the Jaccard index, a distance-based metric, which shows the distances between samples and how each individual (the points) differs from the mean (centroid) of their group. Second, bipartite graphs were produced using the 'plotweb' function from the *bipartite* (v 2.14) package (Dormann, Gruber and Fründ, 2008).

For the richness models, we ran plant and invertebrate GLMMs separately with richness (total number of genera consumed) as the response variable (see Table 5.1 for the error distributions of each model). The behavioural traits were included as explanatory variables in separate models with age, sex and habitat, and site as a random effect.

5.4 Results

As reported in Chapter 3, composition (Table 5.3) and richness (Table 5.4) were related to age, sex and habitat, to varying extents across the different models. This gives us confidence that, compared to our analyses in Chapter 3 with the full dataset, even these reduced samples have sufficient power to detect a range of key patterns observed.

Table 5.3. The association between dietary composition (identity of genera in the diet) and the behavioural traits. Dietary composition is the response variable in each model and the behavioural traits were each in a separate model. The explanatory variables included in each model and the deviance from the likelihood ratio test (LRT) are shown. Age, sex and habitat could not be included in the learning-plant model because of unbalanced sample sizes. A model was not run for learning on invertebrate DNA because of a sample size lower than 15 (see Table 5.1).

Data	Behavioural trait	Explanatory variable	LRT	P value
Plants	Problem solving	Sex	22.44	0.501
		Age	38.70	**0.018**
		Habitat	29.66	0.195
		Problem solving	38.93	**0.043**
	Inhibitory control	Sex	27.73	0.504
		Age	58.70	**0.001**
		Habitat	39.82	0.055
		Detour-reaching	57.40	**0.030**
	Exploration behaviour	Sex	30.11	0.485
		Age	64.12	**0.001**
		Habitat	36.88	0.114
		Exploration	43.66	0.431
	Learning	Learning	14.46	0.574
Invertebrates	Problem solving	Sex	44.84	**0.006**
		Age	45.48	**0.009**
		Habitat	25.17	0.067
		Problem solving	50.25	**0.006**
	Inhibitory control	Sex	57.92	**0.001**
		Age	64.98	**0.001**
		Habitat	18.60	**0.051**
		Detour-reaching	48.03	0.452
	Exploration behaviour	Sex	68.51	**0.001**
		Age	78.86	**0.001**
		Habitat	27.75	0.062
		Exploration	123.29	**0.001**

Table 5.4. The association between dietary richness (number of genera in the diet) and behavioural traits. See Table 5.1 for the error distributions and sample sizes for each model. Each behavioural trait was in a separate model. Age, sex and habitat did not have balanced sample sizes so were not included in the learning-plant model. Model fit was improved when habitat was removed from the exploration-invertebrate model. Three outliers with learning scores above 100 were removed from the learning-plant model. The variance explained by site in each model is as follows for the plant models: innovation: <0.001; detour-reaching: 0.014; exploration: 0.008; learning: 0; and was <0.001 for all the invertebrate models.

Data	Behavioural trait	Explanatory variable	Estimate	SE	CI (95%)	P value
Plants	Innovation	Intercept	1.06	0.26	0.55; 1.57	**<0.001**
		Innovation	0.08	0.25	-0.41; 0.57	0.75
		Age	0.54	0.24	0.07; 1.01	**0.03**
		Sex	0.07	0.23	-0.38; 0.52	0.76
		Habitat	-0.31	0.22	-0.74; 0.12	0.15
	Detour-reaching	Intercept	1.56	0.29	0.99; 2.13	**<0.001**
		Detour-reaching	-0.46	0.51	-1.46; 0.54	0.37
		Age	0.40	0.25	-0.09; 0.89	0.08
		Sex	-0.03	0.20	-0.42; 0.36	0.90
		Habitat	-0.53	0.27	-1.06; 0.00	**0.048**
	Exploration	Intercept	1.38	0.21	0.97; 1.79	**<0.001**
		Exploration	-0.02	0.01	-0.04; 0.00	0.22
		Age	0.40	0.22	-0.03; 0.83	0.07
		Sex	0.13	0.18	-0.22; 0.48	0.47
		Habitat	-0.45	0.24	-0.92; 0.02	0.07
	Learning	Intercept	1.21	0.20	0.82; 1.60	**<0.001**
		Learning	0.00	0.01	-0.02; 0.02	0.96
Invertebrates	Innovation	Intercept	0.76	0.66	-0.53; 2.05	0.25
		Innovation	-0.37	0.58	-1.51; 0.77	0.52
		Age	0.86	0.67	-0.45; 2.17	0.20
		Sex	-0.65	0.56	-1.75; 0.45	0.25
		Habitat	0.060	0.67	-1.25; 1.37	0.93
	Detour-reaching	Intercept	1.28	0.49	0.32; 2.24	**0.008**
		Detour-reaching	-1.03	0.87	-2.74; 0.68	0.24
		Age	0.77	0.56	-0.33; 1.87	0.17
		Sex	-1.50	0.42	-2.32; -0.68	**<0.001**
		Habitat	0.048	0.56	-1.05; 1.15	0.93
	Exploration	Intercept	0.46	0.42	-0.36; 1.28	0.27
		Exploration	0.03	0.024	-0.02; 0.08	0.18
		Age	1.03	0.38	0.29; 1.77	**0.007**
		Sex	-0.97	0.37	-1.70; -0.24	**0.01**

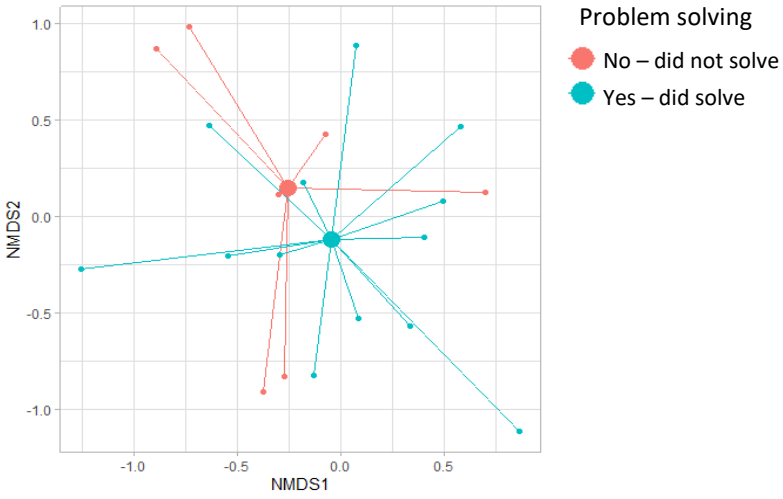
5.4.1 Innovative problem solving

Solvers ate a different composition of plant and invertebrate genera in the winter compared to non-solvers (Table 5.3, 5.5 and S5.1; Figure 5.1). Five plant genera (plantains, alder, oats, sow thistles and violets) were eaten exclusively by non-solvers (N = 10) and ten (heather, ivy, holly, acers, fruit trees, roses, nettles, grasses, ash and willow) were eaten exclusively by solvers (N = 16; Table 5.5; Figure 5.1b). The genera exclusive to each innovating group were largely found in individual birds and our result was not robust to the removal of genera only present in single samples (singletons) (no singletons: LRT = 24.99, P = 0.09). Furthermore, the result of the univariate analysis found no differences between solvers and non-solvers on each genera individually. Thus, we show an overall difference in diet with no single genera driving the effect. Though not significant, *Quercus* (oak) was present in the diets of more non-solvers than solvers (40% of individuals compared to 13%) and *Fagus* (beech) was present in the diets of more solvers than non-solvers (75% of individuals compared to 60%) (Table 5.5; Figure 5.1b). *Rubus* (berry bushes) was eaten by both groups evenly. For the foods provided at the feeders, more solvers had sunflower seeds in their diet than non-solvers (88% of individuals compared to 60%), and more non-solvers consumed peanuts than solvers (60% of individuals compared to 44%) (Table 5.5; Figure 5.1b).

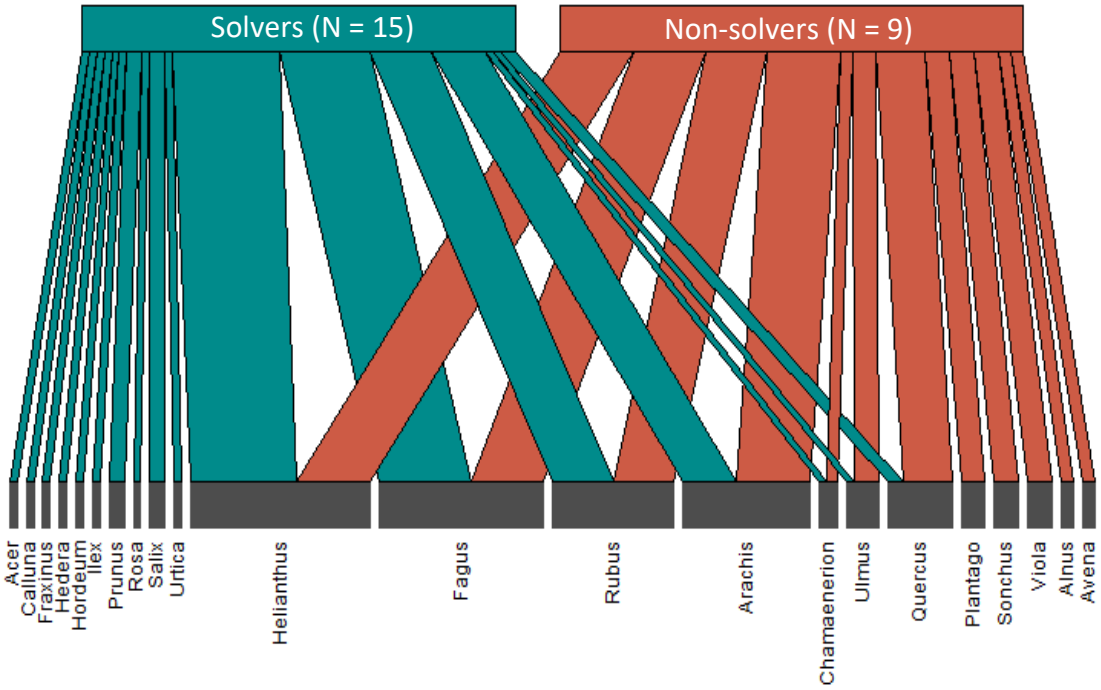
Solvers and non-solvers differed in the composition of dietary invertebrates they consumed (Tables 5.3 and S5.1; Figure 5.1), which was not driven by any particular genera. Five genera (three moths, gall wasps and hoverflies) were consumed by both solvers and non-solvers and all of these (*Bastobasis*, *Neuroterus*, *Diacrisia*, *Orthosia* and *Syrphus*) were present in more non-solver than solver diets (Table S5.1). Nine invertebrate genera (four moths, aphid, mayfly, fungus gnat, moth fly, beetle) were eaten exclusively by non-solvers (N = 5) and 12 (seven moths, two spiders, two flies, parasitoid wasp) were eaten exclusively by solvers (N = 11) (Table S5.1; Figure 5.1d), though we note that all of these were rare and only consumed by a single or two individuals. The significant association between problem-solving performance and invertebrate dietary composition when singletons were removed was marginally non-significant (no singletons: LRT = 17.71, P = 0.06).

There was no difference in dietary richness of either plants or invertebrates between solvers and non-solvers (Table 5.4). This result is unlikely to be due to insufficient power because problem-solving performance remained non-significant even after removing non-significant terms and comparing AIC values.

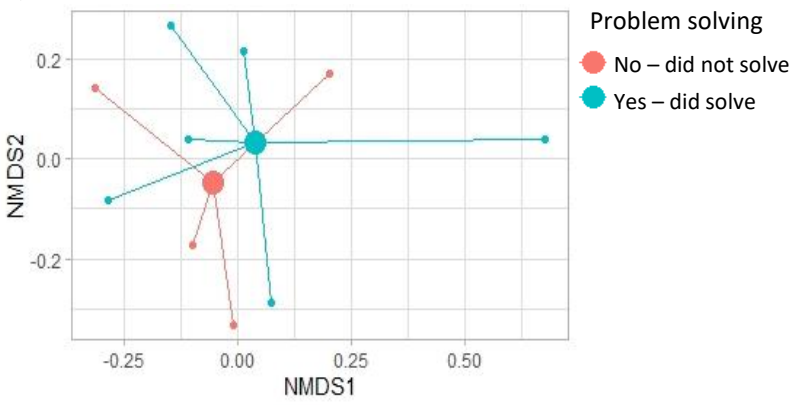
a)


Problem solving
No – did not solve
Yes – did solve
NMDS1
NMDS2
1.0
0.5
0.0
-0.5
-1.0

b)


Solvers (N = 15)
Non-solvers (N = 9)
Acer
Calluna
Fraxinus
Hedera
Hordeum
Ilex
Prunus
Rosa
Salix
Urtica
Helianthus
Fagus
Rubus
Arachis
Chamaenerion
Ulmus
Quercus
Plantago
Sonchus
Viola
Alnus
Avena

c)


Problem solving
No – did not solve
Yes – did solve
NMDS1
NMDS2
0.2
0.0
-0.2
-0.25
0.00
0.25
0.50

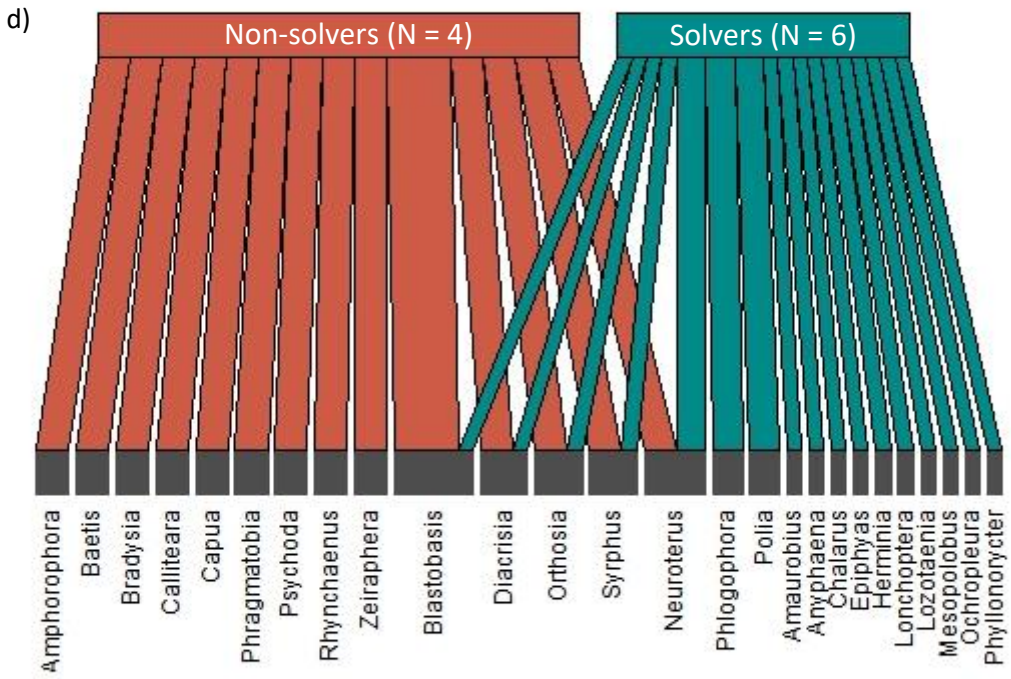


Figure 5.1. Composition of the diet for solvers and non-solvers for plants (a and b) and invertebrates (c and d). Diet is shown with a nonmetric Multidimensional Scaling (NMDS) plot (a and c) and a bipartite plot (b and d). Each point on the NMDS plots represents an individual and the connecting lines join the individual to the mean of its group (plants: N = 23 (two birds had a richness of zero and cannot be shown, and 1 outlier was removed) and invertebrates: N = 10 (six birds had a richness of zero). The Jaccard index was used to calculate the distances between samples. For the bipartite plots, sample sizes are given on each upper bar (plants: N = 24, two birds had a richness of zero so are not shown) and invertebrates: N = 10). The width of the lines joining the top bar to the bottom bars represents the proportion of birds from each solving group that consumed each genus. The width of the lower bars is proportional to the sum of the interactions involving that genus: genera that were involved in more interactions (ie. were present in the diet of more birds) have a wider bar.

Table 5.5. The percentage of solvers (N = 16) and non-solvers (N = 10) that consumed each plant genera (percentage frequency of occurrence) grouped into food provided at feeders, main natural food and other natural food. Many taxa are only eaten by a few individuals.

Genera	Common name	Solvers (N=16) (%)	Non-solvers (N = 10) (%)
Food at feeders			
Helianthus	Sunflower seeds	88	60
Arachis	Peanut	44	60
Main natural food			
Fagus	Beech	75	60
Quercus	Oak	13	40
Rubus	Fruit bushes e.g. bramble	50	50
Other natural food			
Prunus	Fruit trees e.g. plum	13	0
Salix	Willow	13	0
Acer	Japenese Maple	6	0
Calluna	Heather	6	0
Chamaenerion	Willowherbs	6	10
Fraxinus	Ash	6	0
Hedera	Ivy	6	0
Hordeum	Grasses e.g barley	6	0
Ilex	Holly	6	0
Rosa	Roses	6	0
Ulmus	Elm	6	20
Urtica	Nettle	6	0
Alnus	Alder	0	10
Avena	Oat	0	10
Plantago	Plantain	0	20
Sonchus	Sowthistle	0	20
Viola	Violet	0	20

5.4.2 Inhibitory control

The consumption of plant genera varied with detour-reaching score (Table 5.3; Figure 5.2) which was not driven by any particular genera. Oak, willowherb, ash, sowthistle and oats were consumed by birds with the highest scores (high inhibitory control) and walnut, spruce, pine, cabbage and Japanese maple were consumed by birds with the lowest scores (low inhibitory control) (Figure 5.2). Fruit bushes (*Rubus*), beech (*Fagus*), sunflower seeds (*Helianthus*) and peanuts (*Arachis*) were consumed by birds across the whole range of scores. The significant association between detour-reaching and plant dietary composition did not change with the removal of singletons (no singletons: LRT = 33.52, $P = 0.04$). Detour-reaching score was not related to the dietary composition of invertebrates (Table 5.3) or to the dietary richness of invertebrates or plants (Table 5.4).

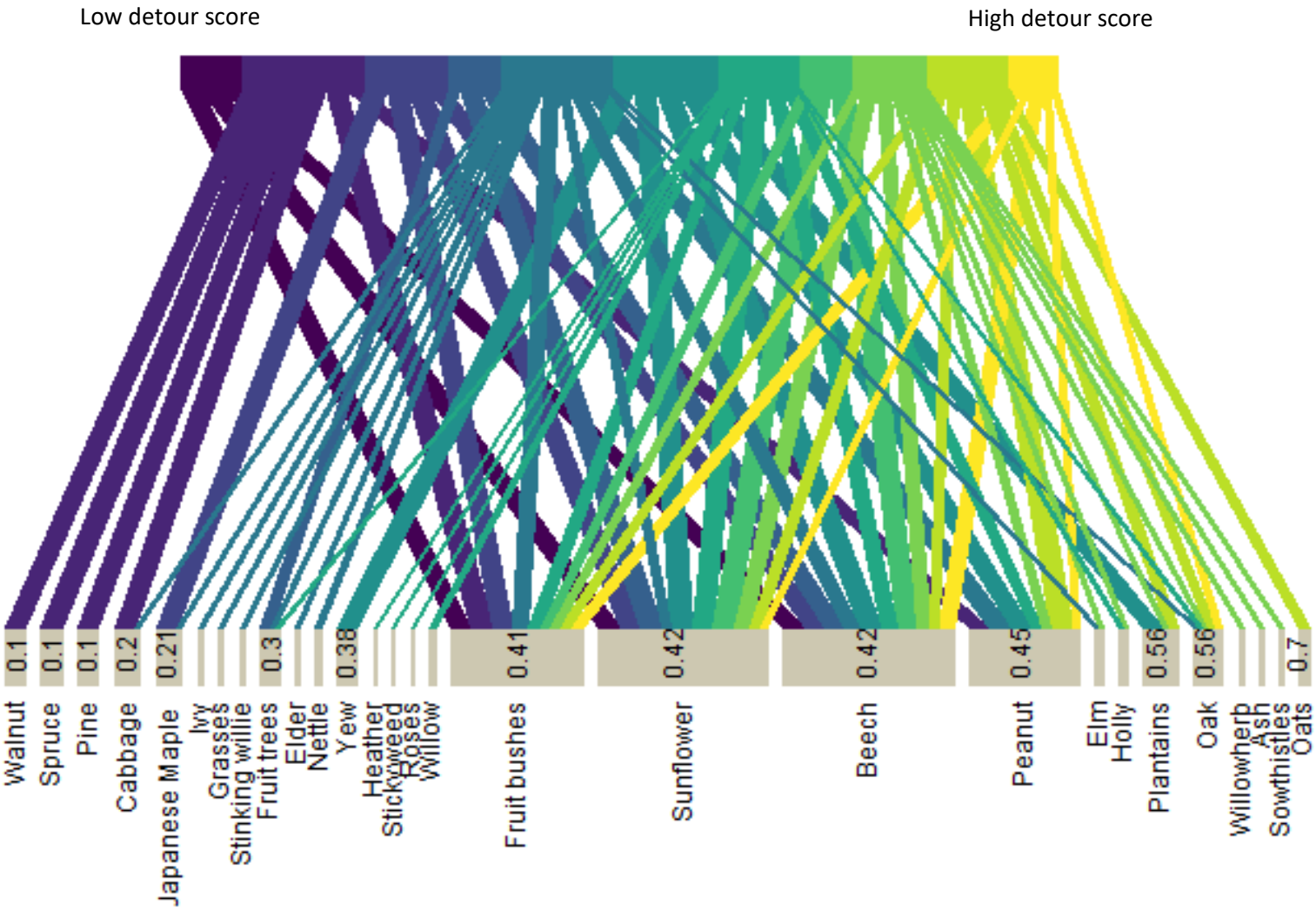


Figure 5.2. The plant genera consumed by great tits with respect to their detour-reaching score. The colour from dark to light (purple to yellow) represents the detour-reaching score from low (0) to high (1) with a high score indicating high inhibitory control. The sample size is N = 28 (one bird had a richness of zero so cannot be shown) which includes 11 unique scores from 0 – 0.8; seven scores were held by more than one bird. Birds are linked by interacting lines to the genera they consumed. The width of the lines represents the proportion of birds of each detour score that consumed each genus. The width of the lower bars is proportional to the sum of the interactions involving that genus. Genera that were involved in more interactions (ie. were present in the diet of more birds) have a wider bar. The mean detour score of all the birds that consumed each genus is shown on the lower bars.

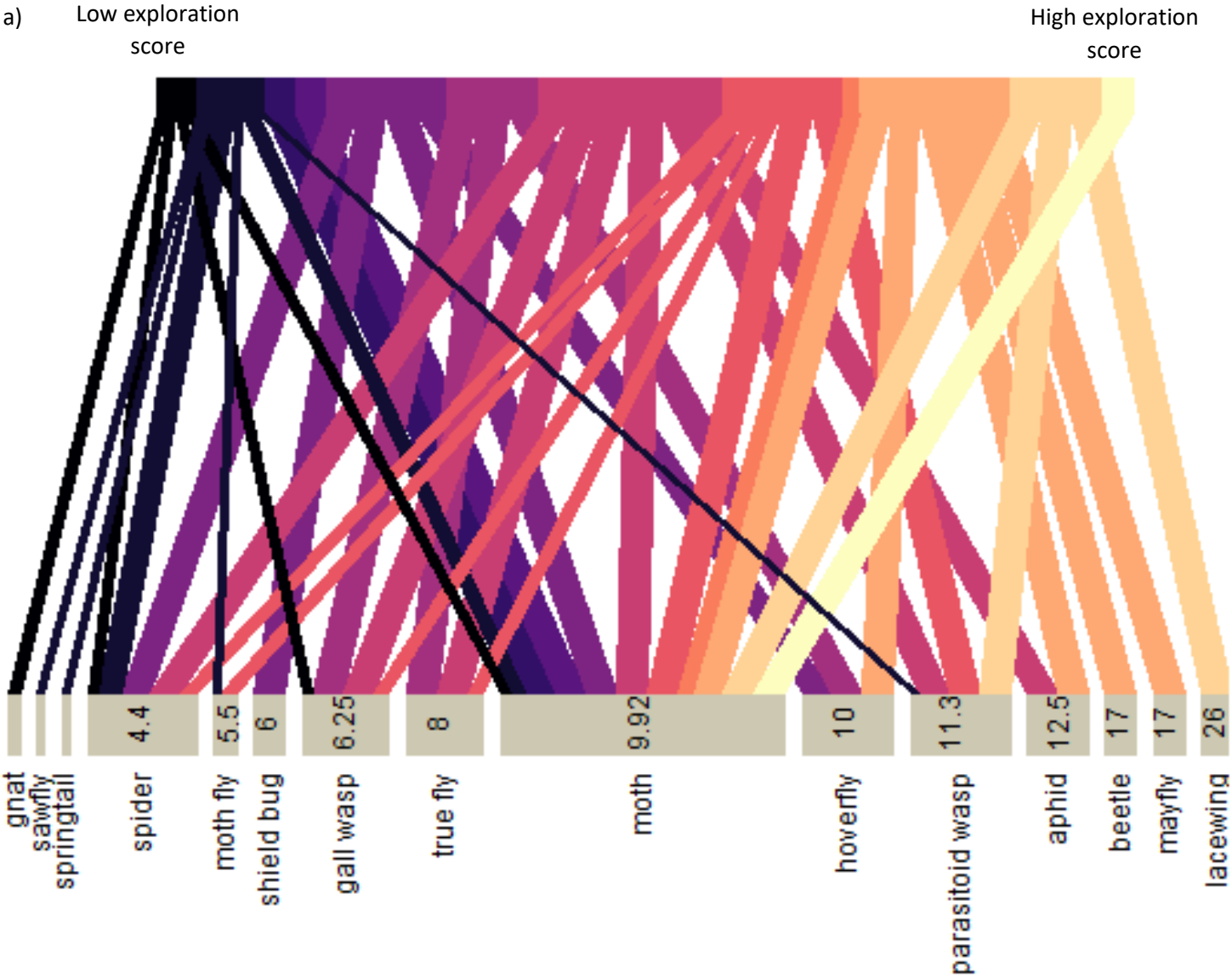
5.4.3 Exploration behaviour

Exploration behaviour was associated with the dietary composition of invertebrates but not plants (Table 5.3; Figure 5.3). Gnats (*Bradysia*), sawflies (*Xestia*), springtails (*Entomobrya*), spiders (*Amaurobius*, *Anyphaena*, *Clubiona* and *Pardosa*), moth flies (*Psychoda*) and shield bugs (*Acanthosoma*) were detected in birds with low exploration scores (mean score ≤6) and lacewings (*Chrysotropia*), mayflies (*Baetis*), beetles (*Rhynchaenus*) and aphids (*Amphorophora* and *Macrosiphum*) were detected in birds with high exploration scores (mean score ≥12.5) (Figure 5.3). The significant association between exploration and invertebrate dietary composition was not driven by any particular genera and did not change with the removal of singletons (no singletons: LRT = 58.0, P = 0.004). Exploration behaviour was not associated with plant or invertebrate dietary richness (Table 5.4).

5.4.4 Learning

We did not find an association between discrimination learning and plant dietary composition or plant richness (Tables 5.3 and 5.4). We acknowledge that we may have insufficient power to detect an association between learning and richness because the sample size was low (N = 19). We did not have a large enough sample size to test for an association between learning and invertebrate composition or richness.

a)


Low exploration score
High exploration score
gnat
sawfly
springtail
spider
moth fly
shield bug
gall wasp
true fly
moth
hoverfly
parasitoid wasp
aphid
beetle
mayfly
lacewing
4.4
5.5
6
6.25
8
9.92
10
11.3
12.5
17
17
26

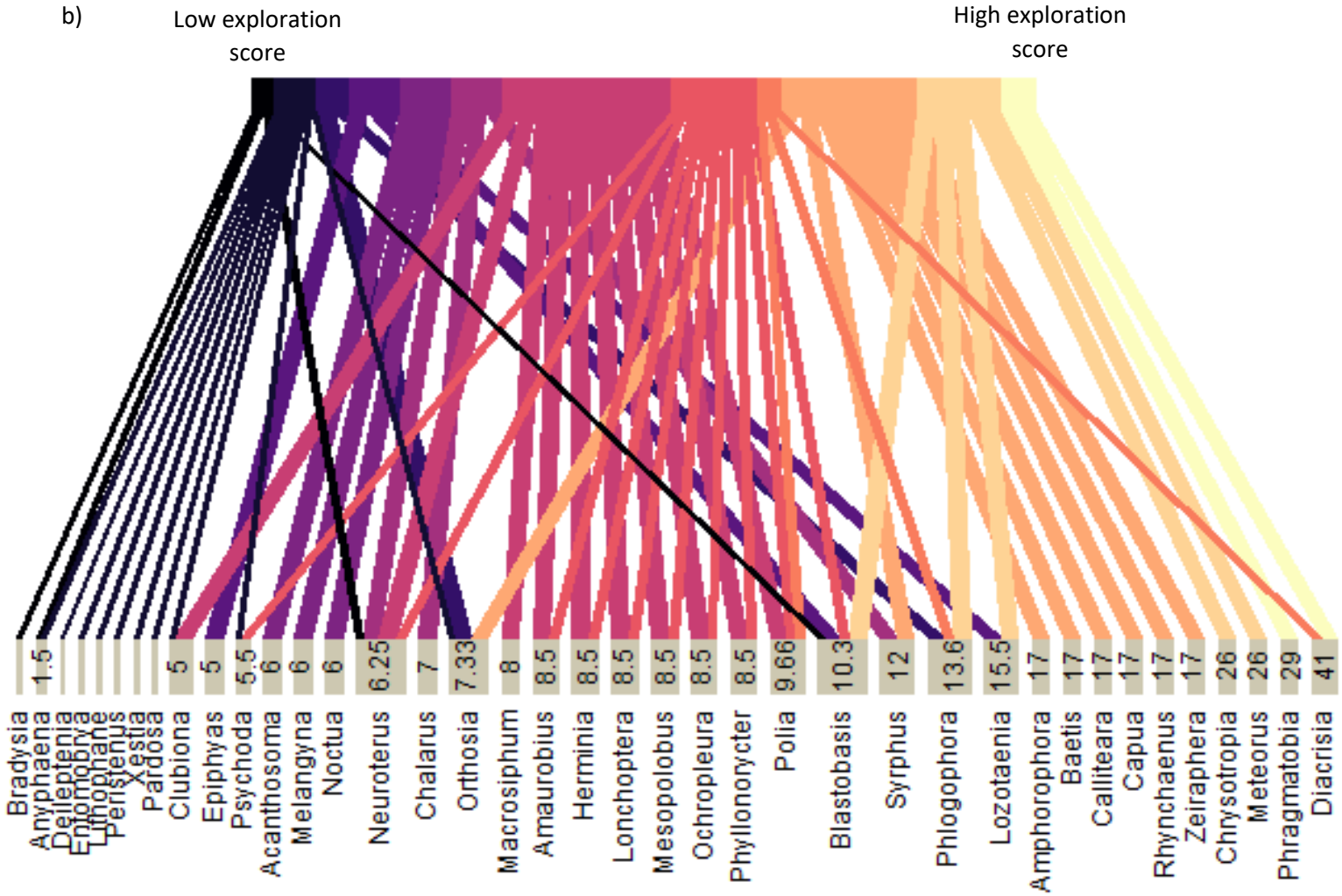


Figure 5.3. The invertebrate genera consumed by great tits with respect to their exploration score for a) the genera grouped by common name and b) the genera in full. The colour from dark to light (dark purple to light yellow) represents the exploration score from low to high (range: 1 – 29). Of the 23 birds in the analysis, 16 are represented on the plot and 7 had a richness of zero so cannot be represented (their scores: 1, 2, 4, 10, 12, 14, 20). The 16 birds are represented by 12 unique exploration scores. The numbers on the lower bars show the mean exploration score of all the birds that consumed at least one genus of the group for plot a, and consumed that genus for plot b. See Figure 5.1 for detail on the creation of the bipartite plot.

5.5 Discussion

We investigated how three measures of cognition and one behavioural trait closely linked to personality were associated with individual variation in the winter diet of great tits. We found that two cognitive measures; innovation and inhibitory control, and exploration behaviour, were associated with dietary composition. Solvers and non-solvers differed in the composition of plant and invertebrate genera in their diet, inhibitory control was correlated with plant dietary composition and exploration behaviour was correlated with invertebrate dietary composition. Discrimination learning was not associated with dietary composition and none of our behavioural measures were associated with dietary richness. We expand on our results below.

5.5.1 Innovative problem solving is associated with dietary composition of plants and invertebrates

The ability to solve a novel problem or use a novel behaviour to solve a familiar problem (Reader and Laland, 2003) is particularly useful for animals when there are opportunities to acquire food from novel sources (Fisher and Hinde, 1949; Ennion, 1962). For instance, innovative foraging has been shown in blue tits opening the lids of milk bottles to get at the cream inside (Fisher and Hinde, 1949), lobtail feeding in humpback whales (Weinrich, Schilling and Belt, 1992) and sweet potatoes washing in Japanese macaques (Kawai, 1965). Our results show that whether great tits succeeded at an innovative problem-solving task was associated with the composition of plant and invertebrate genera consumed in their winter diet, but not the number of genera they consumed. Despite this, both the plant and invertebrate composition results were not robust to the removal of singletons (genera present in a single individual) suggesting that our result is driven by the rare taxa. Singletons for plants were more than twice as common (and for invertebrates were slightly more common) among solvers than non-solvers, perhaps reflecting the tendency for solvers to exploit a range of different food types (Reader and Laland, 2003) and the ability to expand the diet to new food sources (Ducatez, Clavel and Lefebvre, 2015). Despite this, there were more solvers than non-solvers

for both the plant and invertebrate diet data, so any conclusions drawn from these results must remain tentative.

Theory suggests that individuals with a lower ability to compete for a resource are more likely to show enhanced innovation abilities, through avoiding dominant conspecifics and exploiting alternative food sources (Reader and Laland, 2003; Griffin and Guez, 2014). Following this, dominant individuals are not expected to be innovators. Our results show two notable differences in dietary plants between solvers and non-solvers that could be explained by this 'necessity drives innovation' hypothesis. First, oak acorns (*Quercus)* are an important food source for great tits in the winter (Betts, 1955) and oak was detected in a higher proportion of non-solver than solver diets, though we do not know which part of the oak (bud or acorn) was consumed. An explanation for this may be that non-solvers, because they are more dominant, have access to the best territories in winter, which are likely to be deciduous oak woodland (van Balen, 1967; Wilkin, King and Sheldon, 2009). This is supported by evidence that dominant birds retain territories throughout the winter (Krebs, 1971; Dingemanse and De Goede, 2004) and that non-innovators are likely to be dominant (Reader and Laland, 2001; Morand-Ferron *et al.*, 2011). Second, of the foods that we baited the great tits with, more solvers ate sunflower seeds (*Helianthus*) than non-solvers, while in contrast, more non-solvers ate peanuts (*Arachis*) than solvers. We provided the peanuts in a wire mesh feeder that birds had to remain on, in order to feed. If peanuts are the preferred food in winter (they provide more kilocalories per gram than sunflower seeds: 7.18 kcal/g compared to 6.12 kcal/g; Gibb, 1957), the mesh feeder provides more opportunity for highly competitive birds, that are more likely to be non-solvers, to monopolise the peanuts. On the other hand, sunflower seeds, which were eaten by more solvers, could be taken away quickly and whole, to be eaten out of view of competitors.

In great tits, adults are dominant over juveniles (Sandell and Smith, 1991) and males are dominant over females (Verbeek *et al.*, 1999; Dingemanse and De Goede, 2004) so we would expect adult males to be non-solvers, through to juvenile females that would be solvers. Our results do not support this expectation as in our study, all the adult males were solvers, and more juvenile females were non-solvers

than solvers. So, whilst our results show that non-solvers are eating more of the resources that are found in the best territories (oak) and that can be monopolised (peanuts), the identity (age and sex) of those non-solvers is not what we would expect from the necessity drives innovation hypothesis. Other studies have found that more competitive animals are more likely to innovate (Prasher *et al.*, 2019), perhaps because they are the fastest learners when faced with a task to solve (Boogert, Reader and Laland, 2006; Boogert *et al.*, 2008), suggesting that the link between competitive ability, identity of competitors and innovation is system dependent. Additionally, other factors such as experience may influence the tendency of individuals to innovate (Prasher *et al.*, 2019) and the context in which innovation is measured may influence the direction of a link with competitive ability. O'Shea *et al.* (2017) found that innovativeness measured in isolation was not related to competitive ability, and only when birds were tested in a social context did the authors find competitive ability to be related to innovation. Behaviour is flexible and local conditions can change how behavioural traits are expressed (Dingemanse *et al.*, 2012).

Comparative studies commonly use acquisition of novel food types as a measure of innovativeness (Sol *et al.*, 2005; Overington *et al.*, 2009; Navarrete *et al.*, 2016). We might have expected that innovators would consume a greater variety of prey items (Laland and Reader, 1999a) but our results show no relationship between innovation and dietary richness (number of genera) of plants or invertebrates. This finding agrees with other studies that found no association between dietary breadth and innovation (Overington *et al.*, 2011; Reader, Hager and Laland, 2011). Innovation has been suggested to allow animals to exploit novel food types but expanding the total number of different prey items is likely more related to factors such as competition and resource availability (Futuyma and Moreno, 1988). For example, if an animal colonises a new environment, and is released from competition, it may have access to a wider range of truly novel food resources (Bolnick *et al.*, 2010), providing an opportunity to develop innovative skills to exploit them. Thus, innovation may not be linked to how many prey types an animal has consumed but the origin of the food and being flexible to adapt to novel food sources whenever they become available.

5.5.2 Inhibitory control is associated with dietary composition of plants

In addition to innovation, our results showed an association between inhibitory control and dietary plant composition. While we can only speculate as to why the taxa identified were consumed by birds that varied in inhibitory control, a possible reason is that inhibitory control may be linked to the profitability of the plants. Inhibitory control is involved in decision-making and birds with high inhibitory control might be more efficient at avoiding plants that are challenging to open, especially if the energy or time costs to obtain and process the item are greater than the benefit of consuming it (Emlen, 1966; MacArthur and Pianka, 1966). Our results show some support for this as oats, ash and sowthistles (similar to dandelion), eaten by birds with high inhibitory control, have soft seeds that can be acquired easily whereas walnut, spruce and pine, eaten by birds with poor inhibitory control, have tough seeds that require a lot of energy to open. Very few other studies have looked at links between inhibitory control and diet and those that have, have compared multiple species and used broad, generally imprecise dietary information from the literature (MacLean *et al.*, 2014) or have used prey preference in captivity as the measure of diet (van Horik *et al.*, 2018). In Chapter 4 we showed that inhibitory control (of males) was associated with their summer diet and we know that our measure of inhibitory control in the wild (Chapter 4) is validated against the more standard detour-reaching task in captivity (Davidson, *et al.*, 2021, Pre-print). Thus, our combined results from Chapter 4 and 5, shows that inhibitory control is associated with components of the diet throughout the whole year. Our work has investigated individual variation in diet and individual performance in inhibitory control, in a single species, which allows a more detailed understanding of this cognitive measure as a potential driver of individual differences in diet.

5.5.3 Exploration behaviour is associated with dietary composition of invertebrates

Exploration behaviour, a behavioural trait closely associated with the fast-slow personality axis, was associated with the dietary composition of invertebrates. The

composition of invertebrate genera in the diet varies with exploration score, not that the diet is necessarily more diverse with advancement along the continuum (in either direction). This result supports our expectation that fast and slow explorers would vary in the type of prey encountered, due to differences in how they explore their environment. Our results are supported by studies showing that fast explorers have wider home ranges (Schirmer *et al.*, 2019), travel further to find food (van Overveld and Matthysen, 2010) and have a greater capacity to find new food sites (Herborn *et al.*, 2010), thus are likely to travel across different (micro)habitats and come across different food types. Slower explorers are often said to explore their environment more thoroughly, and faster explorers to explore more superficially (Groothuis and Carere, 2005), and our results show some support for this. Spiders were consumed by slower explorers and at least one genus (*Amaurobius*) that was identified lives in small holes in brickwork and bark, and builds tunnels out of silk to hide in. Thus, this genus is likely to require a lot of searching and thorough exploration by the great tits, a characteristic that fits with the expected behaviour of slower explorers. On the other hand, aphids were consumed by faster explorers and these insects are very abundant and widespread so are not likely to require a lot of searching to find, fitting the behavioural type of faster explorers.

Despite our finding that diet varies with exploration behaviour, great tits generally form large, transient flocks in the winter so we might have expected that faster and slower explorers would come across similar prey if they move around together. However, there is evidence that faster explorers are more likely to switch between feeding flocks and have larger spatial movements that slower explorers (Aplin *et al.*, 2013) so may be still likely to cover a wider area and come across different types of prey. In addition to this, exploration behaviour positively correlates with boldness in great tits (Verbeek, Drent and Wiepkema, 1994; Drent and Marchetti, 1999) which may further explain dietary differences between individuals at either end of the continuum. There is evidence that bolder great tits are more willing than shy individuals to choose aposematic prey (Exnerová *et al.*, 2010), bold deer consume more than shy deer when either the food or situation is novel (Bergvall *et al.*, 2011) and bold and shy black-browed albatross feed at different ocean depths (Patrick and Weimerskirch, 2014). We did not find an association between exploration and

the composition of dietary plants, perhaps because invertebrates are mobile and require more activity to acquire. Contrary to expectations, we did not find a link between exploration behaviour and dietary richness. A reason for this may be that, although faster explorers travel further than slower explorers (van Overveld and Matthysen, 2010), they explore their environment less thoroughly (Groothuis and Carere, 2005), so may still consume a similar total number of dietary genera as slow explorers that travel less far but are more thorough in their exploration. Furthermore, faster explorers travel further than slower explorers but to reach the same type of food (when preferred food is taken away) (van Overveld and Matthysen, 2010), supporting our result that faster and slower explorers do not differ in richness.

Personality has been suggested to be linked to individual dietary niche specialisation (Dall *et al.*, 2012; Toscano *et al.*, 2016) as both refer to consistent individual differences over time, in behaviour in the case of personality (Dall, Houston and McNamara, 2004) and in resource use in the case of niche specialisation (Bolnick *et al.*, 2003). Although we did not obtain repeat measures of the diet and could not measure individual specialisation directly, our study provides a first investigation into the correlation between personality and individual variation in diet. This allows a greater understanding of how behavioural traits determine resource use by individuals.

5.5.4 Non-significant effects of learning and limitations of the study

Our results provide some support for a link between cognition and the diet as innovation and inhibitory control were associated with dietary composition. However, one of our cognitive measures, discriminatory learning, was not associated with the diet. It is well known that learning is important for foraging success (González-Gómez and Vásquez, 2006; Janmaat, Byrne and Zuberbühler, 2006; Raine and Chittka, 2008) and instead of it being important for the type and diversity of prey consumed, learning may be more important for foraging efficiency. Our experiment measured the number of trials taken to learn to discriminate a rewarded location from other non-rewarded locations. The slower learners in our

experiment may take longer to learn to identity of palatable and profitable prey but once they do, they are still likely to have the same diet as faster learners. Furthermore, perhaps poor learners are more likely to scrounge off others and so would have the same diet as good learners. This is supported by a study on house sparrows that showed that individuals that performed better on a learning task were more likely to be producers rather than scroungers in a foraging group (Katsnelson *et al.*, 2011).

In addition, two factors in our study may be responsible for the lack of relationship between discrimination learning and diet, and also apply to our entire study. First, our sample size was limited, which greatly reduced the power we had to detect differences in diet between birds with good and poor learning abilities. Second, we sampled the diet once, and faeces only contain prey items eaten in the few hours prior to sample collection. Thus, our diet data is a useful snapshot but does not provide a longer-term examination of the diet, which is likely to show considerable variation over time with fluctuations in prey abundance. This also explains why we identified a large number of rare genera in the diet. Both cognition and personality are likely to be associated with the diet over the medium to longer term, especially as traits associated with them are stable over time (Dall, Houston and McNamara, 2004; Cauchoix *et al.*, 2018). Establishing the diet over a longer time frame, either through repeat faecal samples or a technique such as stable isotope analysis (Bearhop *et al.*, 2002, 2006), would allow us to measure diet consistency. Attaining measures of diet consistency would allow us to investigate links between individual niche specialisation and personality and cognitive traits (Svanbäck and Bolnick, 2005; Dall *et al.*, 2012; Toscano *et al.*, 2016).

In addition to low sample sizes and the lack of repeat dietary measures that apply to our entire study, three more limitations of our study should be mentioned. First, any DNA in the faeces, whether it was consumed directly or secondarily through consumption by the prey eaten by the birds, is revealed at the end of the metabarcoding process (da Silva *et al.*, 2019). Therefore, it is possible that the plants and invertebrates identified were consumed by other invertebrates, which were then in turn eaten by the great tits. If this were the case, our results still

suggest that solvers and birds with high inhibitory control were eating invertebrates feeding on a different composition of plants compared to non-solvers and birds with poor inhibitory control respectively, and still suggest that dietary differences were associated with cognition. Second, particularly for plants, it is possible that birds may accidentally ingest material that is not their target food (da Silva *et al.*, 2019). However, because we found a large proportion of samples that tested positive for plant DNA and a comparatively smaller proportion of samples that tested positive for invertebrate DNA, we feel accidental ingestion of plant material whilst targeting invertebrates is unlikely. This is supported by a study that found plant material to be more commonly consumed in the winter by great tits than invertebrate prey (Vel'ký, Kaňuch and Krištín, 2011). Finally, due to the long sampling period of 4 months, diets may be different between the beginning and the end of the season because of variation in availability of different food types, which could affect the correlations with behavioural traits.

5.5.5 Conclusions

We have shown that innovative problem solving, inhibitory control and exploration behaviour are associated with dietary composition but not with dietary richness. In addition, the significant correlations between the behavioural traits and diet involved a mix of plant and invertebrate dietary taxa, suggesting complex links between personality, cognition and specific aspects of diet. Our results show that behavioural traits often hypothesised to influence foraging behaviour are linked to dietary components, although the fitness consequences of these associations remain undetermined. In addition, the direction of causation for the association between the behavioural traits and diet is unknown. Variation in behaviour may allow individuals to eat different prey types but alternatively, expansion of the variety of food items in the diet may change an individual's behaviour (personality) or allow it to develop enhanced cognitive abilities (Kitaysky *et al.*, 2006; Arnold *et al.*, 2007; Han and Dingemanse, 2015, 2017; Toscano *et al.*, 2016). Future work would need to manipulate cognition and personality, perhaps using hormones or habituation, and examine the diet over time. How cognitive and personality traits

are linked to, or can drive, individual differences in diet may depend on, and differ between, the ecological conditions faced by individuals (Svanbäck and Bolnick, 2007; Araújo, Bolnick and Layman, 2011). Investigating the association between individual variation in diet and cognition and personality allows us to understand more about how animals use and adapt to changes in resource abundance and different environments.

5.6 Appendix D – Supplementary material for Chapter 5

Figure S5.1. Innovative problem-solving device with three solutions. A waxworm is placed on the metal disc in the centre of the tube and a second waxworm is tied to the string that hangs down in the centre of the tube. Birds can either i) push aside the white flap to reach through the hole and take the worm off the metal disc, ii) pull out the cocktail stick lever underneath the flap so the metal disc falls out of the bottom of the tube, bringing the worm with it, or iii) pull up the string from the top of the device to retrieve the worm from the end.

Table S5.1. The percentage of solvers (N = 11) and non-solvers (N = 5) that consumed each invertebrate genera (percentage frequency of occurrence). The common name of the group is given and the taxonomic family that each genera belong to is given in brackets. Many taxa are only eaten by a few individuals.

Genera	Common name (family)	Solvers (N=11) (%)	Non-solvers (N = 5) (%)
Blastobasis	Moth (Blastobasidae)	9	40
Neuroterus	Gall wasp	18	20
Diacrisia	Moth (Erebidae)	9	20
Orthosia	Moth (Noctuidae)	9	20
Syrphus	Hoverfly	9	20
Amphorophora	Aphid	0	20
Baetis	Mayfly	0	20
Bradysia	Fungus gnat	0	20
Calliteara	Moth (Erebidae)	0	20
Capua	Moth (Tortricidae)	0	20
Phragmatobia	Moth (Erebidae)	0	20
Psychoda	Moth fly	0	20
Rhynchaenus	Beetle	0	20
Zeiraphera	Moth (Tortricidae)	0	20
Phlogophora	Moth (Noctuidae)	18	0
Polia	Moth (Noctuidae)	18	0
Amaurobius	Spider	9	0
Anyphaena	Spider	9	0
Chalarus	True fly	9	0
Epiphyas	Moth (Tortricidae)	9	0
Herminia	Moth (Erebidae)	9	0
Lonchoptera	True fly	9	0
Lozotaenia	Moth (Tortricidae)	9	0
Mesopolobus	Parasitoid wasp	9	0
Ochropleura	Moth (Noctuidae)	9	0
Phyllonorycter	Moth (Gracillariidae)	9	0

5.7 Bibliography

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Chapter 6

General Discussion

Great tit in flight

By Gaby Main

Investigating the factors that influence foraging decisions and determine diet choices of animals is of fundamental importance to the field of behavioural ecology as it improves our understanding of how individuals use resources in heterogeneous habitats and the implications of this for life history variation. Cognition and personality have received a lot of attention as behavioural concepts influencing foraging behaviour, especially in terms of finding food in the environment. However, less attention has been paid to how they are linked to dietary composition specifically and how they influence behavioural plasticity of foraging decisions, particularly under different ecological contexts. The aims of my thesis were to explore cognition and personality as potential drivers of foraging flexibility (Chapter 2), to describe the diet and investigate dietary differences between demographic groups (Chapter 3), and to explore how cognition and personality traits are associated with individual variation in the spring and winter diet (Chapter 4 and 5).

In summary, the results of this thesis have:

1) demonstrated that associations between cognition, personality and foraging flexibility depend on environmental context: food value and predation risk;
2) described the diet of great tits across the spring and winter seasons, and across two habitat types (deciduous and coniferous), and examined the role of age and sex as factors influencing individual variation in diet;
3) shown that inhibitory control is associated with the adult diet in spring and have suggested a role for inhibitory control in parental care, since this cognitive measure was associated with nestling diet and provisioning rate;
4) and finally, have shown that cognition (innovation and inhibitory control) and personality (exploration behaviour) are associated with the adult diet in winter.

Here, I will discuss Chapters 2 and 3 in order, followed by a section on the adult diet from Chapters 4 and 5 (section 6.3) and finish with a look at inhibitory control for parental care and other behaviours (section 6.4). First, I will discuss foraging flexibility as a type of behavioural plasticity and the importance of ecological context in revealing associations between traits of interest. Second, I will discuss the limitations of DNA metabarcoding and extensions of the methods in Chapter 3. Third, I will describe individual consequences of the association between the behavioural traits and diet, discuss how cognition and personality might drive individual niche specialisation and how interactions between cognition, personality and demographic variables might be associated with the diet. Additionally, I will discuss the direction of causation for the association between the behavioural traits and diet. Fourth, I will focus on inhibitory control specifically and discuss how this cognitive mechanism may influence parental care and other behaviours. Furthermore, I will point out other cognitive and non-cognitive factors that might affect performance on inhibitory control tasks and the association with the diet, and ask how adaptive this cognitive ability is. Finally, I shall summarise the conclusions of this thesis and suggest future directions.

6.1 The influence of cognition and personality on foraging flexibility

Individual variation in behavioural plasticity allows individuals to respond to changing environments. The role of cognition and personality in driving behavioural plasticity has received increasing attention but we know little about how this occurs under realistic ecological scenarios. Chapter 2 filled this knowledge gap by investigating how inhibitory control and exploration behaviour influence foraging flexibility under two ecological conditions.

In this section, I will discuss i) foraging flexibility as a type of behavioural plasticity and ii) the effect of ecological context in revealing associations between variables of interest.

6.1.1 Foraging flexibility as a type of behavioural plasticity

In behavioural ecology, plasticity is a broad concept and the term is often used to mean different things. Behavioural plasticity is broadly defined as change in behaviour in response to environmental conditions (Dingemanse *et al.*, 2009), and can refer to the extent of change in different situations (Sih *et al.*, 2004). Types of plasticity have been split into those that vary with external factors and those that vary with internal state (Stamps, 2016). Within 'exogenous plasticities' – responses to external stimuli – 'developmental plasticities' are defined as the effects of past experience on current behaviour which includes learning (Stamps, 2016). This is not to be confused with 'ontogenetic plasticity' which specifically refers to past experience at a previous life stage (i.e. childhood), affecting behaviour at a later age (Stamps, 2016). The foraging behaviour I measured in Chapter 2 is a type of exogenous (short-term), developmental plasticity and fits specifically under the term 'flexibility', as defined by Stamps (2016). Flexibility is the extent to which a behaviour in a well-learned situation changes in response to a stimulus, and must involve a learning component (Stamps, 2016). Thus, the behaviour I have measured meets the broad definition of plasticity.

6.1.2 The effect of ecological context in revealing associations

The results of Chapter 2 showed that relationships between variables of interest may only be revealed under different ecological contexts. The effect of inhibitory control on foraging flexibility was only apparent when the food reward options were of equal, high value, whereas exploration behaviour was associated with flexibility most strongly in the presence of a predator (Chapter 2). There is a well-described ecological trade-off between foraging and predation risk (Lima and Dill, 1990), so why does cognition depend on one and personality depend on the other? One suggestion is that cognition is more relevant in the context of foraging and exploration is more relevant in the context of predation. This is likely since exploration behaviour correlates with predation risk-proneness (Koolhaas *et al.*, 1999; Quinn *et al.*, 2011) and the response to predators is more of an innate response drive by fear, whereas the decision to make a choice between food types is more cognitively demanding and so is moderated by a cognitive function. As well as context, how individuals value different choices is likely to influence their flexibility. Some individuals may be less choosy in their food choice so may choose the easiest food option whereas others may be more choosy and have a higher threshold for switching their food choice (Sih and Del Giudice, 2012). Furthermore, if an individual is predation risk averse, this could affect how inhibitory control influences foraging plasticity when the risk of predation changes. We may only understand variation in how individuals value different choices, when testing them under different contexts such as food value and predation risk.

Other ecological contexts in addition to food value and predation risk may also influence the association between behavioural traits and plasticity. For instance, as the reliability of information improves, individuals are expected to switch from unchanging (consistent) behaviour to responsive (plastic) decision making (McElreath and Strimling, 2006). In a study on chacma baboons, personality was found to influence foraging plasticity, only when cues were unreliable (Carter *et al.*, 2013). Therefore, it is important to consider how ecological conditions faced by animals in their natural environment may impact how behavioural traits are associated with behavioural plasticity.

6.2 Dietary differences of great tits according to demographic group

For species that are difficult to observe when foraging, assessing intraspecific dietary variation between demographic groups is challenging. The use of molecular techniques, such as DNA metabarcoding, can overcome this challenge and identify the prey items in the diet, and also facilitates establishing spatial and temporal variation in diet. Chapter 3 provides the most comprehensive study of the diet, and the most detailed investigation into the intrinsic (age and sex) and environmental (season and habitat) factors that influence dietary differences, in great tits to date.

In this section, I will discuss i) the limitations of DNA metabarcoding, and the potential for stable isotope analysis to be employed in combination with metabarcoding to assess the diet, and ii) possible ways this work could be extended.

6.2.1 DNA metabarcoding limitations and stable isotope analysis

The development of DNA metabarcoding in recent years has made it possible to identify the diets of highly generalist species, to a finer taxonomic resolution than previous methods (Shokralla *et al.*, 2012; Clare, 2014). However, there are a number of limitations of DNA metabarcoding. First, no primer pair is completely accurate at detecting all DNA fragments, particularly in samples like faeces where the DNA is very degraded (Clare, 2014). The primers used for COI and ITS2 used in this thesis both target short DNA regions which make it more likely that degraded DNA will be detected. However, certain prey items may still not have been picked up due to having low quality DNA that could not be amplified during PCR (Pompanon *et al.*, 2012; Clare, 2014). Second, secondary ingestion (or secondary predation) where a species is identified that was the target prey of the great tit's own prey, is a known issue in this field and, depending on the focal species, has been considered of little importance (Barrett *et al.*, 2007; Gerwing *et al.*, 2016) or can confer strong bias on the diet of generalist species if other methods such as morphological analysis and behavioural studies are not employed (da Silva *et al.*, 2019).

Third, metabarcoding does not provide information on the size or life stage of invertebrate prey, or on the part of the plant, such as buds or seeds. For this thesis,

the aim was to simply characterise the diet of the great tits with a view to shed light on dietary variation. However differences in diet between age groups (Chapter 3) and associations between diet and behavioural traits (Chapter 4 and 5) may be based on size, life stage or plant characteristics rather than differences between the species eaten. For example, males and females may show differences in prey size as well as type of prey, due to differences between the sexes in morphological characteristics such as beak size and weight (Ebenman, 1986), and adults may provision invertebrates of a different life stage to their nestlings than those that they eat themselves. Currently, the most reliable method to infer size and life stage of prey for species like the great tit is video footage at the nest (García-Navas, Ferrer and Sanz, 2012; Navalpotro *et al.*, 2016; Pagani-Núñez *et al.*, 2017), which is not applicable for determining adult diet, or to use average prey sizes from the literature. To fully understand variation in diet between demographic groups, and make inferences about the benefit to individuals of consuming different prey types, it will be important to delve deeper into characteristics of the prey species consumed.

Fourth, using current methods, it is not possible to quantify the relative abundance of prey species using high-throughput sequencing (Clare, 2014; Krehenwinkel *et al.*, 2017). Differential digestion of prey items make predictions unreliable; for example, a tough beetle carapace will not be digested as much as a soft fly and therefore will have more DNA available in the sample to detect (Clare, 2014) and the same may be true for prey of different sizes. A number of studies have had success using the number of sequences produced for each MOTU (relative read abundance) to estimate the proportion of each prey type in a sample (Thomas *et al.*, 2016; Deagle *et al.*, 2019; Cavallo *et al.*, 2020). However, this approach requires prior information about known diet, together with the relative read abundance, to calculate correction factors for estimating prey biomass consumed, and is not suitable for highly generalist species such as great tits that consume many hundreds of species.

Finally, the diet data that is obtained is only as good as the database it matches to but there has been vast improvement in the detail of taxonomic databases in recent years (Valentini, Pompanon and Taberlet, 2009; Pompanon *et al.*, 2012), and more

improvements to come as the field continues to develop. Despite their shortcomings, high-throughput methods still have substantially more power to accurately detect the diet than traditional approaches like morphological analysis (Pompanon *et al.*, 2012; Alonso *et al.*, 2014) and Sanger sequencing (Soininen *et al.*, 2009), and are applicable to a wide variety of ecological questions.

Stable isotope analysis is another molecular technique used, potentially to infer diet, or more commonly, to infer position in the food chain. It uses ratios of carbon and nitrogen isotopes in body tissue, usually from blood or feathers, to obtain information about the trophic level and spatial scale of prey found in the diet (Bearhop *et al.*, 2002, 2006; Cherel *et al.*, 2008). An advantage of using stable isotopes over metabarcoding is that information is gathered over a longer time frame, i.e. the growth of the whole feather (Bearhop *et al.*, 2006). This means dietary information could be obtained during the entire life of a chick in the nest or a whole moult cycle (several months) of an adult (Bearhop *et al.*, 2006). However, the taxonomic resolution is not comparable to metabarcoding as the actual prey items consumed cannot be identified, unless the focal species is feeding on a small number of prey species at very different levels in the food web, is feeding in different locations, or if previous information of these behaviours are known (Burns *et al.*, 1998). If both stable isotope analysis and DNA metabarcoding were used together, as has been done in mammalian ecology (Soininen *et al.*, 2014; Walter, Kurle and Hopkins, 2014), this would i) allow identification of prey to species level (metabarcoding), ii) establish consistency of prey use over both short (metabarcoding) and long timeframes (stable isotopes) and iii) determine space use of individuals across habitat types. Pagani-Núñez *et al.*, (2017) used stable isotope analysis to determine the diet of nestling great tits and found that mean carbon-13 ratios were negatively correlated with the proportion of oak trees around the nest box (Pagani-Núñez *et al.*, 2017). This suggests that stable isotope analysis can be used to determine the habitat structure the target species is feeding in. This would be a particularly useful addition to Chapter 3 because I suggested that the lack of difference in dietary plants between habitat types was due to great tits feeding at the edges of their fragments. Stable isotope analysis could be used to confirm this.

In addition, using stable isotopes, I could also determine if birds were using particular microhabitats around their nest boxes, see section 6.3.1.

6.2.2 Suggestions for future work looking at niche separation

There are a number of ways that the work in Chapter 3 could be expanded to improve our understanding of dietary niche separation between demographic groups in great tits. First, it would be interesting to explore if certain demographic groups relied more on invertebrates or plants in the winter. I looked at plant and invertebrate consumption separately (Chapter 3) but it might have been the case that, for example, males and females reduced competition between themselves by one sex feeding more on plants and the other more on invertebrates. As males are bigger than females, sex differences in diet are likely because certain sized beaks will be more efficient at handling certain types of food (Gosler, 1986; also see section 6.3.4). Additionally, great tits are assumed to mostly consume invertebrate material in the breeding season (Betts, 1955), which is the reason I only tested for plant material in the winter samples, but a specific aim to test the spring samples for plant material would have provided evidence supporting or refuting this assumption.

Second, instead of having only presence/absence data, investigating the proportion of plant material versus invertebrate material, or indeed comparing the abundance of different plant and invertebrate taxa, in individual diets would be a particularly important extension to this work. Obtaining information on relative abundance of prey is not possible with current metabarcoding methods (see section 6.2.1 above) but advancements are being developed that allow this possibility (Thomas *et al.*, 2016; Deagle *et al.*, 2019; Cavallo *et al.*, 2020). Information on relative abundance of prey would provide a more detailed understanding of the extent that demographic groups rely on certain taxa.

Finally, the multivariate statistical method used in Chapter 3 provides information on whether dietary composition differs, and can inform us about statistical differences in taxa between groups (i.e. is there a significant difference in dietary

composition between males and females), but it does not assess a quantifiable extent of dietary separation. To expand this work, I could assess how the expected amount of overlap in resource use between demographic groups compared to the observed overlap using Pianka's index (Pianka, 1973; Novakowski, Hahn and Fugi, 2008).

6.3 The association between cognition, personality and diet

This thesis has shown that inhibitory control, exploration behaviour and innovation are associated with dietary composition (Chapter 4 and 5), supporting the expectation that individuals vary in prey selection based on their cognitive capacities and a personality trait. Previous studies have shown that these behavioural traits play an important role in foraging behaviour (Clayton and Dickinson, 1998; Toscano *et al.*, 2016; Rosati, 2017; Troxell-Smith and Mella, 2017) but this thesis provides the most comprehensive investigation to date of how cognitive capacities and a behavioural trait associated with a personality axis are linked to prey items in the natural diet.

In this section I will discuss the effects of the behavioural traits on adult diet from Chapters 4 and 5 including: i) the consequences of the association between behavioural traits and diet for individuals and populations, ii) how demographic characteristics might interact with behavioural traits to influence diet, iii) the influence of morphological features, and iv) the direction of causation, between behavioural traits and the diet.

6.3.1 Consequences of the association between behavioural traits and diet

What are the functional implications of the association between the behavioural concepts (personality and cognition) I have investigated and diet? On the one hand, the association may be a by-product of variation in personality or cognitive abilities that arises because of other functional behaviours, and therefore that some individuals consume one diet and others another, is neither advantageous or

disadvantageous to those individuals. Put simply, the implication of the association on individuals may be neutral. On the other hand, there may be costs and benefits for a behavioural type of consuming particular prey, which may lead to no net difference in fitness. Here will consider the potential consequences of the association between behavioural traits and diet for condition, survival and reproductive success of individuals.

The association between behavioural traits and diet may have consequences for body condition, the store of nutrients in the body and the body's ability to store them efficiently (Moya-Laraño *et al.*, 2008). Although I did not measure body condition directly, which is very difficult to do in birds in the non-breeding season when fat levels are very low, results in Chapter 4 showed that there was no association between inhibitory control and carbohydrate, lipid or protein content of prey. This suggests that birds with high inhibitory control were not more efficient at selecting prey based on the qualitative nature of the macronutrient content, as such. Micronutrients are also essential for efficient body functioning, for example the amino acid taurine supports growth and plays an important role in tissue development (Sturman, 1993) and zinc plays a role in motor development (Bhatnagar and Taneja, 2001). Establishing if certain behavioural types, for example individuals with high inhibitory control, select their prey based on micronutrient content, and incorporating weight, fat and muscle scores, would allow us to establish if and how behavioural traits drive individual body condition through diet.

Second, the association between behavioural traits and diet may impact negatively on individuals if certain behavioural types are more likely to consume unpalatable or toxic prey (Exnerová *et al.*, 2010, Chapter 4). More males with high inhibitory control consumed prey with warning colouration than males with low inhibitory control (Chapter 4), and another study showed that bold great tits were more willing to choose aposematic prey than shy individuals (Exnerová *et al.*, 2010). If this prey choice tendency persists over time, the accumulation of toxins may lead to a long-term negative effect on condition (Kokko, Mappes and Lindström, 2003). We might imagine there should be strong selection against this accumulation of toxins, but if there is a short-term benefit of consuming aposematic prey, and this

outweighs a negative effect, particularly if it is not very severe, then animals may continue to consume aposematic prey. In addition, starlings that had experimentally reduced body mass and fat stores attacked aposematic prey more often than controls (Barnett, Bateson and Rowe, 2007), which may suggest that body condition could interact with behavioural traits to influence the consumption of chemically defended prey. More research on the palatability and long-term effects for predators of consuming prey with warning colouration would advance our understanding of the consequences of consuming certain prey types.

The interplay between behavioural traits and diet may have consequences for how efficiently individuals balance their energy budget. For instance, faster individuals on the fast-slow personality axis, are likely to expend more energy than slower individuals (Careau *et al.*, 2008) because they move over larger distances (Boon, Réale and Boutin, 2008), travel further to find food (van Overveld and Matthysen, 2010) and have a more exploratory foraging strategy (Wilson and McLaughlin, 2007). If this expenditure is not offset by increased energy gain through finding high-energy food, fast individuals will pay a greater energy cost than slow ones. Innovators and high inhibitory control birds may also pay a greater energy cost as their neural, instead of physical, energy expenditure may be high. Indeed, there is evidence that cognitive processing in the brain is very energetically costly (Dukas, 1999; Plaçais and Preat, 2013). Animals must balance the need to find enough high-quality food to fulfil requirements and the energy expended, either physical or neural, to acquire it.

Variation in prey consumption determined by a behavioural type may afford individuals greater reproductive success and survival compared to other behavioural types. From numerous studies in both the human and animal literature, it is well established that diet composition can influence mortality and survival (Fernandes, Yunis and Good, 1976; Fortes *et al.*, 2000; Trichopoulou *et al.*, 2005, 2007; Dussutour and Simpson, 2012; Kiilerich *et al.*, 2016). Continuing with the example from above, if bold great tits consume an increased amount of toxic prey over their life, they may have decreased longevity compared to shy individuals. If this is the case, we might imagine that the bold personality type would be selected against,

but, as we know both personality types persist, bold individuals are likely to have an advantage elsewhere. The pace-of-life syndrome hypothesis has been linked to personality traits and proposes a trade-off where shy individuals are expected to live long and reproduce slowly and bold individuals the opposite (Réale *et al.*, 2010; Hall *et al.*, 2015). Bold individuals may consume more toxic prey and have decreased longevity compared to shy individuals, but they may have similar reproductive success. Diet has also been linked to reproductive success (Whitfield *et al.*, 2009; Lorentsen, Mattisson and Christensen-Dalsgaard, 2019), either through improved breeding condition from the adult diet (Chastel, Weimerskirch and Jouventin, 1995) or if nestling diet influences offspring success (García-Navas and Sanz, 2011). In Chapter 4, I explored if the diet provisioned by high inhibitory control mothers afforded benefits to the nestlings in terms of mass on day eight, and did not find a relationship. Future research could expand this to look at fledgling mass (taken just prior to when the nestlings fledge – 15-20 days old) and survival of nestlings post-fledging (acquired by intensive re-capture efforts). It would be beneficial for diet to be sampled at day 8 (as already done) and day 15-20, to compare diet to the same time point as fledging mass, and to generate repeat measures to assess dietary consistency throughout the nestling stage. I suggest that the effects of dietary consumption be incorporated into ideas on how personality and cognitive traits are linked to reproductive success. This has previously not been done due to the difficulty of obtaining detailed dietary information, but molecular techniques to identify the diet are now more available and affordable (Laini *et al.*, 2020). Exploring if and how a behavioural type has increased body condition, survival or reproductive success due to its prey composition would improve our understanding of the fitness consequences of variation in cognition and personality for individuals.

Whether or not there is a functional advantage for individuals of consuming certain prey types, Chapters 4 and 5 suggest that birds are using resources in a way that is associated with their behavioural capacities. Despite this, an alternative explanation for the finding that behavioural traits are associated with the diet is that cognitive variation or exploration behaviour is linked to choice of nesting location so that individuals consistently end up in specific microhabitats depending on their behavioural traits, which may lead them to consume different prey. Thus, the

relationship between cognition or personality and diet may be indirect and mediated through habitat choice or habitat matching. Some evidence suggests that personality is linked to nest location as bold chestnut thrushes chose sites with lower nest density (Zhao *et al.*, 2016) and bold female eider ducks nested further from the shore (Seltmann *et al.*, 2014). Behavioural traits may be linked to diet through habitat choice in spring when the great tits defend nest box territories, but I also showed that cognition and personality were associated with diet in the winter when great tits travel in large flocks through the same microhabitats. This provides some support against the idea that the link between behavioural traits and diet is mediated by habitat type, at least in winter. To confirm that microhabitat use is not influencing my results in spring I would examine diet across years to see if great tits nesting in the same box have the same diet, whilst also measuring their cognition and personality. In addition, food availability is another important factor to consider when understanding how individual variation in behaviour contributes to the use of resources. Assessing if animals have access to the same food types would confirm the association between behaviour and diet and can be achieved by invertebrate abundance sampling. The association between behavioural traits and differential use of resources has implications for how behavioural types may adapt to changes in resource abundance.

Having examined the consequences for individuals, the next step is to consider the consequences of an association between behavioural traits and diet at the population level. First, individuals with different behavioural types consuming different prey will reduce competition at the individual level, which may increase the population size. For the association to act at the population level however, there must be underlying genetic variation (Morand-Ferron, Cole and Quinn, 2016). If this is not the case then early life effects, such as limited nutrition, stress, or poor early-environment conditions (Quinn *et al.*, 2016) may be causing behavioural types to consume different prey, which would not act at the population level. From this thesis, I cannot discern if the association between the behavioural traits and dietary composition are heritable themselves, let alone genetically correlated (Taylor *et al.*, 2012) and this would be an important aim for future research. Examining how the association between behavioural traits and diet might act at the population level

would provide insight into how behavioural trait and resource use variation is maintained, which has consequences for natural selection.

6.3.2 Cognition and personality as drivers of individual niche specialisation

In recent times, attention has focused on repeatable individual variation in diet, over and above variation caused by fundamental state variables, such as age, sex or morphology, termed individual niche specialisation (Bolnick *et al.*, 2003; Araújo, Bolnick and Layman, 2011). A number of mechanisms for this have been proposed (Bolnick *et al.*, 2003; Araújo, Bolnick and Layman, 2011), including the possibility that behavioural capacities when searching for or handling alternative foods influence differences in diet between individuals (Bolnick *et al.*, 2003; Svanbäck and Bolnick, 2005). Competition for resources mean individuals must choose alternative prey when their preferred option is not available and due to variation in cognition and personality, individuals may rank non-preferred resources differently, causing them to specialise on different prey (Bolnick *et al.*, 2003). This thesis has established that behavioural traits are associated with diet variation (Chapter 4 and 5), but to strengthen the argument that personality and cognition actually drive individual niche specialisation through effects on diet, repeat measures of diet and behavioural traits would be very valuable. Alternatively, the cross-sectional data from a single time point, such as I have in this thesis, could be supplemented with long-term data (e.g. stable isotopes; see section 6.2.1) (Bolnick *et al.*, 2003) to determine temporal consistency of diet. Although most behavioural traits are indeed repeatable (Bell, Hankison and Laskowski, 2009), whether this is also true for compositional data which forms a two dimensional matrix, the size of which would be determined by the number of samples x the number of species, is uncertain.

Investigating cognition and personality as potential drivers of individual niche specialisation allows us to understand more about how individual variation in behavioural traits contributes to the use of resources and success in different environments (Araújo, Bolnick and Layman, 2011; Dall *et al.*, 2012; Toscano *et al.*, 2016). Furthermore, establishing if the correlation between diet and the

behavioural traits occurs at the between or within individual level would allow us to investigate to what extent individual plasticity plays a role (Dingemanse and Dochtermann, 2013). If the correlation occurs at the within-individual level, this suggests individual plasticity plays a large role, for example, if inhibitory control ability changes within an individual, perhaps because of hormones, and this affects their diet accordingly. However, if the correlation between a behavioural trait and diet occurs at the between-individual level, this suggests individuals are consistent in how their behavioural capacities influence their diet (e.g. individuals with high inhibitory control will always have a certain dietary composition). This kind of analysis is very data hungry and to my knowledge has not been done in the context of behaviour and a diet matrix.

6.3.3 The effect of an interaction between demographic groups and behavioural traits on diet

In Chapter 3 I showed that two demographic groups, age and sex, varied in diet. From this, we might expect that cognition and personality could interact with age or sex to affect dietary composition. Although these demographic groups were included in the analysis with the behavioural traits (Chapter 4 and 5), I was not able to test for interactions between them due to small sample sizes. Irrespective of their cognitive ability, it may be the case that first years are constrained by their lack of experience of different prey types so all have the same diet, at least in their first winter, whereas adults show the association between cognition and diet (Figure 6.1a). The diet consumed by juveniles may be likely to have a larger effect on fitness than the adult diet because if they do not consume enough of the right foods, their cognitive development may be impaired which will impact them later in life. Particularly in their first winter, first year birds are unlikely to have the skills to find the right food and will have to learn which foods are good to eat, which may lead to them being inefficient foragers, thus having an impact on their energy and condition. Similarly, females that vary in their cognitive performance may not show variation in diet if they are foraging for particular food types needed for egg production (Fig. 6.1a), whereas the male diet should be less constrained. The

reverse situation could also theoretically be the case, with the diet of adults and males being less affected by their behavioural traits than that of first years or females respectively (Figure 6.1b). These scenarios would still show a difference in diet between individuals with 'low' and 'high' behavioural traits on average (Figure 6.1) that is indicated in the results of Chapter 4 and 5 in which birds with different behavioural capacities vary in diet.

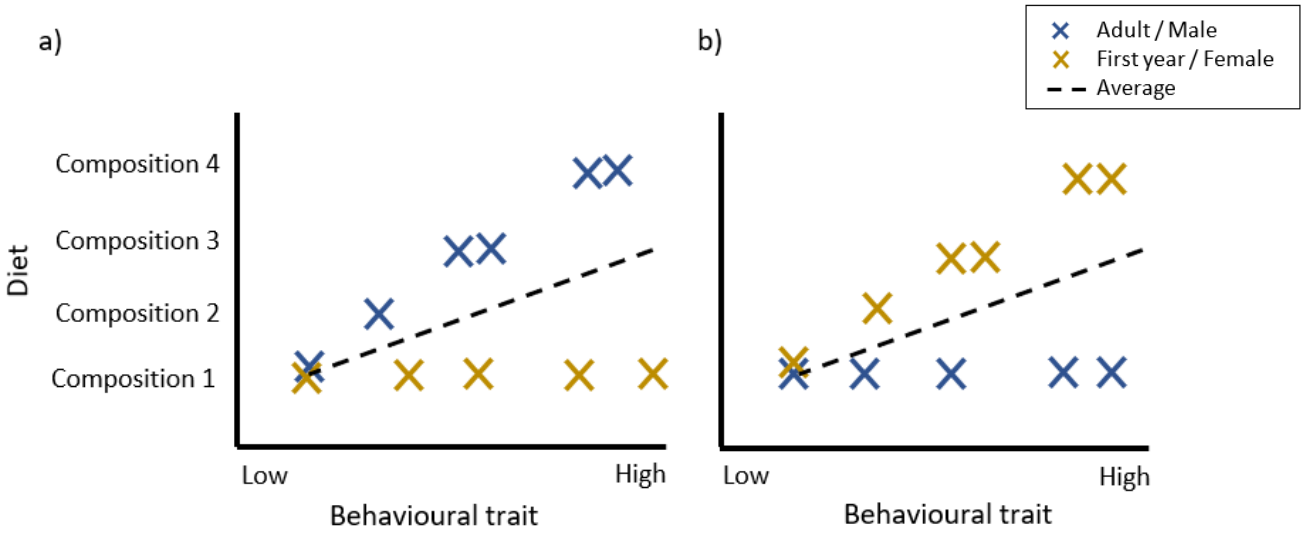

Figure 6.1. Two alternative hypothetical interactions between demographic groups (age or sex) and a behavioural trait, that correlates with dietary composition. Plot a) indicates variation in adult or male diet and a lack of variation in first year or female diet, with a behavioural trait, and plot b) indicates the reverse. The y axis indicates different types of dietary composition and does not imply that one is necessarily more complex than another. There can be any number of different dietary compositions, four are shown here for simplicity. Behavioural traits on the x axis represent two extremes of either ability for a single cognitive trait (e.g. spatial learning) or a personality axis (e.g. fast-slow axis).

6.3.4 Morphological features

Morphological features determine the prey types available to an individual (Aldridge and Rautenbach, 1987; Sampaio, Pagotto and Goulart, 2013), thus, associations

between behavioural traits and diet may be moderated by individual variation in morphology. For example, an animal's morphology may prevent it from innovating; if its beak is not strong enough or its tongue not long enough, it will not retrieve food from a puzzle box, tree trunk or termite mound, and this could affect the diet types it can exploit. In great tits, bill depth is important for handling efficiency of prey (Gosler, 1986) and may be especially likely to moderate the link between behavioural traits and diet in winter when birds consume both plant and invertebrate prey (Chapter 3). Deeper bills are needed for faster processing of beechmast (Gosler, 1986) and thin bills are more efficient for eating invertebrates. In the UK, great tits have longer bills than elsewhere in Europe and there is a suggestion that they have evolved in response to the high provision of seed feeders in gardens (Bosse *et al*., 2017). The interplay between diet, morphology and behavioural traits may not be straightforward. For example, diet can cause changes in morphology (Caumul and Polly, 2005) but morphology can constrain diet types (Wainwright, 1988). Moreover, personality can drive short-term morphological change (e.g. gizzard size; Bijleveld *et al.*, 2014) but selection may act on personality and morphology simultaneously. For example, bold zebrafish had a larger caudal fin, and thus a higher fast-start performance, than shy zebrafish, over four to seven generations and the authors attributed this result to trait coevolution (Kern *et al.*, 2016). Untangling these relationships would allow us to make predictions about how morphology constrains the association between behavioural traits and diet, and how the association might drive changes in morphology.

6.3.5 The direction of causation between behavioural traits and the diet is unknown

I have shown that cognition and personality are associated with the diet (Chapter 4 and 5) but the direction of causation for this relationship is unknown. On the one hand, personality has been shown to be stable in early life (Wilson and Krause, 2012) whereas diet composition frequently changes with age because of physical developments (e.g. larger claws for larger prey) or increased experience (Goss-Custard and Durell, 1987; Daunt *et al.*, 2007), suggesting that personality causes diet variation (Toscano *et al.*, 2016). Moreover, as previously mentioned, personality

traits are likely to influence the food animals encounter (Chapter 5, Troxell-Smith and Mella, 2017). On the other hand, limited and excess nutrients can strongly influence behaviour (Han and Dingemanse, 2015) and manipulation studies have shown effects of diet quality or nutrient availability on personality traits such as boldness, activity and exploration (reviewed in Langenhof and Komdeur, 2018; Han and Dingemanse, 2015, 2017). Resource use may influence energetic traits such as digestive efficiency (Britt, Hicks and Bennett, 2006), leading to an increase in available energy that promotes higher activity or boldness (Careau and Garland, 2012). Thus, the prey consumed by the great tits in one season may change their behaviour in the following season or year. Many studies linking diet to personality investigate the relationship in early life (Groothuis and Trillmich, 2011; Wilson and Krause, 2012). It is possible that early life nutrition could influence personality, which then influences diet in later life, thus the direction of causation goes both ways and may involve feedback loops.

Similarly, the causal direction between cognition and diet could be in either direction. As mentioned in this thesis, cognition is strongly linked to foraging success (Chapter 1, Raine and Chittka, 2008; Pasquier and Grüter, 2016; Rosati, 2017) so cognitive abilities are very likely to determine the prey that animals find, capture and process (Chapter 1, 4, 5). However, there is evidence that dietary components determine cognitive ability. For example, wild blue tit nestlings that received a taurine supplement were more successful than controls on a spatial learning task later in life (Arnold *et al.*, 2007). Furthermore, red-legged kittiwakes that were raised on a high lipid diet learnt to associate a coloured dish with a food reward faster than birds raised on a low lipid diet (Kitaysky *et al.*, 2006).

Because diet can have lifelong effects from an early age, and have short term effects at any stage of life, I suspect that early-life diet influences cognition and personality in the first place, and following this, established cognition capacities and personality traits form positive feedback loops with the diet later in life where both influence each other (Sih *et al.*, 2015; but see Niemelä and Dingemanse, 2018). So far, to look at the direction of causation between behavioural traits and diet, studies manipulate the diet and examine the effect on behaviour. To extend this thesis,

personality could be manipulated using hormone injections to increase activity level, cognition could be manipulated by extensive training to improve learning ability and the effect on the wild diet could be examined.

6.3.6 Behavioural traits may act in combination to influence diet

Due to correlated selection processes and their wide-ranging effects on behaviour, cognitive and personality traits may not act in isolation but instead are likely to interact to affect functional behaviours. So although I looked at effects of cognitive and personality traits independently, a number of them may interact to influence the diet. For example, memory of previous profitable foraging patches may be likely to influence the extent to which inhibitory control is involved in deciding when and what prey to eat (Anderson and Weaver, 2009).

Innovative problem-solving is a composite trait and is likely underpinned by many processes (Reader, Morand-Ferron and Flynn, 2016), but which specific mechanisms are involved in the link with diet is unclear. For example, inhibitory control has been suggested to contribute to how animals solve novel problems because finding a new solution requires inhibition of an old behaviour (Taylor *et al.*, 2009; Manrique, Völter and Call, 2013). In addition, exploration is likely to underlie innovative problem-solving because a high tendency to explore objects or locations increases the likelihood of developing a novel behaviour (Reader, 2015). Inhibitory control and problem-solving were both associated with plant composition, and exploration behaviour and problem-solving were both associated with invertebrate composition in the diet (Chapter 5), supporting the idea that these traits may underlie innovative problem-solving. To fully understand how cognition in particular is associated with the diet, future studies should consider how behavioural traits act in combination to influence functional behaviours such as foraging.

Personality and cognition may be expected to be correlated, as both refer to individual variation in behaviour, but results are inconsistent across species (Dougherty and Guillette, 2018). To understand if cognition and personality are linked, and if they have independent effects on the diet, it may be important to

know how they are controlled by the brain. There is evidence that different personality traits may be modulated by different brain regions. Boldness is related to the number of neurons in the basolateral amygdala in mink (Wiese *et al.*, 2018) but aggression has been linked to the hypothalamus in rats (Toth *et al.*, 2010). The hippocampus is well known as the region where spatial learning and memory operate and there is also consensus on the prefrontal cortex as the site of inhibitory control and other executive functions (Miller, 2000; Bryan *et al.*, 2004; Munakata *et al.*, 2011). Understanding where personality and cognitive traits operate in the brain can inform us whether selection might act independently on specific brain regions. If cognition and personality are independent, selection on cognitive traits involved in foraging will not have consequences for personality effects on foraging, and vice versa.

6.4 The importance of inhibitory control for diet and other behaviours

Chapter 4 focussed on the effect of one particular cognitive mechanism, inhibitory control, on the diet of adults and their nestlings. Despite a surge of interest in inhibitory control in recent years (MacLean *et al.*, 2014; Kabadayi *et al.*, 2016; Kabadayi, Bobrowicz and Osvath, 2018; Miller *et al.*, 2019), few studies have investigated how inhibitory control is associated with ecologically relevant behaviour. Chapter 4 has attempted to fill this knowledge gap by establishing a link between inhibitory control and foraging behaviour, by means of the diet. Additionally, I also explored the role of inhibitory control in parental care by investigating provisioning rate and the nestlings' diet.

I will now discuss i) the influence of inhibitory control and general cognition on parental care, ii) how inhibitory control might influence behaviours other than foraging and diet, iii) non-cognitive factors that might influence inhibitory control performance and other factors that might co-vary with inhibitory control to influence diet, and iv) whether inhibitory control is adaptive.

6.4.1 The influence of cognition on parental care

Parents vary in the amount of care they provide to their young and up to 20% of variation in care can be due to the individual (Westneat *et al.*, 2011). The idea that this variation may be explained by cognition has received very little attention in the literature (Wetzel, 2017). In Chapter 4, I explored whether the association between female inhibitory control and nestling diet had consequences for the offspring, and thus whether there was a link between cognition and reproductive success. Cognition was not associated with nestling mass or a higher content of different macronutrients in the diet but there was an effect of inhibitory control on provisioning rate; parents with higher inhibitory control provisioned their nestlings at a lower rate than parents with low inhibitory control (Chapter 4). Wetzel (2017) also found a relationship between cognitive performance (speed of problem-solving) and provisioning rate, though this relationship was in the opposite direction. It is difficult to know if a high or low rate of provisioning is beneficial for the nestlings without also knowing the quality of prey delivered. In a study on New Zealand robins, males with better memory performance gave a greater proportion of large prey items to their chicks and this was associated with a lower provisioning rate (Shaw *et al.*, 2019). This suggests males are provisioning quality prey over quantity, and this may also be the case for the great tits with high inhibitory control. To expand my work, I would establish the quality (e.g. palatability or energy content) of the diet fed to nestlings by parents with high and low inhibitory control, which would provide greater insight into how cognition impacts parental care.

There may be other consequences of the link between female inhibitory control and nestling diet for the offspring that I did not measure in the great tits, for example, survival, rate of growth or time to fledging. Offspring of male house sparrows that could problem-solve, had increased survival compared to the young of males who did not solve (Wetzel, 2017) and great tit nests with at least one solving parent had increased offspring survival (Cauchard *et al.*, 2013). In addition, the diet provisioned to nestlings may provide cognitive benefits and micronutrient content in particular has been linked to cognitive ability (Kitaysky *et al.*, 2006; Arnold *et al.*, 2007; see section 6.3.5). Furthermore, stress can affect the association between diet and

behavioural traits. Red-legged kittiwakes fed lipid-poor fish during development grew slowly and had increased amounts of the stress hormone corticosterone (Kitaysky *et al.*, 2006). These young then had a lower associative learning performance than kittiwakes fed an unrestricted diet (Kitaysky *et al.*, 2006). Similarly, great tit nestlings fed a lower biomass of caterpillars had a stronger stress response than those fed a higher biomass and this reflected faster exploratory behaviour later in life (van Oers *et al.*, 2015). Further investigation into the consequences of the provisioned diet for nestlings, including how dietary components lead to stress, will shed more light on the consequences of the association between parent cognition and nestling diet.

The cognitive ability of nestlings is likely determined by diet but it could also be determined by the cognitive ability of the parents. Inhibitory control has been found to be moderately heritable in pheasants (Langley *et al.*, 2020) and highly heritable in dogs and humans (dogs: Gnanadesikan *et al.*, 2020; humans: Crosbie *et al.*, 2013). The same may be true for great tits though the heritability of cognitive traits varies among species and populations (Boogert *et al.*, 2018). Even if inhibitory control is heritable in great tits, there is likely to be a genotype by environment effect (Boogert *et al.*, 2018) meaning both parental cognition and nestling diet may interact to influence nestling cognition. However, it is quite likely that the environmental effects are stronger than the genetic effects because an inherited high inhibitory control ability cannot be demonstrated by an individual if nutrition constrains the development of brain regions necessary for strong executive function (Scrimshaw, 1998; Georgieff, 2007; Munakata *et al.*, 2011). There is evidence that malnutrition early in life affects the brain, including regions responsible for cognitive development, which in some cases is irreversible (Levitsky and Strupp, 1995; Strupp *et al.*, 1995).

6.4.2 The influence of inhibitory control on other behaviours

While this thesis has shown that inhibitory control is associated with foraging behaviour and diet composition, other behaviours may also require inhibition of a prepotent response. For instance, inhibitory control may be necessary for a female

when deciding to stop nest building and start laying eggs. Timing of egg laying is determined by photoperiod (Meijer, Daan and Hall, 1990), temperature (van Balen, 1973) and food availability (Visser *et al.*, 1998) but cognition may also play a role. In years with warm springs, females that advance their laying to ensure the peak of caterpillar abundance matches the peak of chick demand will have higher fitness than those that do not (Lack, 1968; van Noordwijk, McCleery and Perrins, 1995). Inhibitory control could be involved in this process if the dominant, prepotent behaviour is to continue building the nest until it is finished. Similarly, females may use inhibitory control to determine when to stop laying and to start incubating their eggs. Results in Chapter 2 showed that birds with high inhibitory control showed greater foraging plasticity (when there was an equal choice between food values), thus, they may have a greater ability to flexibly adjust their nest building and clutch size to respond to environmental cues for successful breeding.

Another scenario in which inhibitory control may be involved during egg-laying and incubation is that of brood parasitism, where species such as cuckoos and cowbirds lay their eggs in the nests of songbirds (Johnsgard, 1997). Research has suggested that cognitive mechanisms such as learning and memory are used by host parents to recognise their own eggs and remove parasitic eggs (Moskát and Hauber, 2007), and inhibitory control may also be involved in this decision. If the dominant, prepotent response is to incubate the eggs, parents must inhibit this and remove foreign eggs from the nest. Similarly, for the brood parasite females themselves, inhibitory control may be involved in the decision about when to lay eggs in a host nest, to best avoid rejection by the host (White, Ho and Freed-Brown, 2009). For example, a brood parasite should inhibit laying eggs when the host is nearby, and should inhibit laying in a nest that already has a number of host eggs, because the host is likely to recognise the new parasitic egg (Moskát and Hauber, 2007).

There is evidence that inhibitory control is important for social behaviours (Amici *et al.*, 2018), for instance, the ability to withhold aggression towards a social partner when competing for food, or rejecting an undesirable partner in favour of a better one in future (Fawcett, McNamara and Houston, 2012; Wascher *et al.*, 2018). Extra-pair mating is a particular social behaviour that might be influenced by inhibitory

control. Great tits often engage in extra-pair copulation to increase fitness (Lubjuhn *et al.*, 1999) and there is evidence that males adjust the amount of parental care they provide to their nests based on the number of offspring they have fathered in that nest (Lubjuhn *et al.*, 1993). If females can inhibit extra-pair matings, they may receive more care from their social partner and have increased fitness. Similarly, if females can tell the extent of extra-pair matings obtained by their mates, and respond by increasing their own extra-pair matings, it may be in the interests of the male to not obtain extra-pair matings himself, so he can ensure full paternity of his social nest.

6.4.3 Other cognitive and non-cognitive factors that affect inhibitory control performance and how it is associated with diet

With the multitude of studies on inhibitory control in recent years (Kabadayi, Bobrowicz and Osvath, 2018), concerns have been raised over non-cognitive factors that may affect performance on detour-reaching tasks used to measure this cognitive trait. For example, motivation and experience with transparent barriers strongly influenced performance in pheasants (van Horik *et al.*, 2018) and orientation of the barrier and reward visibility can also affect how animals perform (Kabadayi, Bobrowicz and Osvath, 2018). There are a number of other tasks designed to measure motor inhibition which can get around some of these confounding factors. The stop-signal, go/no-go and A-not-B tasks do not require the subject to move around a barrier and do not use transparent materials (Amici, Aureli and Call, 2008; Verbruggen and Logan, 2008), so may provide more accurate indications of inhibitory control performance. However, to avoid confounding factors, subjects have been tested on multiple tasks, which does not always result in consistent performance (van Horik *et al.*, 2018), suggesting that inhibitory control is context specific and not all tasks are underpinned by the same cognitive mechanisms (Bray, Maclean and Hare, 2014; Brucks *et al.*, 2017). Although detour-reaching tasks are often used to measure motor inhibition as they require a subject to inhibit a physical response to attain a reward, other cognitive skills such as learning, task-switching and working memory may also play a role (Kabadayi,

Bobrowicz and Osvath, 2018). We still know little about which cognitive mechanisms are targeted by different tasks and studies with this aim will aid in our understanding of the evolution of cognitive abilities.

Whilst non-cognitive factors that might influence inhibitory control performance must be considered, it is also important to acknowledge that there may be other cognitive capacities that co-vary with inhibitory control to affect diet. First, visual perception is likely to play an important role when searching for prey and there is evidence that variation in perceptual performance can affect performance on detour tasks (Kabadayi, Bobrowicz and Osvath, 2018). Performance is improved when the barrier is not completely transparent as the perceptual pull of the reward is lessened (Lockman and Adams, 2001; Zucca, Antonelli and Vallortigara, 2005; Kabadayi, Bobrowicz and Osvath, 2018). Second, the ability to form a search image for a certain prey type may influence inhibitory control; individuals that can more efficiently form a search image and stick to it, will be better at avoiding prey that is not the target species (Langley, 1996). Finally, when deciding whether to choose an immediate reward now or to travel further to find something else, memory of a good patch that was visited previously may influence the decision.

6.4.4 How adaptive is inhibitory control?

Because of the role of inhibitory control in decision making that affects many aspects of life, we expect high inhibitory control to be beneficial for individuals. Indeed the definition of this executive cognitive function describes the inhibited behaviour as 'counter-productive' or 'not appropriate or needed' (Diamond, 2013; Isaksson, Urhan and Brodin, 2018). In the famous marshmallow test that assesses delayed gratification in children, it seems maladaptive to choose the smaller, immediate reward when there is only a small cost in waiting to acquire the larger reward (Mischel, Shoda and Rodriguez, 1989). Moreover, the consequences later in life for children with low inhibitory control are negative and can be extreme (Mischel, Shoda and Peake, 1988; Epstein *et al.*, 2010; Moffitt *et al.*, 2011). However, despite this, there may be situations when impulsive behaviour is not

disadvantageous and may have adaptive value (Bari and Robbins, 2013). For instance, inefficient inhibition may allow individuals to find non-obvious solutions to problems (Harnishfeger and Bjorklund, 1994) and there is evidence that impulsive people perform better than non-impulsive people when there is a short decision window, or when encountering very easy-to-solve problems (Dickman, 1985; Dickman and Meyer, 1988).

Inhibitory control may be more likely in situations where performing an inappropriate behaviour pays a very high cost, than when there is only a mild cost of the 'wrong' behaviour. Instances of such high cost behaviours are suppression of immediate pouncing in stalking predators (MacNulty, Mech and Smith, 2007) or stopping aggressive interactions with high-ranking individuals. Inhibitory control is very likely to be context specific (Tsukayama, Duckworth and Kim, 2012; Bray, Maclean and Hare, 2014; Amici *et al.*, 2018) and there may be some situations where high inhibitory control only confers a mild benefit. In this case, the strength of selection may be weak and there may be greater individual variation in inhibitory control ability. One such situation may be during diet choice. As previously mentioned, we know little about the benefit of diet choice for animals with varying inhibitory control abilities (Chapter 4 and 5) and it might be the case that the diet items consumed by individuals with low and high inhibitory control do not differ in the benefit they provide. Similarly, there may be situations where it is adaptive to show poor inhibitory control. For example, if an animal's diet consists of prey that is very patchy or unpredictable then having a high ability for delayed gratification does not provide an advantage as the likelihood of getting a better reward in the future is too uncertain.

Ecology is likely to play a role in whether a species should show high inhibitory control. For species where their ecology dictates their inhibitory control ability, there is likely to be low individual variation in inhibitory control. Common marmosets rely on tree sap so have to show high inhibitory control because this food product takes time to exude (Stevens, Hallinan and Hauser, 2005). Scrub jays are known for their well-developed delay of gratification abilities due to their reliance on cached food (Thom and Clayton, 2015) but the type of food they are

faced with may determine whether or not they show inhibitory control. For instance, perishable food may go bad if cached so individuals should not inhibit their response to eat it straight away. There is evidence that scrub jays are aware of the perishability of food as they have been shown to retrieve caches that contain perishable food quicker than non-perishable food, and know to avoid caches containing perishable food if a long time interval has passed (Clayton and Dickinson, 1998). Harnishfeger and Bjorklund (1994) suggest the idea that the best possible strategy for an individual is if they can choose to show low or high inhibitory control depending on the task at hand. In Chapter 2 I showed that birds with high inhibitory control had increased foraging flexibility (when the food rewards were equal) compared to birds with low inhibitory control. However, it may be the most beneficial and adaptive for individuals to show flexibility with their inhibitory control ability itself.

6.5 Conclusions and future directions

This thesis has provided insight into the behavioural mechanisms behind diet choice and flexibility of foraging decisions, and has shown the importance of ecological context in revealing how cognitive and personality traits are associated with foraging plasticity. I have explored implications of the association between behavioural traits and diet for energetics, body condition, reproductive success and survival. Chapter 4 suggests a role for cognition − inhibitory control in particular − in parental care that is driven by offspring diet and provisioning rate. Future studies should undertake empirical work to investigate the fitness consequences of individual variation in diet of self and offspring that varies with behavioural traits.

I have shown that cognition and personality are two causes of individual variation in foraging (assuming there is a causal relationship) but a big question still to be answered is why are there effects of personality and cognition on diet, and why is there individual variation in diet, given how critical food resources are for fitness? I primarily suggest that the reason is to reduce competition for resources (Chapter 3). But another possible answer could be frequency-dependent selection, which occurs

when the success of a phenotype depends on its frequency and shows how different behaviours can coexist at equilibrium (Wolf and McNamara, 2012). This selective pressure also may reduce competition if individuals with different behavioural traits consume different diets.

My thesis has investigated consequences for the success of individuals but great tits are social animals that aggregate in large flocks in winter and compete for and defend territories in the spring. Therefore, what are the consequences of the association between behavioural traits and diet variation for social factors such as social network composition, mate choice or dispersal? Perhaps individuals that use their behavioural traits to find the best quality food are more attractive to potential partners, or maybe those individuals that cannot effectively exploit resources in their environment, because they have a poor cognitive ability, are more likely to disperse.

My thesis provides the most comprehensive description of the diet in the great tit to date, and it does so for different life stages, sexes, and across habitat types and seasons. In addition, it provides support for the expectation that intrinsic behavioural traits linked to personality and cognition influence the dietary composition of animals, and shows the importance of ecological context in revealing associations between traits of interest.

6.6 Bibliography

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