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Plasticity of foraging strategies in the blue tit, *Cyanistes caeruleus* and the domestic chick, *Gallus gallus domesticus*

By

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This thesis is submitted in fulfilment of requirements for the degree of Doctor of Philosophy to Trinity College, University of Dublin

Department of Zoology
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February 2014

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Summary

This research was primarily concerned with dietary conservatism in wild blue tits, *Cyanistes caeruleus*. Dietary conservatism refers to the tendency for some individuals of a population to ignore novel foods. Dietary conservatism has been found to occur in a number of species of birds and fish. Previous studies into dietary conservatism have only been concerned with the presence or absence of the behaviour and its consequences for populations of novel prey species. These studies have shown that while there are individuals who readily accept novel food, adventurous consumers (AC), there are a number of individuals in the population who continue to refuse to accept novel food, these individual are referred to as being dietary conservative or DC.

This study aimed to determine whether there were costs associated with DC behaviour and if so could these costs be alleviated through plasticity in the behaviour. In order to investigate these ideas, wild blue tits were used as a study species, and where this was not possible domestic chicks were employed.

Experimental aviaries were used to replicate different ecological conditions, which might be experienced by foraging birds. Firstly the effect of intraspecific competition was considered, to see if the presence of other individuals of the same species would influence the decision to consume novel food. The results showed that DC individuals were more prepared to accept novel food when other foragers were present. A second experiment investigated the effect of the presence of a predator. In this instance the AC foragers began to behave similar to DC foragers indicating that there might some cost associated with evaluating novel food, which may reduce an individual's ability to detect predators.

The next set of experiments were concerned with properties of the novel food itself, such as the rate at which it was encountered and the length of time between encounters. These experiments revealed that the context in which the food was presented mattered greatly. When the food was presented to the birds in their captive housing boxes, they were more likely to refuse to consume novel food when they encountered it more often. Conversely when the food was presented to them in a more natural foraging setting, they accepted the novel food when they encountered it more often. When there was a short space of time between presentations, domestic chicks were willing to accept novel food more than chicks that experienced longer delays between subsequent novel food presentations. These experiments were also carried out using blue tits and deactivation of dietary conservatism did not occur, suggesting that the process is more complex in wild foragers compared to the domesticated chicks.

Finally the relative profitability of novel food was manipulated in an experiment involving domestic chicks. When novel food was more profitable relative to familiar food, AC foraging chicks were more likely to consume it. This was not the case for DC chicks. Their refusal to accept the novel food in these circumstances revealed a significant cost of the DC foraging strategy.

The findings of the experiments were then discussed in relation to overall plasticity of dietary conservatism and how ecological conditions might affect the ratio of AC and DC individuals in foraging populations. The results also reveal what kinds of conditions may have initiated the evolution of the behaviour and how it might be maintained in forager populations.

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1 General Introduction

1.1 Introduction

The central theme of this thesis is dietary conservatism and how it influences an individual's behaviour and decisions relating to novel food. As such, there are a number of areas within the behavioural ecology literature that are pertinent to this theme. Optimal foraging (section 1.2.1) is discussed in relation to the theory behind foraging and some of the empirical studies that investigate the predictions of optimal foraging theory (1.2.2). Within populations there can be differential resource use between individuals (1.2.3), as well as resource generalists and specialists (1.2.4). The next section (1.3) deals with the definitions of neophobia and dietary conservatism. This leads on to what is, to date, perhaps the most significant finding in relation to the study of dietary conservatism, that it may have facilitated the initial evolution of aposematism (1.4). I discuss how dietary conservatism may have first evolved, and how it might be maintained (1.5) and finally why it is an important behaviour to study (1.6).

1.2 Foraging theory and behaviour

1.2.1 Optimal foraging

Much of what is studied in ecology is governed by differences in survival and reproduction, both of which ultimately depend on the successful acquisition of sufficient nutrition. Emlen (1966) stated that finding and consuming food in an efficient manner is vital to the survival of an animal and therefore research into feeding and feeding preferences is essential in the field of ecology. What an animal feeds on is just as important as the techniques it uses to find food, and there are many characteristics of food and foragers that will influence the preferences displayed by individuals (Ivlev 1961), such as total food abundance, relative abundances of food types and the spatial distribution of food, as well as of other foragers.

Emlen (1966) constructed a model that examined these ideas, and, in doing so, made the assumption that individuals will prefer foods that maximise their net rate of energy intake. At around the same time, Mac Arthur and Pianka (1966) were also modelling foraging behaviour and made similar assumptions about how individuals forage. These two seminal papers became the foundations for what is now widely known as optimal foraging theory (OFT). Both papers came to similar conclusions, namely that when resources are scarce, every food item encountered should be consumed. Conversely, in a productive environment, an individual should become more restricted in its diet, concentrating on more preferred sources of food (Emlen 1966; Ivlev 1961; MacArthur & Pianka 1966).

There are many assumptions associated with current OFT, namely: that foragers can evaluate the profitability of food items in terms of energy per unit handling time: foragers can remember the average profitability of food types encountered: foragers can evaluate encounter rates with these varying food types and that they can use all this information to make decisions on what to consume. The main predictions of OFT are that foragers should always consume the most profitable items and that less profitable items should only be accepted when the level of encounters with more profitable foods falls below some critical threshold. In this way a forager's diet should vary in concert with environmental conditions and the characteristics of the food encountered (Hughes 1993; Stephens & Krebs 1986).

1.2.2 Empirical studies in OFT

In addition to this modelling approach to diet choice, empirical studies have highlighted many ways in which both the characteristics of the food, and the environment within which it is found, influence the choices made by foragers. For example Milinski and Heller (1978), found that sticklebacks, *Gasterosteous aculeatus*, foraging on water fleas, *Daphnia magna*, chose to attack the swarm of least density after they were exposed to a predator. This behavioural adaptation to the threat of predation revealed that there are occasions when foraging efficiency competes with some other task, such as avoiding a predator.

When considering foraging tasks in isolation, it may seem that the individual is behaving in a sub-optimal manner. However, when the context of the foraging task is included in our interpretation of the results, we begin to understand why the individual behaved in the manner we observed. In real world situations it would be rare that a forager can simply forage without having to consider any outside influences (Hughes 1993). There are a host of ecological conditions that influence diet choice, which are not limited to maximising net energy gain (Hughes 1993).

1.2.3 Differential resource use between individuals: resource polyphenism

Until relatively recently, much of the literature concerning population ecology has neglected the ecology of individuals, instead assuming that conspecifics were ecologically identical (Bolnick *et al.* 2003). There is, however, growing evidence of differential resource use between individuals of the same population, as touched upon by

Maynard Smith (1962) and then expanded by van Valen (1965). Van Valen (1965) observed that island bird species had a greater variation in resource use than mainland species. He attributed this variation to the fact that there was reduced interspecific competition on the islands, allowing increased between individual variation in resource use; effectively niche expansion in the population as a whole but with greater variation in interindividual resource use.

The occurrence within a population of individuals with differential resource use has been termed resource polymorphism or polyphenism, though perhaps the latter is more appropriate as it describes the existence of different resource phenotypes within a species. In the studies conducted thus far on resource polyphenism, two general conditions appear to be crucial, the existence of an underused resource and a relaxation of interspecific competition (Smith & Skúlason 1996).

The reduction in interspecific competition allows individuals to utilise a resource that may otherwise be used by another species as was the case with Darwin's finch, *Pinaroloxias inornata,* of the Coco's Islands (Werner and Sherry, 1987). These birds exhibit an array of foraging behaviours, which differ between individuals, allowing them to exploit resources that would be otherwise unavailable to them. The question then is why this occurs? If a group of individuals are sharing the same environment, how do they come to use the resources within that environment in a different way? Bolnick *et al.* (2003) state that individuals will use different resources if they have different preferences or abilities to use those resources, and that there must be some mechanism which is maintaining those different preferences and abilities. Ultimately, there is a trade-off between resource acquisition modes, whereby the ability to exploit a new resource diminishes the ability to use other resources (Ackermann & Doebeli 2004). Otherwise all individuals would have the same preferences and abilities when it comes to resource use. One therefore must assume that there is some cost (e.g. reduced efficiency in utilising other resources) to adapting to utilise alternative resources, but that cost is offset by the benefits brought about by being able to specialise on a particular resource, such as a reduction in intraspecific competition, improved foraging efficiency (Terraube *et al.* 2010) or improved breeding success (Golet *et al.* 2000).

1.2.4 Niche width, generalists and specialists

The idea that individuals within a population could use the available resources in different ways was further explored by Roughgarden (1972a) who coined the term niche Width which he defined as the variety of resources a population exploits. Roughgarden (1972) imagined that these resources could be ordered along a resource axis with a given width relating to the amount of resources available to a population. Within this population there are individuals of various phenotypes which utilise resources at different intervals along this axis. The example Roughgarden (1972) used were a species of *Anolis* lizards, which take prey of different sizes according to their jaw size, a morphological difference. It could equally be some behavioural or physiological difference, which causes the differential resource use. Roughgarden (1972) formulated a model, which predicted that there are an optimum number of individuals of each phenotype for a given set of resources and a given regime of intraspecific competition. When a balance is reached between these various phenotypes the largest population size is achieved with the minimum amount of intraspecific competition. If the thresholds of any phenotype go beyond the optimum number, a smaller population size is the result.

Subsequently there have been a number of studies revealing widespread interindividual variation when it comes to resource use within and across a wide range of taxa including insects (Howard 1993; Singer *et al.* 1989), fish (Fry *et al.* 1999) and birds (Werner & Sherry 1987). These and other studies have suggested the presence of individual specialists within populations. Bolnick *et al.* (2003) describes these specialists as "an individual whose niche is substantially narrower than its population's niche for reasons not attributable to its sex, age or discrete (*a priori*) morphological group". In order for an individual's niche to be narrower than its conspecific's niche, it is logical to assume that these individuals are not utilising some of the resources, which the rest of the general population are using, otherwise their respective niches would be the same width.

1.3 Neophobia and dietary conservatism

1.3.1 Neophobia

Foraging animals continually encounter novel items in their environment. Some of these items could be potentially valuable nutritional resources, while others could be harmful or possibly lethal. A choice must be made whether or not to consume the item. Most foraging animals display an aversion to such novel items, termed neophobia (Barnett 1958). This aversion is short lived and is generally overcome after repeated exposure to the novel item (Coppinger 1969).

A good example of this behaviour can be seen in rats, *Rattus norvegicus and R. rattus.* In the presence of man, both species have been subject to selection, such that avoidance of novel objects in their environment has been beneficial. They are viewed as pests by man and therefore every effort is made to eradicate them, including the laying of baits/traps intended to kill them (Cowan 1977). Neophobic reactions to novel items allow rats time to inspect and evaluate the potential danger of these items. This kind of avoidance behaviour has been observed in other mammals such as house mice *Mus musculus*, marmosets *Callithrix jacchus* ,sheep, *Ovis aries* (Burritt & Provenza 1997; Voelkl *et al.* 2006; Wolfe 1969) and in birds; blue jays *Cyanocitta cristata*, grackles *Quiscalus quiscula*, red-winged blackbird *Agelaius phoeniceus*, (Coppinger 1969), great tits *Parus major*, blackbirds *Turdus merula,* and robins *Erithacus rubecula,* among others (Exnerová *et al.* 2003; Exnerová *et al.* 2006; Marples *et al.* 1998) as well as in other taxa such as fish and amphibians (Mappes *et al.* 2005; Marples *et al.* 2005)

1.3.2 Dietary conservatism

Long term aversion to novelty, much beyond that of neophobia, is referred to as dietary conservatism (Marples *et al.* 1998). More specifically it is a refusal to include a previously unfamiliar item in the diet, despite the fact that it is no longer novel or unfamiliar (Marples and Kelly, 1999). This behaviour has so far been reported in some individuals in eight species of birds (Kelly & Marples 2004; Marples & Kelly 1999; Marples *et al.* 2005; Marples & Mappes 2010; Marples *et al.* 2007; Marples *et al.* 1998; Thomas *et al.* 2004) and five species of fish (Richards *et al.* 2011; Thomas *et al.* 2010). In contrast to individuals who are dietarily conservative (henceforth DC) there are individuals that are adventurous consumers (henceforth AC), who have little or no hesitation in incorporating novel items into their diet once their initial neophobic reaction has been overcome. The ratio of AC:DC individuals varies from around 3:1 to 2:1 for birds (Marples *et al.*, 1998) and a similar ratio of 2:1 in three-spined sticklebacks (Thomas *et al.*, 2010), but can be as high as 9:1 for some poeciliid fish (Thomas *et al.* in prep). So clearly there are individuals within a population with different food preferences and in most cases the DC individuals are in the minority. DC individuals prefer familiar foods, foods with which they have had some experience, while AC individuals will feed more or less indiscriminately on both novel and familiar foods, once neophobia has been overcome (Thomas *et al.* 2004; Thomas *et al.* 2010).

Marples and Kelly (1999) describe DC has having four distinct stages:

1 Visual inspection only

In this stage, novel foods are not manipulated in any way, they are simply observed but avoided.

2 Occasional sampling or acceptance only when familiar food is absent

Once individuals have become somewhat accustomed to the presence of the novel food, they will eat it, but only when familiar food is absent. The novel food is still regarded as a less attractive food source. If familiar food becomes available again, the novel food will then be avoided.

3 Regular acceptance as the last food eaten

At this stage the novel food is more readily accepted; it is becoming more familiar and is avoided less, but is still avoided more than the familiar food.

4 Full acceptance as a familiar food

The food is accepted as familiar with no avoidance, even in the presence of other familiar foods.

1.4 Dietary conservatism and the initial evolution of aposematism

1.4.1 Aposematism

Charles Darwin commented on the conspicuousness of some butterfly larvae, stating that he had become puzzled as to the reason for their conspicuousness. He could see no reason why they should be so brightly coloured (Darwin 1871). Wallace reasoned that in order for the larvae's distastefulness to be effective, they would need some outward sign to advertise the fact (Wallace 1867). It was from Wallace's observations that the theory of aposematism was developed; unprofitable prey gains an advantage by being brightly coloured or conspicuous, such that they are easily recognisable (Darwin, 1871). It was actually Poulton (1890) who coined the term aposematic colouration defining it as "an appearance which warns off enemies because it denotes something unpleasant or dangerous; or which directs the attention of an enemy to some specially defended or merely non-vital part" (Poulton 1890).

1.4.2 The problem of the initial evolution of aposematism

The evolution of aposematic colouration has been considered to be something of a paradox among empiricists and theoreticians alike. Many have argued that aposematism must have first emerged in an already defended cryptic species (Engen *et al.* 1986; Leimar *et al.* 1986; Sillen-Tullberg & Bryant 1983; Speed 2001). However the emergent species would face two immediate obstacles. Firstly they would be no longer protected through crypsis and, therefore, more open to predation from inexperienced predators. Secondly, by virtue of their rarity, they would be less likely to survive long enough to reproduce (Ruxton *et al.* 2004) as predators wouldn't know the meaning of their signal.

Aposematism works through the education of predators. Predators sample a number of defended individuals and, through experience, learn to avoid them. This strategy can only be successful when there are sufficient numbers of aposematic individuals present to counter the numbers lost during this education period (Ruxton *et al.* 2004). If there are low numbers of novel aposematic individuals present, then their survival rate is likely to be very low, with a large proportion of the population being killed as soon as they have been encountered by predators (Lindström *et al.* 2001; Speed 2001). Therefore, there must be some way in which the problems of conspicuousness, novelty and rarity can be overcome.

Mallet and Singer (1987) showed that once conspicuous defended morphs reach some critical frequency, their fitness would be greater than cryptic undefended morphs, as the cost of educating predators would be shared by a greater number of individuals. This, however, does not address the problem of initial rarity. To get around this, Mallet and Singer (1987), and then later Mallet and Joron (1999), suggested that stochastic factors, such as genetic drift and low predator numbers, could alleviate the problem.

1.4.3 Dietary conservatism and the evolution of aposematism

One other factor that has been investigated in relation to aposematism, is dietary conservatism (Lee *et al.* 2009; Lee & Speed 2010; Thomas *et al.* 2004; Thomas *et al.* 2003). In their study, Thomas *et al.* (2003, 2004) showed that it was possible for novel (artificial) morphs to survive and reach fixation (100% of the population) through the dietary decisions made by wild birds; more specifically, through their refusal to incorporate these novel morphs into their diet when familiar morphs were available, i.e. DC. It has been suggested that the design of the above experiments do not accurately reflect the foraging tasks experienced by wild birds (Marples & Mappes 2010) but they do at least hint at the possibility that dietary conservatism can play a role in alleviating the initial predation pressure felt by novel prey morphs.

Until relatively recently it was thought that there were only a limited number of conditions in which aposematism could have evolved (Guilford 1990), however, as reviewed in Ruxton *et al.* (2004) there are, in fact, many more ways in which it may have been possible, and some studies have indicated that the psychology of the predator could have been an important factor (Ruxton *et al.* 2004; Servedio 2000; Sherratt 2002; Speed 2001). Marples *et al.* (2005) discussed the importance of dietary conservatism as a contributing factor in the initial evolution of aposematism. They demonstrated that a novel conspicuous morph could, in some circumstances, have a selective advantage over cryptic morphs, even in the absence of chemical defences. Using wild birds in both natural and laboratory settings, they started by presenting the birds with artificial prey, most of which were familiar and only one of which were novel (Thomas *et al.* 2004). Presentations occurred on a daily basis and the proportions of novel and familiar prey were determined by their relative survival on the previous day. In most of the prey populations the novel prey went extinct but in some cases the novel prey survived and reached fixation (100% of the population).

1.5 The origin and maintenance of DC in populations

1.5.1 The origins of dietary conservatism

This all raises some important questions about dietary conservatism. Firstly, whether it was necessary for DC to be present in the predator/forager (henceforth I will just refer to foragers) population for aposematism to have evolved, and secondly by what mechanism it could have arisen and been maintained. Thirdly, whether there are any other conditions that could have selected for DC in forager populations. In order to answer these questions, one needs to have an understanding of the decision making processes of foragers, in the context of food preferences and ecological conditions.

If dietary conservatism aided in the initial evolution of aposematism, as has been suggested (Lee *et al.* 2009; Lee & Speed 2010; Marples *et al.* 2005; Thomas *et al.* 2010; Thomas *et al.* 2004; Thomas *et al.* 2003), then it must have arisen as an adaptation to something other than toxicity in prey species. There may be some set of ecological conditions that exist where a cautious approach to novelty would be advantageous. The environment is changeable, conditions vary temporally and spatially, there cannot be a single behaviour that is suitable for all conditions. If we focus on foraging behaviour, a strategy that is advantageous or beneficial in one set of environmental conditions may not be in another (Mery & Burns 2010). By investigating different ecological conditions and foraging contexts, this thesis hopes to determine what kinds of conditions are necessary for DC to have arisen and subsequently be maintained.

1.5.2 The maintenance of polyphenisms

There are a number of ways that behavioural polyphenisms may be maintained in a population (Roulin 2004). One is if the polyphenism is selectively neutral. However it seems unlikely that alternate foraging strategies could be selectively neutral. I have already mentioned how important foraging is to animals, so to suggest that the strategies they use to find food would not be shaped by evolution seems improbable.

It is also possible that AC/DC could be maintained through density dependent and/or frequency dependent selection, also referred to as balancing selection (Subramaniam & Rausher 2000). These conditions arise when the alternate phenotypes increase or decrease depending on their density or frequency within the population. For example, Losey *et al.* (1997) studied the effect of predation and parasitism on two colour morphs of the pea aphid, *Acyrthosiphon pisum*. They found that when parasitism was prevalent the red morph increased at the expense of the green morph, but when the level of predation increased, the green morph increased at the expense of the red morph. Something similar could be occurring for AC and DC birds, but until we investigate the influence of ecological and environmental conditions on these alternate foraging strategies, it would be unwise to speculate.

In my view, the most likely way the AC/DC dichotomy could be maintained is through disruptive selection, (Maynard

Smith 1962). For some measurable trait disruptive, selection favours the individuals at the extremes of a population. Disruptive selection is particularly influential when the selection regimes vary in either time or space or both (Maynard Smith 1962). If conditions which favour alternate behaviours change through time and fluctuate between conditions, this allows the polyphenism to be maintained. Similarly, when environmental conditions vary spatially, and in these spatially varied environments different phenotypes are favoured, these conditions can result in the maintenance of polyphenisms (Maynard Smith 1962; Roulin 2004)

1.6 Why is dietary conservatism important?

Studying dietary conservatism is important for a number of reasons. Firstly, studies investigating dietary conservatism are in their infancy. At the moment it is unclear why this behaviour evolved in the first place. Dietary conservatism is likely to have evolved as a response to some ecological selective pressure related to food choice. It may have simply been a response to the unknown profitability of novel food. Investigating the responses of both AC and DC foragers under different ecological conditions and presenting novel food in different contexts, should reveal whether there are other existing conditions, which could have facilitated the evolution of dietary conservatism.

Another reason to study dietary conservatism concerns the costs and benefits of the behaviour. Avoiding novel prey can be beneficial, especially if those novel prey are defended. If they are not defended, then ignoring these prey could represent a significant cost to the forager, if these items are profitable. It is not currently known how the relative profitability of novel prey influences diet choice. It is also unclear whether there is any degree of behavioural plasticity associated with dietary conservatism. This is perhaps the most important question of all. Plasticity in this trait might then alleviate some of the apparent costs of avoiding novel profitable prey. However, there may also be unknown costs associated with consuming novel prey, which may also be revealed through investigation.

There are also broader applications to the study of dietary conservatism. Though this field of research is in its infancy, dietary conservatism has been found in a diverse range of animals, most notably fish and birds. There is also unpublished evidence of existence of the trait in frogs, newts and possibly *Drosophila* also. Thus the influence of dietary conservatism could be quite far reaching. This would make the findings of this study quite important; there have been numerous studies that have identified range shifts among a wide range of species (Davis & Shaw 2001; Li *et al.* 2010; Parmesan *et al.* 1999) attributed to climate change and habitat destruction. Additionally changes in species phenology have become increasingly frequent (Robinet & Roques 2010; Visser *et al.* 2003; Visser *et al.* 2004), all of which could lead to mismatches between foragers and their familiar prey.

An understanding of when individuals will choose one type of prey over another and the conditions in which these choices occur is vital to future studies into behavioural and evolutionary ecology. More accurate insights into diet choice will aid in the construction of more complete models, as well as improving our ability to conserve and manage dwindling populations. As highlighted above it may also improve our understanding of evolutionary processes, such as the emergence of aposematic individuals.

1.7 Study subjects: The blue tit and the domestic chicken

1.7.1 The blue tit, Cyanistes caeruleus

Blue tits are small passerines which belong to the family *Paridae* (Svensson *et al.* 1999). They mainly inhabit lowland deciduous woodland and farmland but can also be found in suburban parks and gardens. They feed on a variety of different foods, including fruit, insects and seeds (Perrins 1979). They are more generally leaf gleaners, feeding on the insects found on the leaves of trees, but will feed on the ground on occasion. Their breeding season begins in April/May and clutch sizes can range from 7- 13 eggs (del Hoyo *et al.* 2007). Blue tits are extremely common in the greater Dublin area, and by far the most common bird caught while mist netting for test subjects (*pers. obs.*) in scrub and woodland habitats.

The fact that they are easily captured and cared for makes them very suitable for behavioural studies. Though sample sizes of wild birds cannot match what could be achieved through the use of standard laboratory animals, such as the domestic chick, research involving wild birds is more likely to yield results which are more reflective of the behaviour of wild birds.

1.7.2 The domestic chick, Gallus gallus domesticus

The chicks used in this study were one day old males of the strain Cobb 500. These chicks are commonly used in laboratory experiments. They arrivedv in the lab on the day they hatch and this makes them very suitable for diet choice experiments. Upon arrival in the lab they are still feeding off their yolk sac and will have never experienced any kind of food. This 'naivety' in relation to food makes them particularly suitable for the work contained in this thesis. They are easily kept and it is easy to obtain much larger numbers of chicks compared to wild passerines, thus they are useful for experiments requiring larger sample sizes.

1.8 Chapter summaries

This thesis aims to investigate the effect that ecological and environmental conditions have on the foraging strategies displayed by birds, and whether or not the underlying level of dietary conservatism exhibited by the forager plays a role in these decisions. Of particular interest are the differences between AC and DC foragers and whether these differences remain under different ecological conditions.

Chapter two describes the general methods and husbandry common to all the experiments contained in this thesis. The method of capture and husbandry of the blue tits was the same for every group of birds used. The methods of training and familiarisation may have varied slightly between groups but where that occurred it is highlighted in the relevant chapter. Similarly, the chicks were all sourced from the same hatchery and kept in the same conditions and where training methods were different these are highlighted in the relevant chapter.

Chapter three attempts to answer some important general questions, which I feel needed to be answered before delving into some of the broader topics explored further on. One such question involves the administration of the 'DC test', and specifically, whether, having taken part in a DC test, individuals' subsequent reactions to novelty were influenced by having done so.

A second question involves the working definition of neophobia. The behaviour we investigated is dietary conservatism, which becomes active once neophobia has waned, so it is important to know exactly when neophobia ends. Some studies use the latency to approach novel food as an indication of the end of neophobia (Brigham & Sibley 1999), while others have used contact with the novel food itself (Marples *et al.* 1998). These two alternatives were investigated and discussed.

Next I looked at the possible correlation between DC and neophobia. This was important for a number of reasons. Firstly, if the two behaviours are not correlated then this adds further weight to the suggestion that they are distinct from one another. Secondly, if any correlation does exist examining this would make it possible to determine whether or not DC and neophobia are part of a broader behavioural syndrome.

I then took the analysis a step further by examining the data for grouped clusters of similar data points. If clusters exist within the data, then examining where these clusters occur should provide clues as to the nature of the relationship between AC and DC foragers and whether or not they represent distinct foraging strategies.

Chapter four looked at intraspecific competition and asks whether the presence of a competitor reduces the level of dietary conservatism displayed by foraging blue tits. Competition reduces food availability through both interference and exploitation competition. Chapter four focused on exploitation competition, but, specifically the effect the presence of a potential competitor has on the dietary decisions of the forager.

Chapter five looked at the influence of the threat of predation on diet choice. Prior to this experiment it was unclear how dietary conservatism might affect behaviour in relation to diet choice and predation threat. Generally speaking dietary decisions made under the threat of predation have evolved to increase the ability of foragers to detect the predator; how that is achieved when novel foods are among the foods available was previously unknown.

Chapter six investigated the context in which novel foods were encountered by foragers and whether that influences their decision to eat them. Foraging theory dictates that when profitable foods are encountered at high rates they should be exploited. If those foods are novel, and the forager is DC, is a high encounter rate enough to deactivate their aversion to the novel food? Similarly, did the temporal distribution of the encounters alter the decision of whether or not to eat them?

Chapter seven looked at the influence of handling time on diet choice. By increasing the handling time of familiar food compared to that of novel food, we hoped to determine how AC and DC foragers responded.

The thesis ended with a discussion chapter drawing together the findings of all the experiments, firstly in relation to general forager behaviour and ecology. Then, by looking at the broader implications of the results, I considered how the AC/DC ratio might be influenced by different ecological conditions and how differences between the behaviour of AC and DC foragers contribute to the hypothesis that they represent distinct foraging strategies. Finally I discuss how these two alternate foraging strategies might be maintained in populations of foragers.

2 General Methods & Husbandry

2.1 Blue tit capture, housing and training

2.1.1 Capture

There were two methods used to capture blue tits throughout this project. The first was traditional mist netting, which involves the use of fine nets approximately two metres in height and of lengths varying from ten to twenty metres. A number of sites were used in and around Dublin city. These were: the Trinity College Botanical Gardens in Dartry, a wooded area adjacent to Trinity College sports grounds in Santry, the grounds on the Trinity College campus itself and in Dublin Zoo in Phoenix park. Wild birds captured using this method were aged and sexed and standard biometrics were taken according to the guidelines set out by Svensson (1992). The birds were then ringed using coloured rings, as well as a metal ring containing a unique identification number. Birds were then placed in an aviary at Dublin Zoo or in the Trinity Botanic Gardens.

Mist netting was carried out under the supervision of Drs. David Kelly and Nicola Marples under license number R(B) 17/2007 from the National Parks and Wildlife Service of Ireland and F/CF/4601 from the British Trust for Ornithology. In addition to the licences of both Dr. Kelly and Dr. Marples, I also hold a ringer's permit licence no. BTO 5913 and NPWS 046/2013, which was only acquired in the third year of the study. Birds were held in captivity under the licence held by Dr. Marples B100/2756 (Dept. of Health and Children, Ireland). All experimental procedures have been vetted by the animal ethics committee of Trinity College Dublin.

Mist netting was carried out before, during and after the breeding season. No adults were taken during the breeding season; only fledged juveniles were kept for use in experiments at this time of the year. Outside the breeding season birds of all ages were used for experiments. Once it had been established that birds were in good condition they were used in the experiments.

For some experiments, see chapter 6, hand raised blue tit chicks were used. These were obtained from nest boxes which were located in the wood in Santry, Co. Dublin. Twenty-five nest boxes were placed on trees in the wood and their positions were noted. From early April, the nest boxes were checked on a weekly basis. Initially the presence of nesting material was noted, followed by the presence of completed nests. Once the nest boxes were occupied and in use by a breeding pair, the date of laying of the final egg was noted through daily checks. Once the last egg had been laid, the hatching date could then be calculated by adding the incubation period for blue tits to the date the final egg had been laid. The incubation period for blue tits is 12-19 days. When chicks were between ten and twelve days old they were removed from the nest box. We did not wish to remove entire broods so more than half the brood was always left behind in the nest box to avoid abandonment by the parents. Chicks were transferred to an insulated box containing heated gel packs and an artificial nest. This is where the chicks were housed until they fledged.

2.1.2 Housing

For this project there were two experimental aviaries available for use. The first of these were located on the grounds of Dublin Zoo and consisted of twelve individual housing units arranged in rows of six facing one another (See Figure 2.1.1 below) divided by a green mesh screen, which obscured observation of opposite units during experimental procedures. Each unit measured 2m high by 1.6m wide by 2m deep and had a bare earth floor with sticks and wooden perches, plants and other woody debris to simulate natural conditions. Each unit also contained a feeding hatch and platform which allowed easy delivery and removal of water and food dishes. These feeding hatches were easily observable during experiments as this was where the birds came to feed. The hatches were surrounded so as to obscure the view of the feeding dishes from neighbouring pens, in that way birds could not see what a neighbouring bird was eating. Part of the roof of each unit was exposed to the environment through wire mesh ceilings allowing experience of natural weather and light patterns while the other half of the ceiling was covered by solid metal sheeting to provide some protection. Each unit also contained a nest box with bedding material, should the birds decide to roost there overnight. Inside the aviary building, a walkway allowed front-access to each wire-mesh unit through individual full length doors. Birds were housed individually during the breeding season while still having auditory and visual contact with their neighbours and were held in groups of two to three outside the breeding season. This was in part to allow for the natural flocking behaviour of adult blue tits in the winter and of newly fledged juveniles in the summer. It also served to allow the younger birds to feed more easily on food sources they were perhaps unfamiliar with (*pers. obs.*)

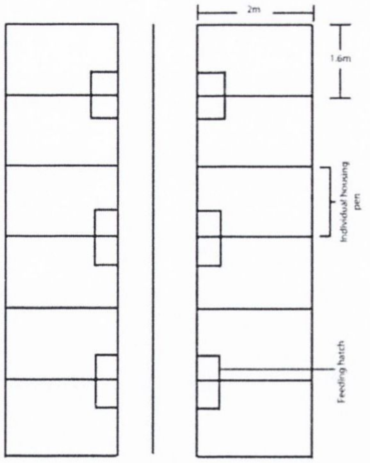


Figure 2.1.1 Diagram of the Dublin Zoo aviaries.

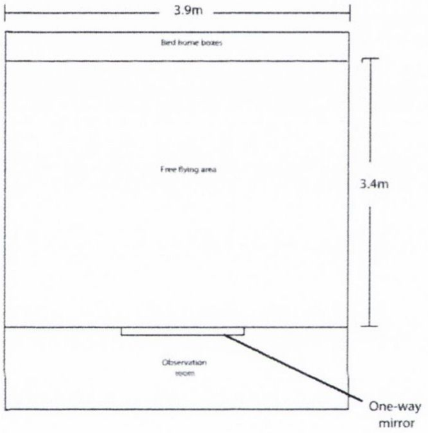


Figure 2.1.2 Diagram of the Dartry aviary

The second of the experimental aviaries was located in the Trinity College Botanic Gardens in Dartry. This aviary consisted of twenty individual plywood housing boxes (65cm x 80cm x65cm). These boxes were placed on shelves in a four x five grid at one end of the aviary. The rest of the aviary was made up of an free flying room, with the floor 3.4m x 3.9m (height of the room was 2.5m) covered in sand. External to this room was an observation room which allowed the monitoring of the free flying room through a one-way mirror. The interior of this mirror (the side which was in the free flying room) was covered by a fine mesh to prevent the birds from colliding with the mirrored glass or seeing their reflection in it (fig 2.1.2).

The individual housing boxes had two doors (not shown in figure 2.1.2), one larger door for letting birds in and out and a smaller flap at the bottom for the delivery of food and water. Each individual box contained a removable floor to allow for disposal of waste food and bird faeces, these could be washed and replaced into the boxes. They also contained a number of perches, both solid and flexible, which the birds could use to perch on when feeding, as blue tits habitually feed in this manner. There was no source of external light so behind each box was an L.E.D light source to simulate day light, controlled by a timer. Birds were observed through either the flap at the bottom or a sliding viewing window on the door.

The birds could be easily let out from their boxes by simply opening the main door of that box, and they could be enticed back into their housing box from the experimental room by turning the lights out in the room, but leaving the light of the required box on, as blue tits tend to fly towards a light source. Alternatively they could be caught by simply turning out all the lights and retrieving the bird from the wherever it landed. The first of these methods was preferable as it avoided any stress involved with being caught.

At both locations birds were fed with a mixture of wild bird seed, insect pate (Bird jungle, Keeper Road, Drimnagh Dublin 12, Ireland) and nuts *ad libitum*, supplemented with 2-3 live meal worms, *Tenebrio sp*. per day and suet balls. Water was available through gravity feeders, which were replenished daily as well as shallow dishes, provided for bathing. The individual boxes were cleaned and replenished with fresh supplies daily.

Blue tit chicks were kept in insulated polystyrene boxes with a maximum of four birds to a box. These boxes were filled with insulating materials such as wool and tissue paper, formed into an artificial nest. Heated gel pads were used as supplementary heat. Once fledged, the chicks were transferred to wooden boxes containing perches. These boxes were big enough (1m long x 40cm high x 40 cm deep) that the birds could fly around inside them, a maximum of four birds were kept in each box. Each bird was let out of their box two-three times per day so that they could fly around in a larger room. Until they were fledged the chicks were fed a mixture made of the ingredients in table 2.1.1 below.

Table 2.1.1 Ingredients which made up the paste fed to blue tit chicks prior to fledging.

Dried food	Amount (in cups)
Dried dog biscuit crumbs	3
Chick starter crumbs	1
Insect pate	1
1 hardboiled egg (including shell)	
10 drops of avian multivitamin syrup	

The dry ingredients were ground into a fine powder then sieved, water was then added to make a paste. The paste was stored in food grade freezer bags and placed in a freezer. When needed, the paste was thawed and fed to the chicks via a syringe. Chicks were fed every 45 minutes until they stopped begging for food. All faecal sacs were removed during the feeds and the nests were replaced daily. Upon fledging, the chicks were gradually weaned off the paste mixture onto meal worms, seed mix and green-dyed kibbled peanut.

2.1.3 Training

For the purposes of all the experiments, it was necessary that all the birds were familiar with green coloured kibbled peanuts. Some individuals would eat these straight away, while others would not. In order to ensure that the birds incorporated this food into their diet, a training scheme was devised. At all times the birds had green kibbled peanuts mixed in with their regular food so they became aware that it was food, then, for 2 hours every day they were given only green food. This period of time has proven to be long enough so as not to starve the birds, but at the same time encourages them to consider eating the green food. As well as green coloured food, the feeding and bathing trays were also green. Every effort was made so that the only food colours the birds saw were either green or that of their regular food (black, white, various browns). Individuals were observed until they were seen eating the green food, at which point they were considered to be trained to consider green a familiar colour. The period of time for an individual to be trained varied from one day to two weeks.

The green dye (and all subsequent dyes) for the food was prepared by mixing O'Brien's 'liquid green 90' food colouring in the ratio of 5ml dye to 500ml water for 500g of peanut. The kibbled peanut was then soaked in the dye for five minutes. The dye was then drained from the peanut along with any excess liquid and the food was dried at a low heat (~ 80-90 ^{o}C) in an oven for approximately 40 minutes depending on the quantity of peanut used. Drying the peanut in the oven kept the food from spoiling so that it lasted for 4-6 weeks. Table 2.1.2 below shows the recipes and food colourings used to prepare other coloured foods.

Table 2.1.2 Recipes for preparing the dyed kibbled peanut

Food Colour	Name of Dye	Quantities used
Green	O'Briens Liquid green 90	5ml of dye/500ml water/500g peanut
Red	O'Briens Liquid Col Christmas Red	5ml of dye/500ml water/500g peanut
Blue	O'Briens Liquid Col Blue	5ml of dye/500ml water/500g peanut
Orange	O'Briens Liquid Col Orange	5ml of dye/500ml water/500g peanut
Pink	O'Briens Liquid Pink	5ml of dye/500ml water/500g peanut

2.1.4 DC test

Once an individual was considered to be trained, they could then take part in the DC test. The purpose of these trials was to establish the baseline levels of DC which individuals expressed. The tests were carried out as follows. Before an individual took part in a trial they were deprived of food for one hour to ensure that they would be hungry and, therefore, motivated to eat during the trial. Food was offered in the green feeding trays to which the birds had already become accustomed. Three pieces of green food were offered alongside three pieces of novel coloured food; novel in the sense that the birds had never been offered food of this colour. The food was arranged in a circle with alternating colours. In the case of all the DC trials undertaken, the novel colour was red, and was prepared as described in table 2.1.3. Once the food was in place the trial began and the following times were recorded;

- Latency to make first contact with the feeding tray
- Latency to for each individual piece of familiar (green) food to be eaten
- Latency to make first contact with novel food

- Latency for each individual piece of novel food to be eaten

Each trial lasted for a total of twenty minutes or until an individual ate three pieces of novel food. Individuals were retested the following day if they did not eat three pieces of novel food up to a maximum of three trials at which point they were awarded the maximum time of one hour or 3600 seconds (3 x twenty minute trials). Using these data it was possible to calculate the following:

- Dietary wariness; the latency to eat three pieces of novel food, including the time taken to overcome neophobia
- Dietary conservatism; the latency to eat three pieces of novel food once neophobia had been overcome
- Neophobia; the latency to make contact with the dish containing the novel food.

2.2 Husbandry, training and experimental methods concerning domestic chicks

2.2.1 Source of chicks and housing

In each experiment, male chicks of the 'Cobb 500' strain were obtained from a commercial hatchery (Annyalla Chicks Ltd., Castlebury, Co. Monaghan, Ireland). They were held under licence number B100/2756 held by Dr. Nicola Marples.

The chicks were one day old when they arrived and were housed together in a wooden holding pen which was 200cm long x 60cm wide with 60cm high walls. The holding pen was subjected to 12:12 light: darkness at an ambient temperature of 24°C±4°C. Additional heat was supplied using two infrared heat lamps which were suspended in the wooden holding pens. The floors of the holding pens were covered in wood shavings to provide insulation and absorb chick waste. These pens were cleaned every two days and replenished with fresh wood shavings.

Upon their arrival at the laboratory, the chicks had not been fed, being reliant on the nutrients contained in their yolk sacs. This made the familiarisation with the green food required for use in the experiment all the easier. Upon their arrival, the chicks were fed on starter crumbs (William Connolly & Sons, Red Mills, Goresbridge, Co. Kilkenny, Ireland) which were dyed green. The procedure for dying chick crumbs was slightly different from that for kibbled peanut and is laid out in table 2.2.1 below Water was provided from gravity feeders placed within the holding pens. The dyed green starter crumbs were the chick's first meal, which resulted in their subsequent treatment of green food as familiar. Food and water were available *ad libitum* throughout the duration of the study, except for an hour prior to the commencement of the trials, when the chicks were deprived of food but still had access to water. This was done to encourage active foraging during the tests. Each chick was food deprived for an equal amount of time by ensuring that a chick was removed to an additional holding pen at the same rate each test was being carried out. Each chick was marked with a unique colour combination on the head for identification purposes, which had no adverse effect on the chicks. The marking also had no detectable effect on the chick's response to novel colours and, as shown in previous studies, the chicks did not respond to their own markings (Marples *et al.* 2007). Chicks were randomly assigned to treatments according to the experiment they were taking part in. The last 8 chicks to be assigned were designated as "buddy chicks" for the duration of a particular experiment, and were used as companions to prevent the experimental chick trying to locate the flock rather than feeding.

Table 2.2.1 Recipes and quantities for preparing coloured chick crumbs.

Food Colour	Name of Dye	Quantities Used
Green	Sugarflair Spruce Green	0.5mldye/90ml water/150g chick crumbs
Red	O'Briens Col Christmas Red	1ml dye/90ml water/150g chick crumbs
Blue	O'Brien's liquid Col Blue	1ml dye/90ml water/150g chick crumbs
Yellow	Sugarflair Egg Yellow/Cream	0.5ml dye/90ml water/150g chick crumbs

2.2.2 Pre-training

When the chicks were two days old, they were familiarised with their respective foraging areas (fig. 2.2.1). Over the course of either four or five pre-training sessions, each chick was placed in the foraging area and offered familiar green food. The sessions began with four chicks in the testing area at a time for two minutes, but each session contained progressively fewer chicks over less time, so that the final round consisted of one lone chick foraging with two buddy chicks behind a barrier, present for 30 seconds. Familiarisation is an important aspect of the experimental training, as it combats any contextual neophobia, which may occur during the testing stage (Brigham & Sibley 1999; Marples & Kelly 1999; Richards *et al.* 2011). During the pre-training sessions it was important to ensure that all the chicks ate the food once in the foraging area.

Buddy chicks were used in the pre-training and the experiments. They acted as companions for the foraging chicks, so that they did not become agitated or distressed at being alone while foraging. Buddy chicks were placed in a separate section of the foraging area and partitioned using chicken wire fencing. The benefit of using chicken wire is that visual and auditory contact could still occur between the test and buddy chicks, but the buddy chicks could not interfere with the test chick's foraging (Marples *et al.* 2007).

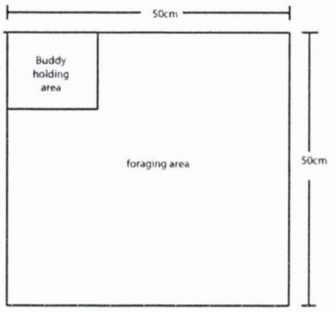


Figure 2.2.1 The chick foraging area

2.2.3 DC test

Once chicks had become familiar with the green food and the foraging arena to be used in a given experimental set up, they were ready to take part in the DC test. As with the blue tits, the chicks took part in these tests to establish baseline levels of dietary conservatism. The procedure was slightly different to that of the blue tits. Chicks tend not to be able to direct their attention to foraging tasks for much longer than 3 minutes, as after this time they begin to sleep or call out incessantly (*pers. obs.*). With that in mind, the DC tests needed to be tailored specifically for the chicks. As described above, before taking part in any experimental treatment the chicks were food deprived for an hour. All chicks were deprived of food for the same amount of time. This was achieved by partitioning the holding pens into an area containing food and an area containing only water. Chicks were then transferred into the area containing only water every three minutes. Once a chick had been food deprived for an hour, it was ready to begin its DC test. The chick was placed in the foraging area with two buddy chicks also present. Prior to transferring the chick to the area, three pieces of novel food and three pieces of familiar food were arranged alternately in a circle in front of the area containing the buddy chicks (the chicks tended to concentrate on this area of the foraging arena). The chick was then placed in the opposite corner of the foraging area and allowed to forage for a period of three minutes. As with the blue tits, the following information was recorded

- latency to eat each piece of familiar (green) food
- latency to first make contact with novel food
- latency for each piece of novel food to be eaten

Each trial lasted for a total of three minutes or until an individual ate three pieces of novel food. Individuals were retested the following day (or afternoon if time permitted) if they did not eat three pieces of novel food in the first trial. This was continued up to a maximum of three trials at which point they were awarded the maximum time of 540 seconds. Chicks were designated as DC if they did not eat three pieces of novel food within the three trials. Using these data it was possible to calculate the following:

- Dietary wariness; the latency to eat three pieces of novel food, including the time taken to overcome neophobia
- Dietary conservatism; the latency to eat three pieces of novel food once neophobia had been overcome
- Neophobia; the latency to make contact with the novel food.
-

2.3 Data analysis

The data were analysed using survival analysis. Survival analysis is generally used in medical studies, where time to an event (usually death) is the outcome of interest. As the latency to eating the novel food could be considered survival time for that food item, it is an analogous problem and therefore an appropriate way to analyse the data. In each experiment we were interested in a time to an event, such as the end of neophobia or dietary conservatism. These data are rarely normally distributed and mainly consist of many early events followed by fewer late ones (Clark *et al.* 2003). Additionally some events may not occur within the time frame of the experimental treatment, if at all, thus only some of the individuals in the experiment will experience an event. In traditional analyses such as ANOVA, this would bias the output of the analyses by underestimating the true (but unknown) time to the event; survival analysis however allows this to be dealt with by "censoring" these data. For example, the time taken for a blue tit to eat three pieces of novel food is the event of interest. Not all the individuals will do this before the experiment ends, so these data would be censored in the analyses. Where any other analysis was employed, it will be described in detail in the relevant section.

In some instances generalised linear model were employed to investigate the interaction between foraging trait (dietary wariness, dietary conservatism or neophobia), foraging strategy (AC or DC) and experimental treatment. Significant interactions in these analyses would suggest that the reactions of AC and DC birds to the treatments were different and thus warrants separate analysis of individuals with these foraging traits.

3 Pilot Studies & Preliminary Questions

3.1 Blue tits and neophobia; when does it end?

An important question to consider in the following studies is when exactly does neophobia end? In pilot studies carried out prior to beginning the work presented here, I was marking the end of neophobia as when the birds made physical contact with the novel food (Marples *et al.* 1998). However, in the course of the pilot studies, I observed individuals taking longer to approach the feeding dishes when novel food was present. This led me to hypothesise that perhaps the neophobic reaction to the novel food extends to the dish containing the food, and rather than making contact with the novel food, an approach towards it signals the end of neophobia. This aligns with the classic definition of neophobia (Brigham & Sibley 1999), which states that "neophobia is the initial avoidance of novel objects in an otherwise familiar location". With that in mind, the following experiment was designed to determine whether there would be justification for measuring neophobia as an approach towards novel foods rather contacting it. In order for the blue tits participating in these experiments to feed on familiar food, they must land on or in the small feeding dish (approx. 8cm in diameter) and pick up the familiar food which is no more than 1-2cm away from a novel piece of food; most individuals then carry the food away to eat on a perch, though some do eat directly from the dish. There is also the problem that many of the DC birds never make contact with the novel food so using contact as a measure of neophobia ending seems inappropriate for blue tits.

3.1.1 Methods

Twenty five blue tits (10 AC and 15 DC) were taken at random from a number of different studies and randomly assigned to either the control or experimental group. Birds were food deprived for one hour prior to taking part in the experiment. Birds in the control group were given a small food dish containing six pieces of familiar green food arranged in a circle. Birds in the experimental group were given three pieces of familiar food and three novel pink pieces, arranged alternately in a tight circle approximately 3cm in diameter. Birds from each group were tested consecutively and trials lasted as long as it took for the birds to make contact with the dish. The latency for each bird to make contact with the dish was recorded as well as the latency to eat from the dish. In addition to performing the experiment described above, data from the all of the blue tits (n = 63, 21 AC birds, 42 DC birds) used in the studies contained here were explored in order to determine which measure of neophobia was more reliable.

3.1.2 Data analysis

All of these birds had previously undergone a DC test (as described in Section 2.1.4) therefore their underlying foraging strategy was known. Gaussian generalised linear models with log links were used to investigate the 3-way interaction between latency to contact the dish, latency to eat from the dish and underlying foraging strategy.

3.1.3 Results

The three way interaction between latency to contact the dish, latency to eat from the dish and underlying foraging strategy was significant (Gaussian GLM, link= log, $F_{7,\ 42}$ = 5.135, P<0.001). Therefore it was necessary to analyse AC and DC individuals separately. For AC birds the 2-way interaction between latency to eat and latency to contact the dish was not significant (Gaussian GLM, link = log, $F_{3,\ 16}$ = 0.023 P = 0.881), therefore there was no difference between contacting the food and dish and eating from it. There was however a significant difference between treatments groups for latency to contact the dish; those birds whose treatments were without novel food were faster to make contact with the dish (Gaussian GLM, link = log, $F_{1,18}$ =23.316 P <0.0001). Similarly for DC birds the two-way interaction between latency to eat and latency to contact the dish was not significant (Gaussian GLM, link = log, $F_{3,26}$ = 0.359 P = 0.554). The difference between treatment was significant (Gaussian GLM, link = log, $F_{1,28}$ = 11.434 P < 0.01). Birds in the treatment without novel food were faster to approach the feeding dish.

Table 3.1.1 below shows that overall contact to the feeding dish as a measure of neophobia had lower variance and standard deviation compared to contacting the novel food (which was measured in experiments in the chapters to follow). Likewise for DC birds, measuring neophobia as the latency to contact the feeding dish was more reliable. There is however an important caveat for these data, there was a ceiling of 3600 seconds imposed on these values. Out of the 42 DC birds tested 20 never made contact with the novel food. Thus the mean and standard deviation calculated from these data have been underestimated, which makes any inference tentative. That said figure 3.1.2 below in conjunction with some of the figures in table 3.1.1 reveals just how variable these data were.

Table 3.1.1 Measures of variance, standard deviation and coefficient of variation for both methods of measuring neophobia. The value for coefficient of variation is expressed as the ration of the standard deviation to the mean.

	Contact Dish		Contact Novel Food	
	Variance	Standard Deviation	Variance	Standard Deviation
AC birds **n = 21**	18232	135	26465	162
DC birds **n = 42**	60752	246	2032579	1426

3.1.4 Discussion

It is clear from the results above that the presence of the novel food in the feeding dishes caused the birds to hesitate to approach the dish, therefore I would argue that this hesitation indicates an aversion to the novel food within the dish and their eventual approach to the dish therefore must indicate a waning of this response. Neophobia was first described in rats by Barnett (1958) and more recently reviewed by Brigham and Sibley (1999), who characterised neophobia as an avoidance of novel objects (including food) which waned over time when individuals had become familiar with the novel objects. Marples and Kelly (1999) described dietary conservatism as having four discrete stages: (1) visual inspection only; (2) occasional sampling or acceptance when familiar food is absent; (3) regular acceptance; (4) full acceptance as a familiar food. Somewhere between stages one and two neophobia has been overcome, and that may vary depending on the species in question. If we take the end of neophobia, as was originally proposed (Barnett 1958; Brigham & Sibley 1999), to be when novel food is approached, then it follows that approach to the food is regulated by neophobia whereas physical contact with the food is more likely to be regulated by the more complex dietary conservatism.

It was also interesting that there was no difference between the latency to approach the food dish and the latency to eat familiar food from the dish for both AC and DC birds, it adds weight to the suggestion that neophobia has indeed been overcome. Greenberg (1990) described a set of experiments on feeding neophobia in two species of sparrow (*Melospiza geogiana and M. melodia*), which demonstrated that there was a greater latency to feed in the presence of novel objects near to the sparrows' food source. Greenberg's results, combined with the analyses carried out here on the latency to feed once the food dish has been approached, further underline the argument that neophobia has been overcome.

Figure 3.1.2 (coupled with the data contained in table 3.1.1) provides a visual representation of the variation associated with each method of determining the end of neophobia, it would seem that for AC birds there is little difference between the methods, yet for DC birds the difference is quite marked. There is also the fact that many of the DC birds never made contact with the novel food but did feed on familiar food in the presence of the novel food, which, if Greenberg's (1990) results are applicable to blue tits, suggests that their neophobia has been overcome. Therefore, measuring neophobia as contact with the novel food grossly over estimates this figure.

In light of the results shown here, contact with the feeding dish in the presence of novel food seems a far more appropriate measure of neophobia for blue tits and such is the measure which will be applied in the experiments that follow.

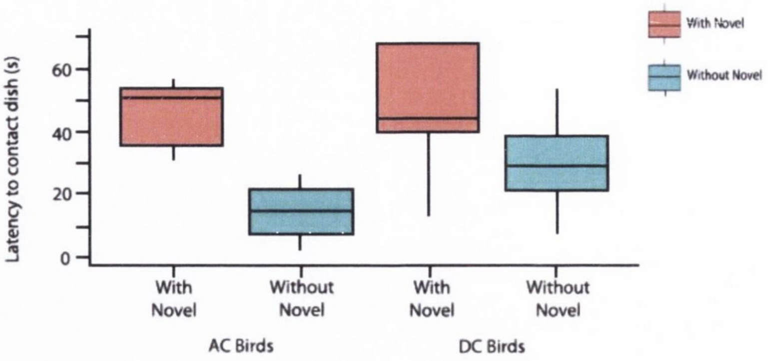


Figure 3.1.1 1 A boxplot of the latency to contact the feeding dish for both treatments

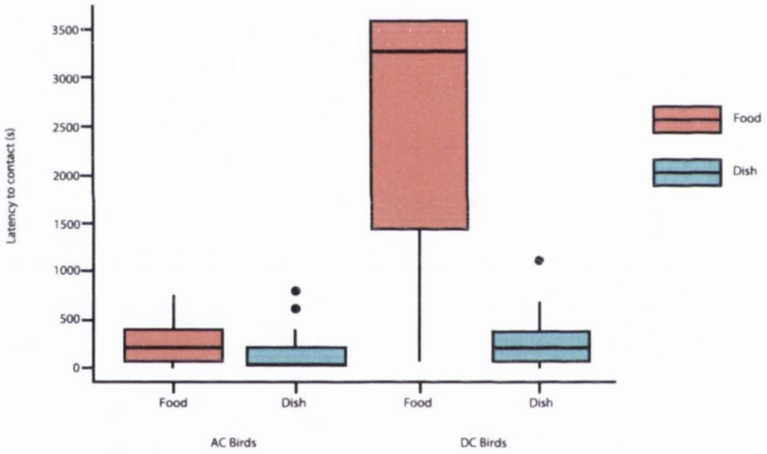


Figure 3.1.2 Boxplots showing the results of both measures of neophobia. The results come from the initial DC tests performed on all blue tits used in this project.

3.2 Does DC testing reduce subsequent levels of DC?

All of the experiments contained within this body of work require the individuals involved to take part in a DC test. This is necessary to establish whether those individuals exhibit a conservative foraging strategy (DC) or an adventurous one

(AC). Without knowing this before assigning individuals to treatment groups, would prevent the balancing of the two strategies across the treatment groups. Moreover, the purpose of these studies was to investigate differences between AC and DC foragers. The treatments that individuals took part in were specifically designed to either increase or decrease their levels of dietary conservatism, therefore attempting to ascertain what these were after the fact would be of no value because they would have been influenced by the treatments they had received.

With that in mind, it seems pertinent to ask the question, "does the administering of a DC test (as described in the general methods section) reduce dietary wariness in subsequent tests?" Marples *et al.* (2007) examined the effect of experience with novel food and the deactivation of dietary wariness in domestic chicks. They demonstrated that, if an individual consumed novel food, their dietary wariness would be reduced. However the extent of exposure needed to reduce wariness was quite prolonged. Those experiments revealed that without direct experience of eating the novel food themselves, as opposed to watching others eat it, there was no reduction in the chicks' overall wariness. The amount of experience with novel food required to reduce wariness varied according to the social context that the food was presented in, varying from at least 40 minutes to an hour.

The DC test exposes the chicks to novel prey for a relatively short period of time, so, based on the findings above, we would not expect the test to influence the response of the birds to the next novel object they encounter. However, it is necessary to test this directly, and to quantify any effect.

3.2.1 Methods

Thirty-three chicks were used in this experiment and were housed and marked as described in section 2.2.1. Before taking part in the experiment, the chicks underwent a two day training period. As soon as the chicks arrived at the laboratory they were marked to allow individual identification and placed in their holding pens (section 2.2.1) and pre-training was carried out as described in section 2.2.2.

Chicks were randomly assigned to either the control group or the treatment group. There were thirteen chicks assigned to the control group and sixteen to the treatment group. The remaining four chicks were designated as buddy chicks. Both groups of chicks received a DC test as described in section 2.2.3; the only alteration to the test was for the control group. Instead of three novel and three familiar pieces of food, the control group received 6 pieces of familiar food. The treatment group received the standard DC test of three familiar and three novel pieces of food. The novel colour in this instance was red and was prepared as described in table 2.2.1. On the day after these treatments were given, all chicks were tested for their response to a differently coloured novel yellow food in a second DC test. For each chick the latency to contact the novel food was recorded, as was the latency to eat each piece of food. From this I calculated the end of neophobia (contact with the novel food), dietary conservatism (the latency to eat three pieces of novel food minus neophobia) and overall dietary wariness (neophobia and dietary conservatism combined). The data were analysed as set out in section 2.3

3.2.2 Results

The results of the survival analyses are shown in table 3.2.1 below. They reveal that for all of the foraging traits investigated, the administering of a DC test had no significant effect on any of them. This is also clear from plots of the

Kaplan-meier survival curves in figure 3.2.1.

Table 3.2.1 Summary of the results of the survival analysis.

Foraging trait	**Survival anlysis results**			
	Z	Degress of freedom	P value	Distribution
Dietary Wariness	0.539	26	0.590	Weibull
Dietary Conservatism	1.05	26	0.296	Weibull
Neophobia	-0.44	26	0.660	Weibull

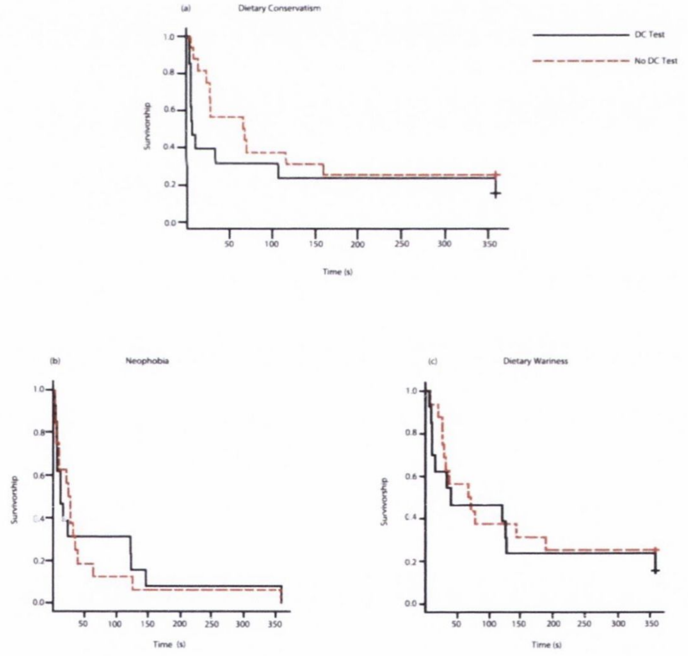


Figure 3.2.1 Survival curves for (a) dietary conservatism, (b) neophobia and (c) overall dietary wariness for both the DC test and No DC test treatments.

3.2.4 Discussion

Though it could be implied that deactivation of wariness can be achieved through experience with novel food, the results presented here, and those of Marples *et al.* (2007), demonstrate that it is only after certain amounts of time and social contexts that this occurs. The DC tests carried out on the chicks had no subsequent effect on the foraging traits investigated here. The type of exposure to novelty experienced in the DC test was not enough to deactivate or reduce any aspect of their dietary wariness. The chicks in the treatment with novel food experienced a total of nine minutes exposure to the novel food, which was not enough to reduce their neophobia effectively. This was also shown by Marples *et al.* (2007), who showed that at least 12 minutes was needed to reduce neophobia successfully. As dietary conservatism forms part of an individual's overall dietary wariness (Marples & Kelly 1999; Marples *et al.* 1998), if neophobia is yet to be overcome then it follows that dietary conservatism would remain unaffected until the neophobia has been.

Tests of these kinds have not been carried out on blue tits, but one would assume that because domestic chicks are selectively bred to gain weight, they are likely to be less wary than any wild bird. Thus it is also likely that deactivation of chicks' dietary wariness should be more readily achieved than it is for wild birds. In the absence of any reduction in wariness caused by the DC test, it is reasonable to assume that carrying out these tests prior to other experiments on dietary wariness will not alter subsequent reactions to novelty.

3.3 Are neophobia and dietary conservatism correlated?

Marples and Kelly (1999) argued that neophobia and dietary conservatism were two distinct processes which operated on different time scales and levels of complexity. Whereas, neophobia is short-lived and easily deactivated through experience of novel foods, dietary conservatism is longer lasting and deactivation occurs over a number of stages (see discussion in 3.1 above). Consequently, it is likely that neophobia and dietary conservatism operate independently. Initially, neophobia prevents the individual from approaching the novel food. Once this has been overcome neophobia has no influence over whether or not a food item will be consumed; this will be governed by dietary conservatism. If that is true, then there should be no significant correlation between neophobia and dietary conservatism.

Correlated suites of behaviour which are consistent across different contexts are referred to as behavioural syndromes (Sih *et al.* 2004b). It might be argued that neophobia and dietary conservatism are two behaviours which are part of a foraging behavioural syndrome, and therefore, by measuring neophobia one could accurately predict an individual's level of dietary conservatism. Studies into dietary conservatism have thus far neglected to investigate this relationship, instead concentrating on the existence of the trait (Marples *et al.* 1998; Richards *et al.* 2011; Thomas *et al.* 2010), its deactivation (Marples *et al.* 2007) and its role in the initial evolution of aposematic organisms (Lee *et al.* 2010; Marples *et al.* 2005).

The present study attempted to investigate the relationship between neophobia and dietary conservatism by investigating whether or not these two behaviours are in fact correlated.

3.3.1 Methods

For every experiment performed in this study I recorded the baseline levels of DC and neophobia for each individual before they took part in any experiment, as described in section 2.1.4. I examined these data for correlation using the R statistical software package (R Core Team, 2013) using the "cor" and "cor.test" functions. The non-parametric version of the test was used, the spearman's rank correlation. AC and DC birds were analysed separately.

3.3.2 Results

Table 3.3.1 below shows that the correlation between neophobia for both AC and DC birds was very weak. Further illustration of this point can be seen below in figure 3.3.1 and the associated r^2 values presented in the table.

Table 3.3.1 Correlation values of neophobia and dietary conservatism and their respective P values for AC and DC birds. R^2 values are also presented for figure 3.3.1

	Correlation	P Value	r^2
AC Birds **n = 20**	0.046	0.667	0.002
DC Birds **n = 43**	0.21	0.206	0.047

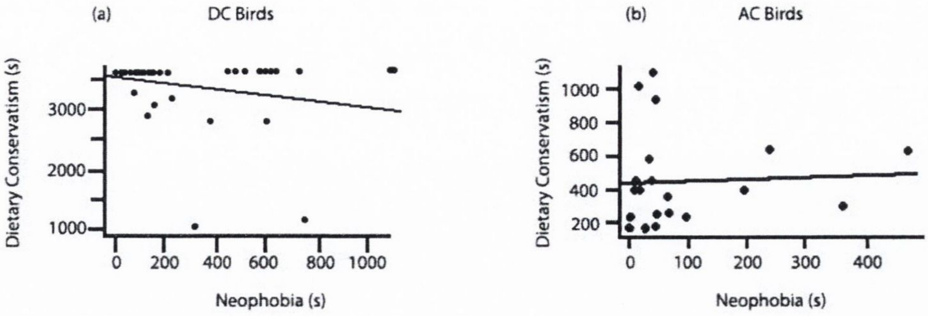


Figure 3.3.1 The relationship between neophobia and dietary conservatism for (a) DC birds and (b) AC birds.

3.3.3 Discussion

There was no relationship between the level of neophobia displayed by any individual and their level of dietary conservatism and this is important for a number of reasons. Firstly, this strongly supports the view that neophobia and dietary conservatism are two distinct processes (Marples and Kelly 1999). Secondly, it also indicates that neophobia and dietary conservatism do not form part of a behavioural syndrome. It might be tempting to assume that if an individual has a low level of neophobia, then that same individual would have a low level of dietary conservatism. However, the results reported here suggest that to do so would be incorrect.

Convergent validity (Campbell & Fiske 1959) investigates whether two tests measure the same trait, the test for neophobia and dietary conservatism are not correlated so represent two different traits (Carter *et al.* 2013). However, in order to categorically state that this is the case, would require a multi-trait, multi-method approach (Campbell & Fiske 1959), in which alternative measures of both neophobia and dietary conservatism would have to be derived and tested for convergent validity (Réale *et al.* 2007). Furthermore, by definition, for traits (measureable behaviours) to be considered part of a behavioural syndrome, they must be consistent across contexts (Réale *et al.* 2007; Sih *et al.* 2004b) and it will be shown in the experiments contained within this thesis that this was not the case for neophobia and dietary conservatism. There were many contexts where neophobia was reduced but DC was not.

While the work of Réale *et al.* (2007) does not intend to provide a structure for all behavioural studies, their framework is helpful nonetheless. They define each behavioural trait and also describe how best to measure it, they consider neophobia to be part of the exploration avoidance axis. Exploration of novel objects or areas provides information about them, thereby reducing their novelty (Greenberg & Mettke-Hoffman 2001), whereas dietary conservatism can only manifest itself once the object has been discovered and explored. Thus, while an individual may overcome their neophobia to novel foods in a very short space of time, their reluctance to consume that novel food may last much longer. The requirement to gather information about the food, it seems is governed by neophobia, while the decision of whether or not to eat it is governed by dietary conservatism (Marples *et al.* 2007).

3.4 Dichotomy or Continuum?

The existence of AC and DC foraging strategies as a dichotomy, rather than as a continuum of latencies to attack novel prey, is a matter of some debate, which has yet to be resolved. The genetic basis, and speed with which the two populations diverged under selective breeding (Marples & Brakefield 1995b), together with the consistency between the response to a DC test and subsequent behaviour (see experiments contained here), support the view that these strategies are distinct. However, if differences in behaviours other than latency to accept novel foods are found, which correlate with the two foraging strategies, then this would constitute stronger evidence that they are distinct strategies, rather than being a continuum of the extent to which a single strategy is expressed.

For the purposes of this study, it may also be revealing to carry out a cluster analysis to investigate the existence of groups within the data set. If the analysis reveals two separate groups, this would strengthen the argument further that AC and DC are two separate and distinct foraging strategies (Marples & Kelly 1999).

The identification of a clear dichotomy between AC and DC foraging strategies could be very important in future behavioural and ecological studies. Marples and Brakefield (1995) have already shown that reaction to novel food was a heritable trait in Japanese quail, and the results of the studies in subsequent chapters of this thesis reveal differences in reaction to novelty by AC and DC foragers. Therefore, knowledge of an individual's foraging strategies would allow a more accurate prediction of behaviours under different ecological conditions.

3.4.1 Methods

Using the entire data set from the blue tits and their initial DC tests a k-means cluster analysis (Hartigan & Wong 1979), but using the k- medoids method (Zhao 2013), was carried out. This method is more robust than the k-means method when considering smaller data sets and data sets containing outliers. This method of clustering also does not need the number of clusters to be specified prior to applying the analysis, unlike the k-means method. The analysis was carried using R statistical software (R Core Development Team 2013) and the ‘fpc’ package (Hennig 2010). The analysis returns the most likely number of clusters and the amount of variation that those clusters explain in the data. The function *pamk()* in the *fpc* package, returns a “clusplot” which plots the distance between the clusters as well as the clusters themselves and a silhouettes plot which gives an indication of the goodness of fit of the clusters.

The same analyses were carried out on data from chicks, but this was not the total number of chicks used in experiments. A separate batch of 32 chicks were obtained, cared for and trained as described in section 2.2. They were given a DC test as described in section 2.3 but instead of a maximum of three trials each of two minutes, these chicks were given a maximum of 14 trials. This was an attempt to eliminate any ceiling effects. However even after 14 trials with novel food eight of the chicks did not eat the novel food, yet these results should provide a clearer picture than that of the blue tits, because fewer of the data points are present as maximum latencies.

3.4.2 Results

Blue tits

There were a total of 63 blue tits used in the analysis, of which 22 had been identified as AC and 41 as DC using the methods described in section 2.1. The *pamk* function in R identified 2 clusters within the data, which contained 22 and 41 birds respectively (fig. 3.4.1 below). The silhouette plots revealed that these clusters were a good fit to the data (with 1.0 being a perfect fit) with S_i scores of 0.87 and 0.94 respectively.

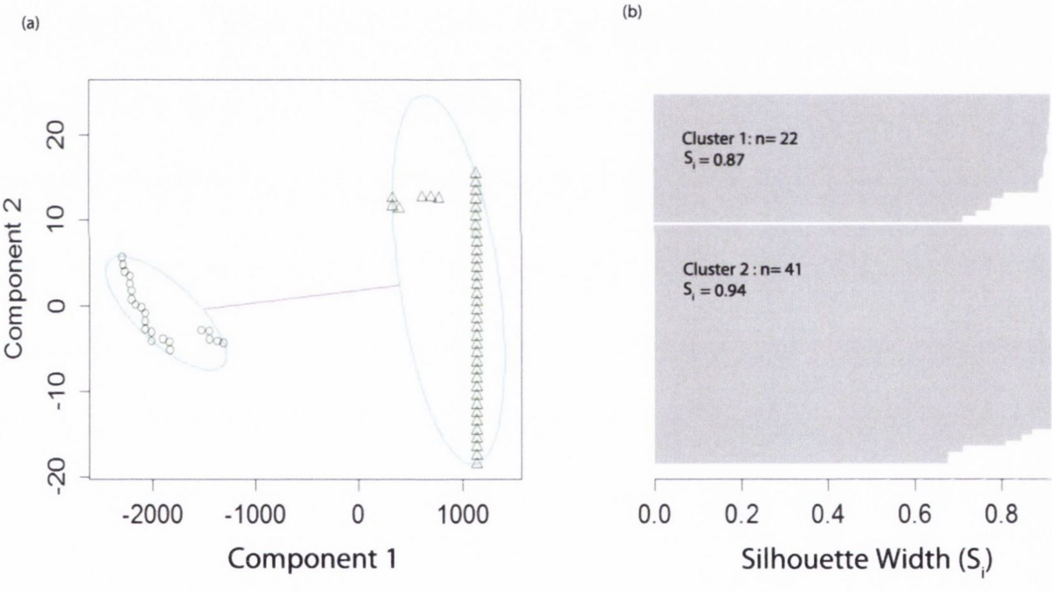


Figure 3.4.1 The results of the blue tit cluster analysis. (a) The 'clusplot' showing the 2 clusters and the distance between the clusters. (b) The silhouette plot, indicating the cluster size (n) and the associated S_i (silhouette information), values close to 1 indicate a perfect fit.

Chicks

There were a total of 32 chicks, and the cluster analysis revealed that they were grouped into two clusters of 20 and 12 chicks (fig. 3.4.2 below). The chicks in both clusters are split into the same groups as they had been previously by the methods outlined in section 2.2. The silhouette information (S_i) for the clusters was 0.95 and 0.77 respectively (fig. 3.4.2 below)

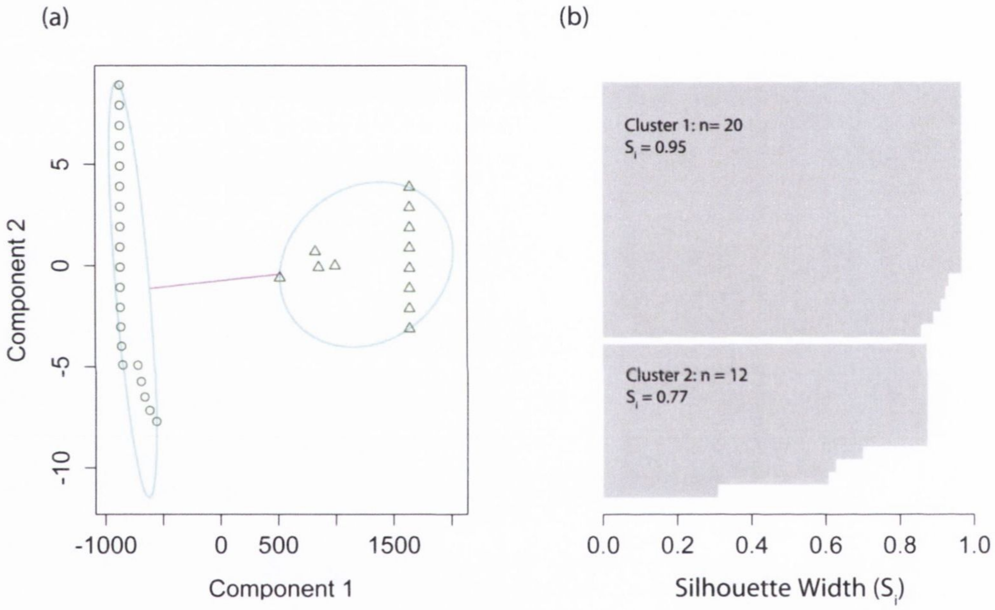


Figure 3.4.2 The results of the chick cluster analysis. (a) The 'clusplot' showing the 2 clusters and the distance between the clusters. (b) The silhouette plot, indicating the cluster size (n) and the associated S_i (silhouette information), values close to 1 indicate a perfect fit.

3.4.3 Discussion

The results have shown that there are potentially two, well defined clusters in each of the blue tit and chick data sets. The cluster analysis has split the blue tits and chicks in exactly the same manner as I did through the implementation of the DC test. However, the blue tit data contained many values that were simply maximum values. These data came from DC tests carried out before experiments and 34 of the birds never ate three pieces of novel and where thus given the maximum score for those trials (see section 2.1). Therefore even though the blue tit cluster analysis has revealed two well defined clusters, there is a possibility that those individuals, which never ate the novel food, may have carried on doing so for much longer. It is therefore possible that we would see a third cluster of more extreme DC latencies even further away from the first cluster containing the AC birds.

The chick analysis was an attempt to alleviate the inclusion of 'ceiling' data, maximum values attributed to birds that did not eat novel food over the course of the trials. However there were still some individuals that, even after two weeks of testing, still refused to eat novel food. Though there were fewer (only 8 individuals) in this non-eater group, compared to the blue tits, these could still represent a third group, consisting of more extreme DC individuals.

Nevertheless the analysis lends weight to the argument, that there are at least two distinct groups of foragers; one that contains birds willing to consume novel food (AC foragers) and one or more other group(s) that contains birds less willing to do so (DC foragers), and that the DC test separates them accurately.

The inclusion of the 'ceiling' values in the analysis is somewhat unsatisfying and a number of potential solutions exist. One would be to carry on recording latencies until all the individuals had eaten novel food. However, as stated above, a number of chicks continued to refuse to eat novel food even after two weeks of trials. The strain of chick used grows very quickly, and after two weeks they are difficult to manage and become less reliable for behavioural studies. Similarly wild birds can take weeks and even months to accept novel food (Marples *et al.* 1998), therefore finding a suitable animal model may prove difficult. A second solution might be to exclude these maximum values and impute the missing values, but this also has its problems. There are vast arrays of methods for imputing missing values, yet most of these rely on using mean or median values (Little & Rubin 2002), which I believe would be inappropriate for these data. We have no idea how long individuals might continue to refuse the novel food, so using the mean or median of the sampled individuals might grossly underestimate the true value. As yet, I have failed to find an appropriate method of imputation.

The AC/DC split in the groups of birds resulting from the DC tests was identical to the clusters found in the analysis. It may have been argued that this split was somewhat arbitrary, but the cluster analysis suggests otherwise. Even though there may be more than two groups, there are two distinct groups, which differ in their reaction to novel food.

4 Competition influences conservatism in the blue tit

4.1 Introduction

Individuals which feed in groups are often subject to increased intraspecific competition and, therefore, lower levels of resource intake (Cresswell 1998a; Cresswell 1997, 1998b; Davis *et al.* 2011; Sansom *et al.* 2008). Cresswell (1997), for example, demonstrated that even with relatively few competitors, significant reductions of resource intake can occur in foraging blackbirds. Individuals' ability to cope with competition will not only affect their fitness but also their distribution both locally and in more general terms. Sansom *et al.* (2008) illustrated how flocks of foraging redshank, *Tringa totanus*, suffered reduced food intake, increased movement within local foraging patches as well as movement to less competitive sites. Many species have dealt with interspecific competition by carving out their own particular niches, but for species which feed socially, the most direct competition they will face will be from conspecifics. Here we investigated the effect of just such competition on the expression of dietary conservatism in wild blue tits, which are known to move around in flocks at certain times of the year (Hegner 1985; Hogstad 1987, 1989) and thus likely to experience just such intraspecific competition.

Familiar foods are the preferred resource of DC foragers and these may become scarce due to the presence of competitors. Optimal foraging theory (Stephens & Krebs 1986) states that if this happens, some other, less preferred resource should be utilised, in order to reduce foraging costs. If DC foragers do not attempt to broaden their diet by including unfamiliar items, then the cost of being DC will increase under these conditions.

Some studies have already revealed that the presence of a competitor can act as a signal, to an individual, of imminent resource depletion (Lucas 1987; Plowright & Landry 2000; Plowright & Redmond 1996). In their studies on pigeon foraging behaviour, Plowright and Redmond (1996), and subsequently Plowright and Landry (2000) demonstrated that it was possible to separate the effect of resource depletion and the presence of conspecific competitors. They did this by obscuring the amount of resources available to the pigeons in a foraging bout in the presence of a competitor that resulted in the pigeons becoming less choosy about the food they ate. They argue that this was due to the fact the pigeons were able to associate the presence of conspecifics with a potential depletion of resources, thus, reducing the amount of time left to forage. Others have argued that in this situation individuals should become less choosy to maximise resource use in a foraging bout (Davis *et al.* 2011). Mc Mahon *et al.* (in prep.) studied the effects of competition on foraging domestic chicks, in relation to dietary conservatism and found differences in behaviour between conservative and adventurous foragers. DC birds became less conservative when competitors were present, when both novel and familiar foods were conspicuous, as did AC birds. However, when familiar food was cryptic and all food was harder to see, they found that DC birds remained strongly DC whereas AC birds showed a reduction in DC. The authors interpreted this difference as a suggestion that the AC birds considered the competing forager as a rival, while the DC birds treated it more as a social partner, copying its food choice when able to see it.

The present study extends the work of Mc Mahon *et al.* (in prep) in two ways. Firstly, it separates the effects of social learning from the effects of competition by using a rival forager that avoided both the familiar and the novel food type. In the

McMahon *et al.* paper the rival forager birds ate both food types readily, making it impossible to tell whether the experimental bird was copying the food choice of the rival, or refusing to broaden its diet due to competition for the food. Secondly, wild caught blue tits were used to extend our understanding of the effects of competition on dietary conservatism to a non-domesticated bird species, as domestic chicks show shorter lived DC (Mc Mahon *et al.* in prep) and are selectively bred to gain weight. So far there have been no direct studies on how competition influences the dietary decisions of DC wild birds and the extent to which the DC trait expression is plastic. Understanding the plasticity of this trait under changing ecological and social conditions is important for our understanding of predator behaviour as well as the ecology and evolution of predator-prey interactions.

4.2 Methods

Twelve blue tits were captured and housed in the Dublin Zoo avairy as described in section 2.1 (fig. 2.1.1)

4.2.1 Pre-training

One bird was chosen at random to be the competitor for all other individuals over the course of this experiment. All individuals were trained (see below) to regard green dyed kibbled peanuts as their familiar food, and this was presented in green feeding trays. The length of time required for birds to accept the familiar food varied between individuals, ranging from one to four weeks. In order to facilitate the acceptance of the green food, individuals were given food mixtures that were made up of approximately 90% green food and 10% regular food mixture for a 2 hour period every day. This was repeated until all individuals were observed consuming the green food. Once all individuals readily accepted the familiar green food, the experiment began. Birds took part in a DC test as described in section 2.1.

4.2.2 Effects of Competition

The novel colour chosen for the experimental trials was blue. In contrast with McMahon *et al.*'s (in prep) study on domestic chicks, where the competitor was familiarised with both food types, in the present experiment the competitor bird was trained actively to avoid both novel and familiar food types. This was achieved by presenting it with green and blue food flavoured with Bitrex® (denatonium benzoate), a bittering agent which gives the food a foul taste but does not harm the bird (Marples & Roper 1997). The competitor was not considered trained in avoidance until it was observed picking up and rejecting (i.e. not ingesting) the foul tasting food, after which it was allowed to take part in the trials. Prior to every test it was again given bitter flavoured coloured foods to reinforce its previously learned aversion to these food colours. The reason for making the competitor dislike both food types was so that it did not interfere with the decision made by the focal bird. If the focal bird observed the competitor eating the novel food, it may have had a social learning effect (see McMahon *et al.* in prep). Similarly if the competitor ate the familiar food, he may have forced the focal bird to eat the novel food due to a reduction in the amount of familiar food available. The experiment was therefore designed so that the focal bird would be making a decision based on the presence of the competitor *per se* and not based on what the competitor did or how it altered the availability of food types.

There were 11 test birds, and one competitor bird, housed in 12 identical enclosures, either side of a viewing gallery, which blocked the view of the birds to the opposite side. There was a feeding hatch opening onto a small platform in each enclosure, where food could be delivered without entering the aviary. This platform was shielded on the sides by wooden boarding to prevent neighbouring birds observing the food choices of the occupant. Those birds housed on the same side of the gallery as the competitor bird were tested with a competitor (five experimental birds) while those on the other side of the gallery were tested without a competitor (six control birds). This arrangement ensured that the control birds did not see a competitor entering the enclosures of the experimental birds.

All traces of food were removed from the enclosures of individuals about to take part in a trial and the birds were food deprived for a total of one hour prior to beginning a trial to ensure motivation to feed (Hegner 1985). The competitor was allowed to feed freely in its enclosure before and after each trial. Trials were alternated between experimental and control groups to ensure that there were no confounding factors relating to the timing of experimental treatments versus controls.

The competitor was first introduced to the aviary, if the test was for an experimental bird, then the food tray was placed in the feeding hatch of the enclosure. The observer moved behind a semi-opaque curtain down the centre of the viewing gallery and observation began. As with the DC trials described in section 2.1, the following latencies were recorded for both groups of birds, experimental and controls: latency to first make contact with the feeding tray, latency to eat each piece of familiar (green) food, latency to first make contact with novel food (blue) and times at which each piece of novel food was eaten.

Trials ran for twenty minutes or until three pieces of novel food had been eaten. Once a trial had been completed, individuals were given only their familiar food type for one hour, then they were given their maintenance food (wild bird seed mix, insect mix peanut and suet) with familiar food mixed into it. All traces of the novel coloured food were removed from the enclosures after each trial. Birds which had not eaten three peices of novel food in the first trial were given a second trial after a minimum gap between trials of 24 hours, and a third trial was given a further day later if they continued to avoid the novel food. After this time, as with the DC test, they were assigned the maximum latency of one hour or 3600 seconds. These data were analysed as set out in section 2.3.

4.3 Results

The birds were initially given a "DC test" to identify their underlying foraging strategy, by offering them novel food and familiar food and measuring how long they took to consume three novel food items. This latency was taken as their "DC score" (Fig 4.3.1)

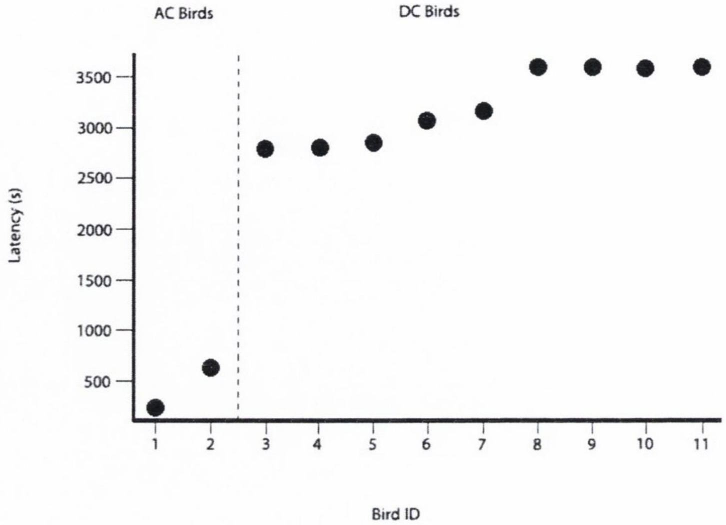
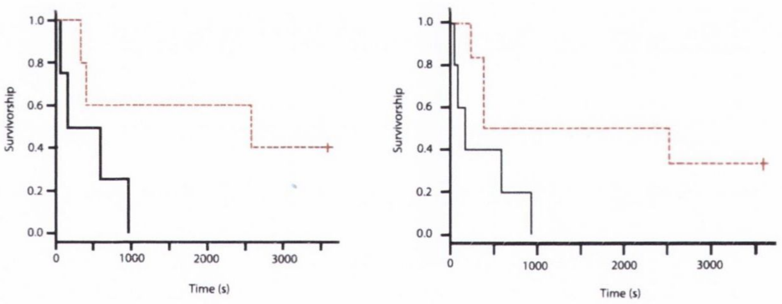


Fig 4.3.1.The latency for each individual bird to eat three pieces of novel food, the dotted line represents the split between AC and DC birds. Birds 8-11 were assigned the maximum score of 3600 seconds because they did not eat the novel food.

Interestingly most of the birds showed high levels of dietary conservatism which is in contrast with all other studies undertaken thus far (Marples *et al.* 1998; Richards *et al.* 2011; Thomas *et al.* 2010). Only two of the birds (PR and NR) displayed what could be referred to as an adventurous foraging strategy. This result contrasts with existing studies which report the AC:DC ratio as somewhere in the region of 2:1 (Marples *et al.* 1998) whereas here we have a ratio of approximately 1:4 AC:DC birds.

Only the most DC birds were used in the subsequent analysis to ensure that those birds with an adventurous foraging strategy did not bias the data, leaving a total sample size of nine. Total wariness includes both the effects of neophobia and DC. Figure 4.3.2(a) shows the Kaplan-Meier survival curve for total dietary wariness for both the experimental birds (those experiencing competition) and control birds (those foraging without a competitor). The group experiencing competition had significantly lower total wariness than the group without competition (z= 2.74, n=9, p=0.006). In order to explore these data further and discover whether both neophobia and DC were reduced with competition, these two sections of the food incorporation process were analysed separately.

Survival analysis on neophobia (Fig. 4.3.2b) revealed no significant difference between the two groups, indicating that competition did not affect neophobia (p=0.206). There was no correlation between neophobia and dietary conservatism (Pearson's product-moment correlation t= 0.765, d.f. = 9, p= 0.463, ρ=0.247), low levels neophobia were not correlated with low levels of dietary conservatism and vice versa.


(a) Dietary Wariness

(b) Dietary Conservatism

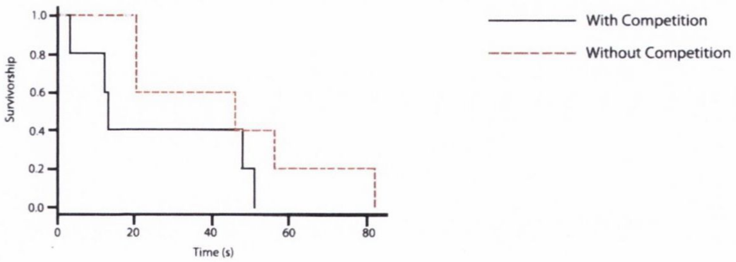

(c) Neophobia

Figure 4.3.2. Kaplan- Meier survival curves for (a) total wariness, (b) Neophobia and (c) dietary conservatism. The curves indicate the latency for the birds to eat three pieces of novel food. In the cases of total wariness and dietary conservatism the latencies measured were lower in the group experiencing competition (p= 0.006 and p=0.005 respectively). In the case of neophobia there was no effect of competition (p=0.206).

To calculate DC, the measure for neophobia was subtracted from the figure for total wariness (Marples *et al.* 2007). Survival analysis for these data (Fig. 4.3.2c) revealed that DC was significantly lower, and time to consume the novel food was shorter for those individuals that experienced competition, compared to the control group (z= 2.78, n= 9, P=0.005).

4.4 Discussion

The level of DC displayed in this blue tit population was very different from that found in other species of bird, and from levels of DC that have been found in fish (Marples *et al.* 2005; Marples *et al.* 1998; Richards *et al.* 2011; Thomas *et al.* 2010; Thomas *et al.* 2004; Thomas *et al.* 2003). The causal reasons for this unusually high ratio of DC birds are currently unclear. It could be argued that the DC ratio may have been influenced by capture method, as capture sites were baited with bird feeders in the days prior to catching. It may be that DC individuals become reliant on this familiar food source and therefore become more likely to be caught compared to more adventurous foragers who could perhaps seek out other sources of food more easily. However, in a small number of hand raised blue tits (not involved in this study), a similar ratio was found, with five out of seven birds classified as conservative foragers (see chapter six), so the trait could be simply more prevalent in this population of blue tits. Studies on other populations of blue tits would be necessary to ascertain whether the high degree of conservatism found here was a feature of this one population or of the species as a whole.

The results also showed that, at least under laboratory conditions, foragers who had previously displayed high levels of dietary conservatism were able to alter their underlying foraging strategy and became more adventurous when the perceived cost of being conservative was increased by the presence of a potential competitor. This suggests that the blue tits behaved optimally, as they were more likely to incorporate a novel food item into their diet when there was increased risk of familiar objects being depleted by competitors. Plowright and Landry (2000) demonstrated that foraging pigeons, *Columbia livia* use the presence of competitors as an indication that resource depletion is imminent. It is likely that the blue tits in this study employed the same strategy. The results suggest that the blue tits became less choosy about what food they would eat because continuing to be conservative would be costly in terms of a reduced intake of food.

In contrast, neophobia was not altered by the presence of a competitor, as there was no difference in the latency to approach the novel food with or without the competitor present. Marples and Kelly (1999) suggested that neophobia and dietary conservatism are distinct processes and as such are not regulated by the same mechanisms. The results presented here add further weight to this view. These results, however, contrast with the results of Mc Mahon *et al.* (in prep) when considering the neophobic response. They found that foraging domestic chicks became less neophobic in the presence of a competitor, and this was true of both AC and DC birds when both foods were equally conspicuous. There could be a number of reasons for these different results. In Mc Mahon's (in prep) study, the event used to indicate the end of neophobia was contact with the novel food, and, as explained above, this might include some of the dietary conservatism portion of the wariness response. In addition, domestic chicks are bred selectively for weight gain so perhaps the neophobic portion of their overall dietary wariness is more plastic compared to wild birds. It might be more important for wild birds to retain a minimum level of neophobia to avoid too rapid an approach into potentially dangerous situations. The present study showed, for the first time, a plastic response in dietary wariness in wild caught birds due to the presence of a competing forager. The portion of dietary wariness that was affected was dietary conservatism and not neophobia. As mentioned above, it may be more important to retain a minimum level of neophobia in order to avoid potentially dangerous situations or novel items, but plasticity in dietary conservatism may be adaptive as a response to higher costs of foraging caused by the presence of a competitor.

Marples *et al.* (2007) showed that dietary conservatism could be deactivated in domestic chicks but only through direct contact with a number of novel foods coupled with lengthy exposure to the novel food, not by observation of another individual eating the novel food. We have demonstrated that such direct contact was not neccessary for our group of wild blue tits. The presence of a competitior was enough to encourage previously conservative foragers to become more adventurous. This finding could be extended to investigate how the level of resources influences dietary choices in a competitive environment by allowing depletion of the resources by the competitor.

The results presented here are the first evidence of plasticity in the degree of dietary conservatism displayed by wild birds. If the behaviours reported here are representative of the same foragers when free flying, they provide an important insight into foraging ecology. So far all bird populations tested for DC have a proportion of the population that display high levels of dietary conservatism (Marples *et al.* 1998; Thomas *et al.* 2004; Thomas *et al.* 2003). The cost of maintaining a high level of dietary conservatism would increase should profitable items be refused when preferred resources are depleted through competitive exploitation. However, the plasticity reported here would reduce the costs of being a DC forager by allowing these individuals to forage in a more adventurous manner when resources are limited.

5 Threat of predation influences level of dietary conservatism in the blue tit

5.1 Introduction

Throughout the animal kingdom there are countless examples of the ways in which species have adapted to avoid predation; crypticity, aposematic colouration and chemical defences (Edmunds 1974; Ruxton *et al.* 2004), to name but a few. Failure to avoid predators can result in death or serious injury, both of which severely affect individual fitness. Consequently predation must be viewed as one of the strongest selective forces when viewed over evolutionary timescales.

As well as morphological, physiological and biochemical adaptations to avoid predation, there are also behavioural adaptations, particularly when it comes to foraging. When an individual is foraging it is focussed on finding food and cannot look out for approaching predators as effectively as when it is not foraging. Depending on where and with whom an individual is foraging, it may find itself at greater risk from attack due to decreased vigilance and increased attention given to the foraging task. Thus, when an animal is engaged in foraging, there is a trade-off between finding food and becoming food (Godin & Smith 1988; Lima & Dill 1993). It is, therefore, not surprising to learn that individuals engaged in foraging activities do so in such a way as to reduce their chances of being attacked. Many species forage in groups to reduce time spent being vigilant (Lima & Dill 1993), leaving more time for consuming resources and reducing the risk of predation through the dilution effect (Caldwell 1986; Hamilton 1971). On the other hand, those who must forage alone make decisions based on the lowest risk of predation for the greatest net gain in resources, for example Milinski and Heller (1978) used sticklebacks to investigate the influence of a predator on optimal foraging. They found that, after presentation with a model predator, the fish preferred to forage on less dense swarms of water fleas, *Daphnia magna*, thus reducing their net intake of food but increasing their ability to detect a predator. Such behaviour is believed to be as a result of limited attention (Dukas & Kamil 2000), as devoting attention to one task reduces efficiency in another. By attacking the swarm of lowest density, the stickleback should be better able to detect approaching predators (Godin & Smith 1988). The results of these and other studies into decision making under threat of predation (Caldwell 1986; Clarke 1983; De Laet 1985; Hamilton 1964; Hegner 1985; Lima & Valone 1986; Watanuki 1986) suggest that individuals involved in foraging tasks are able to assess the level of threat and act accordingly.

One of the many decisions facing foragers is what to eat, and in the face of a predation threat this decision can become even more difficult. Some studies have revealed that in the face of a predation threat, some foragers often appear to choose sub-optimally; in the sense that there are more profitable foods available. However, their behaviour may in fact be optimal overall, as it allows the animal to both find food and look out for predators simultaneously (Lima & Valone 1986; Milinski & Heller 1978). Until now, there are no studies into how dietary wariness may influence these decisions under the threat of predation.

Many of the studies involving predation threat to foraging individuals are interested in the underlying personality of the individuals involved (De Laet 1985; Hogstad 1988; Jones & Godin 2010; Quinn & Cresswell 2005; Waite & Grubb 1987). More specifically, researchers are interested in the presence of behavioural syndromes (Sih *et al.* 2004a; Sih *et al.* 2004b), a correlated suite of behaviours which are consistent between individuals and across contexts. It is not yet clear whether dietary conservatism and neophobia form part of a behavioural syndrome, though there is some evidence for the contrary (Marples and Brakefield 1995). It has been shown that neophobia is part of the 'exploratory' behavioural syndrome (Réale *et al.* 2007) but studies showing DC to be part of a behavioural syndrome are lacking.

The aim of the present study was to investigate the decisions made by both AC and DC foragers following a predation threat, by offering blue tits a choice between novel and familiar foods. Blue tits show relatively high levels of dietary conservatism (chapter 3 & 8) and, as such, are a good model species for the study of this trait.

If blue tits behave in a similar manner to Milinski and Heller's (1978) sticklebacks, then we would expect that the novel food should be ignored by both sets of foragers, but in particular by the AC foragers because under less threatening circumstances they would be expected to eat it, as they are more prepared to exploit novel resources. Evaluating novel food might require some thought on behalf of the blue tits and, consequently, might result in divided attention (Dukas and Kamil 2000) between foraging and looking out for the predator. This is also the case for the DC birds, but they would usually avoid the novel food even in the absence of a predator, so no difference in their behaviour is expected. On the other hand, when a predator is present, and hence the time available for assessing food is more limited, it is possible that the birds would grab the first or nearest item to them, ignoring the type of food taken. Under this scenario, AC birds, which would eat novel food fairly readily, would become slightly quicker to eat the novel food, while the DC birds, which would normally avoid novel food for an extended period, would be expected to become very much quicker to eat it. The final possibility is that AC birds might respond to this time pressure on foraging in a different way from the DC birds. We carried out the foraging tests to discover which of these responses to predation threat were shown by AC and DC birds.

5.2 Methods

A total of 19 wild blue tits were caught and housed in the indoor aviaries in Dartry, as described in section 2.1 (fig. 2.1.2). Food (green-dyed kibbled nut pieces, insect pâté, wild bird seed mix was always available except for one hour prior to experimental trials, and water was available *ad libitum*. None of the food available *ad libitum* was the same colour as the novel baits used in the experiments. The light cycle matched outdoor conditions, with birds experiencing a light period of 8h. All procedures were assessed and agreed by the Ethics Committee of Trinity College Dublin. Dyed foods were prepared as described in section 2.1 and table 2.1.2.

Birds were trained to regard green-dyed kibbled peanuts as familiar, which was achieved by gradually increasing the amount of green food available in each individual's feeding dish. At the end of the experiment all birds were returned to the wild in the same site as they were caught, and using a "soft release" technique in which food was provided for them at the release site for a week after release.

Individuals were given a DC test as described in section 2.1 in order to establish baseline levels of dietary conservatism. In addition to training the birds to accept familiar green food, the birds were trained to feed out in the open aviary (fig 2.1.2). This was achieved by allowing the birds to fly freely in the aviary after a period of food deprivation. Food was available on a platform positioned in front of the one-way mirror. All of the birds eventually became accustomed to feeding in this way.

5.2.1 Experimental treatments

Birds were randomly assigned to either the non-predator treatment or the predator treatment, while trying to keep a balanced number of both AC and DC individuals in each group. Prior to taking part in the experiment, birds were food deprived for one hour before being released into the free flying area. Birds were subjected to their respective experimental treatments one at a time. A dish containing three pieces of familiar food and three pieces of a new colour of novel food (blue–dyed kibbled peanut, see table 2.1.2) was placed on the platform in front of the one way mirror. Once the bird made contact with the food dish, but before it had eaten anything, a model of a pigeon (non-predator treatment) or a sparrowhawk (predator treatment) was made visible. The model was presented on the observation room side of the one way mirror. The model was housed inside a box, which was attached directly to the glass. When the lights in the observation room were switched off the birds were unable to see the model. The model became visible by means of a light inside the box in which it was contained, thus lighting the model but not the entire observation room. In conjunction with this visual signal, a conspecific alarm call was played on presentation of the predator model, while conspecific flocking calls were played on presentation of the non-predator model.

The following data were recorded: the latency to return to the feeding platform after presentation with the model; the latency to contact the dish containing the food; the latency to eat each piece of novel and familiar food. From these data we were able to calculate the length of neophobia for each individual, taken as the latency to contact the food dish (before presentation of the model), each individual's overall dietary wariness, which is the total latency to eat three pieces of novel food (neophobia plus dietary conservatism) and each individual's DC score, which the latency to eat three pieces of novel food after neophobia has been overcome (dietary wariness minus neophobia). Data were analysed as described in section 2.3.

5.3 Results

Figure 5.3.1 below shows the results of the DC test. Seven birds were classified as AC and twelve classified as DC, on the grounds that there was a discontinuity in their latencies to eat the novel food. While this may seem an arbritrary division, previous studies have shown that birds which consumed three novel food items during the time of the DC test trials, consistently go on to consume novel prey very quickly, while those which took longer to consume novel prey consistently acted like DC foragers and ate subsequent novel foods slowly or not at all. Almost all species studied so far have found the proportion of AC individuals much greater than that of DC (Marples *et al.* 1998; Richards *et al.* 2011; Thomas *et al.* 2010), whereas here we saw that for every AC bird there were almost two DC birds

Table 5.3.1 reveals the results of the GLMs used to investigate the two-way interactions between foraging trait and foraging strategy. In other words it asks whether AC and DC foragers reacted differently within their treatments. The two way interactions were significant for dietary wariness and dietary conservatism but there was no significant interaction for neophobia. Thus AC and DC foragers did react differently to the treatments and are therefore analysed separately

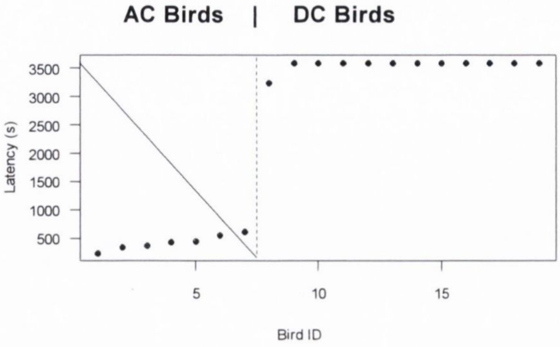


Figure 5.3.1 DC scores for all individuals. The DC score is the latency to consume three pieces of novel food. Birds that did not consume three pieces were given a maximum score of 3600 seconds.

Table 5.3.1 Summary of the results of generalised linear model analyses on the 3 foraging traits of interest. *indicates a significant interaction between foraging trait and experimental treatment.

Foraging trait	GLM Results				
	F	Degrees of freedom	P value	Family	link
Dietary Wariness	10.114	3,15	<0.01*	Gaussian	Log
Dietary Conservatism	8.660	3,15	<0.05*	Gaussian	Log
Neophobia	0.764	3,15	0.395	Gaussian	Log

Table 5.3.2 below summarises the results of the survival analyses for both AC and DC birds. For AC birds, overall dietary wariness and dietary conservatism were significantly higher for the predator treatment compared to the non-predator treatment, (Fig. 5.3.2a), but the presence of a predator had no effect on neophobia. Similarly the time it took AC birds to return to feeding after seeing the predator was no different compared to those in the non-predator treatment. DC birds showed no differences between treatments, Fig. 5.3.2(a), for any of the foraging traits, but it took them significantly

longer to return to feeding after seeing the predator compared to the non-predator treatment, fig. 5.3.2(b).

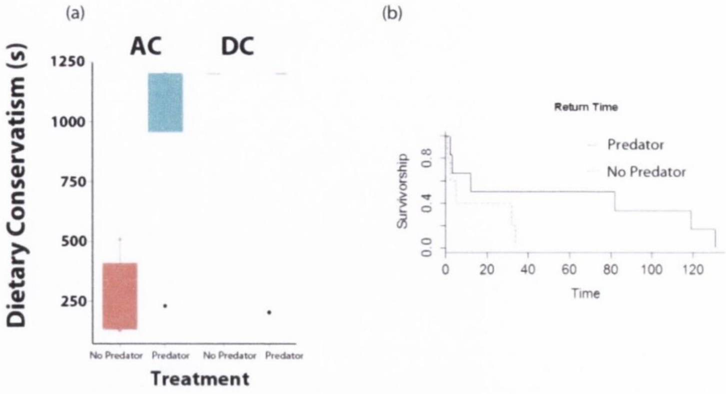


Figure 5.3.2 (a) latency to eat three pieces of novel food after the experimental treatment for both AC and DC birds, for both treatments. (b) The survival curves for the latency to return to feed for DC birds with and without a predator.

Table 5.3.2 Summary of the results of the survival analyses on both AC and DC birds for the difference between the two treatments, non-predator and predator.

	Foraging Trait	Results of Survival analyses			Distribution
		Z	D.F.	P Value	
			(n = 8)		
AC birds	Dietary Wariness	-2.16	5	<0.01*	Exponential
	Dietary Conservatism	-2.32	5	<0.05*	Exponential
	Neophobia	-0.83	4	0.41	Exponential
	Return Time	0.471	5	0.638	Exponential
			(n = 11)		
DC birds	Dietary Wariness	<0.001	10	0.99	Exponential
	Dietary Conservatism	<0.001	10	0.99	Exponential
	Neophobia	0.827	9	0.408	Loggaussian
	Return time	-2.26	10	<0.05*	Exponential

5.4 Discussion

Both AC and DC foragers behaved according to type in the non-predator treatments, with AC birds being quick to consume novel prey, and DC birds being much slower. However in the predator treatment, AC birds behaved like DC birds, and refused to eat the novel food (with the exception of WAL, table 5.3.3). DC birds in the predator treatment continued behaving as DC foragers, refusing to eat any of the novel food (tables 5.3.2 & 5.3.3).

Table 5.3.3 The latencies for each piece of food to be eaten for each individual bird. F = familiar; N = Novel; † indicates food not eaten

Foraging Strategy	Treatment	Bird Id	F1	F2	F3	N1	N2	N3
DC	Predator n = 6	CL	107	132	150	249	269	304
		GNR	70	92	111	1200†	1200†	1200†
		WGL	65	76	91	1200†	1200†	1200†
		ACR	582	618	636	1200†	1200†	1200†
		WBL	246	272	312	1200†	1200†	1200†
		GBR	188	199	216	1200†	1200†	1200†
	Non-predator n = 5	GSL	290	317	336	1200†	1200†	1200†
		SR	101	139	149	1200†	1200†	1200†
		ABR	66	106	185	1200†	1200†	1200†
		WWL	648	687	731	1200†	1200†	1200†
		WBR	171	209	237	1200†	1200†	1200†
AC	Predator n = 4	SGL	143	173	201	1200†	1200†	1200†
		WCL	175	175	182	1200†	1200†	1200†
		ANL	173	174	177	1200†	1200†	1200†
		WAL	286	351	391	325	401	445
	Non-predator n = 4	WCR	23	68	80	58	124	139
		GCL	266	434	487	382	401	465
		WRL	65	82	107	147	166	178
		ARL	346	375	413	365	566	658

Previous studies into diet choice and the threat of predation have revealed similar results. Milinski and Heller (1978) found that sticklebacks feeding on water fleas attacked less dense swarms after seeing a potential predator. The authors concluded that by doing so they were able to direct some of their attention to detecting an approaching predator while feeding at the same time. They hypothesised that sticklebacks attacking a dense swarm would have to direct more of their attention to capturing prey, thus leaving themselves more prone to attack from a predator, due to the confusion effect caused by the swarming prey (Miller 1922). This idea was later tested using guppies *Poecilia reticulata* by Godin and Smith (1988) who found that guppies attacking increasingly dense swarms of water fleas suffered greater mortality caused by their inability to detect an impending attack from a predator.

The more difficult the task an individual is engaged in, the more of their attention must be devoted to it (Desimone & Duncan 1995; Dukas & Kamil 2000) - a mechanism which has been termed 'limited attention' (Dukas & Kamil 2000). The results of the present study suggest that, upon encountering novel food, the decision of whether to eat it or not was one which took careful consideration, and a substantial cognitive effort on the part of the forager. Particularly for AC foragers, the fact that they refused to eat any of the novel food presented in the predator treatment suggests that they either did not have sufficient time to consider the value of the novel food or decided that, in the face of a predation threat, it would be more beneficial to simply eat familiar food and devote some of their attention to predator detection.

Up until now the emergence of DC as a foraging trait has been explained as a strategy for avoiding chemically defended prey (Thomas *et al.* 2003). However these results suggest that there may have been another route by which this trait has evolved. The DC strategy eases foraging effort; by simply concentrating on food that is familiar, individuals may not need to divide their attention between tasks to as large an extent, compared to AC individuals, that may have to spend more time evaluating novel prey items. Thus, in certain circumstances, DC individuals can forage more efficiently and devote attention to other activities, such as predator detection. An AC individual that does not concentrate on familiar prey types may have its attention directed to a number of different food sources and therefore perform the task of obtaining food in a less efficient manner (Dukas & Kamil 2000). The 'information-processing hypothesis' (Bernays 2001; Egan & Funk 2006) predicts precisely this. If we consider that the niche width of AC individuals should be wider than that of DC individuals, because they are willing to exploit resources which DC individuals will not, then we could consider AC and DC to be a particular case of generalist and specialist foraging behaviour (Roughgarden 1972). There are many studies extolling the efficiency of specialists foragers compared to more generalist foragers.

More generally speaking, these results imply that an AC foraging strategy is somewhat costly in a cognitive sense. By considering whether to accept each novel food item, AC foragers necessarily direct attention away from, perhaps more important tasks, such as predator detection (Dukas 2002; Dukas & Kamil 2000), whereas DC foragers have no such dilemma. Their simple strategy of ignoring novel food may actually allow them to be more vigilant during foraging tasks. Dukas and Ellner (1993) explored a related idea when modelling the amount of attention a forager should devote to a given number of prey types. They found that, in order to maximise net rate of energy intake, foragers should allocate all of their attention to just one prey type, in a manner similar to search image theory, although that is usually considered to be restricted to cryptic prey. This is because the mechanism of visually processing information is costly and the devotion of attention to more than one visual task reduces efficiency in those tasks (Dukas 2002). Consequently, when faced with the additional task of looking for a predator *and* a novel food, our AC blue tits decided against accepting the novel food, and concentrated solely on what they were familiar with and knew to be of value, in order to reduce their risk of not detecting an approaching predator.

When DC birds were threatened by the presence of a predator, they were slower to return to feeding in comparison to those in the non-predator treatment. This is perhaps not a surprising result if you consider DC birds alone (De Laet 1985; Hegner 1985; Waite & Grubb 1987), but it is not clear why AC birds did not react in the same way. They showed no difference in return time between treatments. It might be argued that AC individuals are also bold individuals (Wilson *et al.* 1993), since boldness has been defined as an individual's reaction to a risky situation, such as a potential predator (Réale *et al.* 2007). It should not, however, refer to a situation where novelty is involved, such as the novel foods presented here. Instead fast-slow exploration behaviours should be invoked in these situations (Réale *et al.* 2007). However the design of the experiment was such that we did not explicitly test for such behavioural correlations, though it is perhaps something to consider in future studies. It might be tempting to suggest that the AC/DC traits form part of a behavioural syndrome, however in order for a behavioural syndrome to exist the behaviour must be consistent across different contexts (Sih *et al.* 2004a) and we have clearly shown here that this was not the case.

We have shown here that the exhibition of the AC/DC foraging trait is somewhat context dependent and not consistent across different ecological conditions. DC foragers did not alter their foraging strategy because to do so may have increased their risk of attack, whereas the AC foragers displayed a level of plasticity in their foraging strategy by ignoring the novel food and instead concentrating on what was familiar. In doing so they may have been increasing their chances of detecting a predator. A degree of plasticity has been shown in other contexts also, such as when competitors are present (chapter 4). Plasticity in this foraging trait would allow individuals to react to changing conditions. Further exploration of the range of plasticity and the types of conditions required to bring about change in this trait would advance our understanding of how the trait will affect the behavioural ecology of the individuals that exhibit it.

6 Encounter rate and temporal distribution of novel food: influence on dietary conservatism in blue tits and chicks

6.1 Introduction

The way in which foraging animals search for, find and consume food has interested ecologists and evolutionary biologists alike for many years. Tinbergen (1960) was one of the first to comment on the nature of the relationship between prey abundance and diet choice by predators. From his own observations Tinbergen noted that some members of the tit family (*Paridae*) altered their foraging behaviour in response to changes in abundance of prey. He proposed that the birds altered their intake of prey because chance encounters with the newly abundant prey led to an increased efficiency in the bird's ability to find these prey, a process he termed "adopting a searching image". The concept of the search image has been debated (Guilford & Dawkins 1987; Plaisted & Mackintosh 1995) but now seems to be generally accepted as an explanation for one of the ways visual predators search for and find cryptic prey (Blough 1991; Bond & Kamil 1999; Dukas & Kamil 2001). The search image hypothesis is also consistent with many studies into apostatic selection (Clarke 1972), where more numerous prey items are incorporated into the diet in a proportion far greater than their occurrence in the environment, and rarer prey are overlooked and, therefore, at a selective advantage. Foraging behaviour, such as this, is referred to as switching or frequency-dependent predation (Oaten & Murdoch 1975) and is believed to be important in maintaining genetic diversity and polymorphism (Bond 2007; Clarke 1972; Oaten & Murdoch 1975).

When Tinbergen (1960) first observed this frequency dependent foraging behaviour, it occurred when a previously rare prey species suddenly became abundant in the environment. He noticed that there was a lag of a number of days between the initial emergence of the prey species, and the incorporation of the prey into the diet of the birds. He posited that this was due to the fact that the birds began to encounter these more abundant prey species on a more regular basis, thus becoming more familiar with them and acquiring a search image for them, making them easier to find in relation to rarer prey species. It is this ease of capture and consumption which leads to apostatic selection (Allen & Clarke 1968), which is preferential selection of the most abundant food. In an investigation into apostatic predation by birds, Allen and Clarke (1968) showed that when birds were offered green and brown artificial baits in differing ratios, the most abundant colour was the most predated upon. Consequently the birds, having encountered the more common bait more frequently, then adopted a search image for them and predated on them more often.

There is, however, one foraging process which neither Tinbergen (1960) nor Allen and Clark (1968) have taken into account and that is dietary conservatism (Marples *et al.* 1998). In their experiments, Allen and Clark (1968) familiarised birds with two coloured baits and then offered them a choice between these colours in different ratios. The design of this experiment, therefore, does not allow for any DC effect to occur, but since they looked at population averages the results would have been biased by the larger proportion of AC individuals. The results showed that the birds predated most heavily upon the most abundant colour (apostatic selection) but once they had experienced many encounters with the other less abundant colour, they began to incorporate these into their diet gradually. They attributed the initial preference for abundant baits to the formation of a search image for those baits. They also found that the preferences could be reversed through increasing the encounter rate with the least abundant colour. This suggests a possible mechanism for the observed preference for the more common bait. The less abundant baits may have been ignored due to a low initial encounter rate and thus the birds were not as familiar with them as the other more common bait. However, this can also be explained by invoking dietary conservatism. If the initial preference was brought about through initial contact with the more common bait, and therefore a DC avoidance of the less common bait, then the results reported when the bait frequencies were switched suggests that the conservatism can be overcome by encountering unfamiliar prey (prey previously not included in the diet) on a more regular basis. If this is analogous to situations which might occur in the wild, where there are fluctuating levels of prey abundance, such that one prey type increases at the expense of another and vice versa, then it is important to know how this will alter the predator-prey dynamics of the local environment.

The experiments of Allen and Clark (1968) suggest that foragers will eventually learn to accept previously unfamiliar prey types after a number of encounters whereas the results of Marples *et al.* (1998) suggest that there will be individuals among the population of predators who will continue to avoid these previously unfamiliar types for an extended period. Allen and Clark would not have detected these DC individuals as they only looked at the average response of the total population, not the individual responses of DC and AC birds.

The following experiments explore these ideas using wild caught blue tits held in experimental aviaries, and domestic chicks, held in laboratories in Trinity College Dublin. Previous chapters have shown that DC can be regulated through competition and predation threat. The aim of this study is to extend this to how food is encountered and if this influences the expression of dietary conservatism.

Following Tinbergen (1960), Allen & Clark (1968) and the results reported by Marples *et al.* (1998) it seems reasonable to assume that AC individuals should react to high encounter rates with novel prey by incorporating them into their diet, but it is not yet known how DC individuals should react. Refusal to incorporate novel profitable food into the diet upon many encounters would represent a significant cost to the forager. Similarly encountering high numbers of novel prey over a short period of time should indicate to foragers that they are a resource that should be exploited in order to maximise net energy gains (Stephens & Krebs 1986). If dietary conservatism prevents individuals from reacting to prey encounter rates by driving them to exploit only what is familiar, then the DC forager would be a distinct disadvantage in highly variable and unpredictable environment, where resource densities and relative abundances are fluctuating.

6.2 Methods

Both blue tits and chicks were captured or sourced as described in chapter 2, blue tits were housed in the indoor aviaries in Dartry described in section 2.1 and shown in figure 2.1.2. Husbandry and familiarisation with foods are as described in sections 2.1 and 2.2 respectively. Additional training and methodology are outlined below.

6.3 Experiment 1 Part I: How does the number of encounters with novel food influence dietary conservatism in blue tits?

Prior to starting tests, the birds were trained to eat from a specialised feeding tray, consisting of a circle of Perspex, 20mm in diameter with 20 small wells, 12mm in diameter, around the circumference, where food items could sit (figure 6.3.1). The tray was placed into an individual's box through a hatch in the bottom and could be rotated from outside so that only one prey item was presented to the bird at any particular time. Training consisted of leaving the tray in the aviary overnight with food on top in order to familiarise the birds with the set-up.

This experiment aimed to determine whether changing the number of encounters with a novel prey type, over the same time period, affected the duration of dietary conservatism. Birds were allocated to two treatment groups semi-randomly, with the condition that each group had an equal number of wild-caught members and equal numbers of individuals showing an AC foraging strategy. Both treatment groups were food deprived for one hour prior to the start of each test. Both groups were then shown a single familiar food item (a green dyed kibbled nut piece) every minute for a total of 20 minutes, using the specialised feeding tray. The first treatment group were also shown a novel food item (a blue dyed kibbled peanut piece) during the first minute and last minute in the same well as the familiar food item, giving a total of 20 encounters with familiar food and two encounters with novel food. The second treatment group were shown a novel food item with every familiar one, giving a total of 20 encounters with familiar food and 20 encounters with novel food. There were an equal number of familiar items in each treatment so that hunger levels would not influence any of the decisions made by the birds. After each treatment, birds were food deprived for a further hour, and then given a second DC test, as described in section 2.1 using blue as the novel colour.

The dyed foods were prepared as described in section 2.1 and table 2.1.2. Data were analysed as described in section 2.3

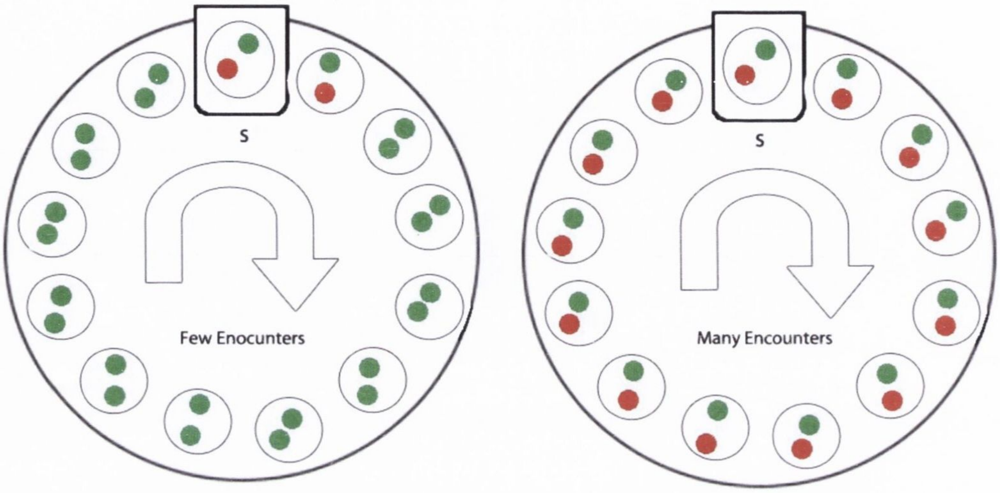


Figure 6.3.1 Disc Feeding Apparatus layout. Only one well was able to be seen at one time by the birds at one time. Treatment 1 is located on the left and Treatment two on the right. Filled circles represent novel food and open circles represent familiar food. The starting well of the experiment is marked with an S and tray was moved in a clockwise direction until the final well (well left of starting well) was made visible

6.3.1 Results

In total there were 40 blue tits used in this study, 18 of which were juveniles and the remainder were adults. Of those 18 juveniles, six were hand reared. Figure 6.3.1, below shows initial DC scores for all birds, measured as the latency to eat three pieces of novel food. Individuals were classified as AC if they ate three pieces of novel food within the first trial and DC if they did not.

Table 6.3.1 shows the results of the generalised linear models. The interactions between dietary wariness, foraging strategy and treatment were significant, as were the interactions involving dietary conservatism. There was no significant interaction involving neophobia. AC and DC birds were analysed separately owing to these differences in dietary conservatism and overall wariness.

Table 6.3.1 Summary of the results of generalised linear model analyses on the 3 foraging traits of interest. *indicates significant differences.

Foraging trait	GLM Results				
	F	Degrees of freedom	P value	Family	Link
Dietary Wariness	8.674	3, 36	<0.001*	Gaussian	Log
Dietary Conservatism	8.474	3,36	<0.001*	Gaussian	Log
Neophobia	2.640	3,36	0.08	Gaussian	Log

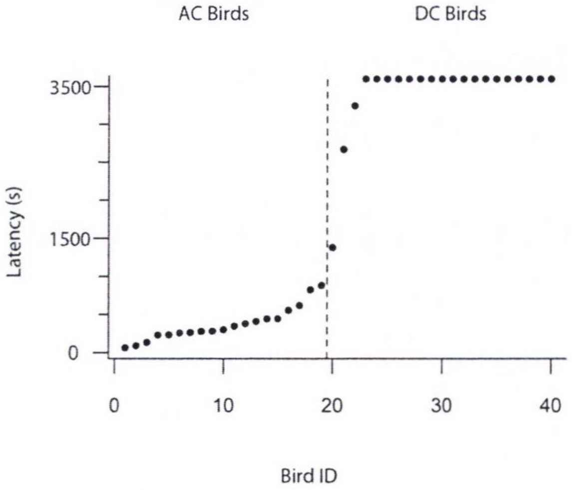


Figure 6.3.1 DC scores for all individuals. The DC score is the latency to consume three pieces of novel food. Birds that did not consume three pieces were given a maximum score of 3600 seconds.

Table 6.3.2 below shows that the makeup of the experimental groups was almost identical, with the exception of the underlying foraging strategy; group 1 has six more individuals due to the death of three individuals from group B over the course of experiments.

Table 6.3.2 Summary of the characteristics of the individuals within each group, including method of rearing, age and under lying foraging strategy.

Group	**Encounter rate**	**Total**	**Hand-reared**	**Wild caught**	**Juvenile**	**Adult**	**AC**	**DC**
A	Low	23	3	20	9	14	8	15
B	High	17	3	11	9	8	7	10

Table 6.3.3 below shows the results of the survival analyses for both AC and DC birds. There was a difference in overall wariness (dietary conservatism + neophobia) between the treatments. In contrast to the expected direction of this effect, those birds that encountered the fewest numbers of novel foods had the lowest wariness scores of the two groups. They were more likely to incorporate the novel food into their diet having only seen it twice previously. Figure 6.3.2 (b), below, shows the survival curves for both groups, where time on the x-axis represents overall dietary wariness.

The dietary conservatism shown by the AC birds was also significantly affected by the treatments. The trend was in the same direction as that for dietary wariness. Birds from group A, which had experienced fewer encounters with the novel prey, were less conservative than birds from group B that had experienced more encounters with novel food, fig.(6.3.2(c)). In contrast to dietary wariness and conservatism, neophobia showed the opposite trend; individuals in group B, which had encountered the novel prey many times were less neophobic than those in group A, (fig. 6.3.2(d)), a trend which contrasted with previous results, however there was no significant difference in this instance.

Table 6.3.3 Summary of the results of the survival analyses on both AC and DC birds for the difference in survival between the two treatments; low encounter rate with novel prey (Group A) and high encounter rate (Group B). *indicates significant difference

	Foraging Trait	Results of Survival analyses			Distribution
		Z	D.F.	P Value	
			(n = 15)		
AC birds	Dietary Wariness	3.05	13	<0.01*	Exponential
	Dietary Conservatism	3.18	13	<0.01*	Exponential
	Neophobia	0.198	13	0.843	Exponential
			(n = 25)		
DC birds	Dietary Wariness	2.50	23	<0.05*	Exponential
	Dietary Conservatism	2.52	23	<0.05*	Exponential
	Neophobia	-3.04	23	<0.001*	Weibull

In summary those individuals who experienced more encounters with novel food, were less neophobic than individuals who experienced fewer encounters, but this difference was not significant. Interestingly those individuals who experienced more encounters with the novel food were more wary and more conservative compared to those in the fewer encounters treatment.

The results for DC birds were similar to those for AC birds; dietary wariness was significantly lower for individuals who had had the fewest encounters with novel, (fig. 6.3.3(b)). Similarly dietary conservatism was lower for those in the fewest encounters treatment fig 6.3.3(c). Interestingly there was also a significant difference between the groups for neophobia, (fig. 6.3.3 (d)), but it was those in the "many encounters" group whose neophobia was lower.

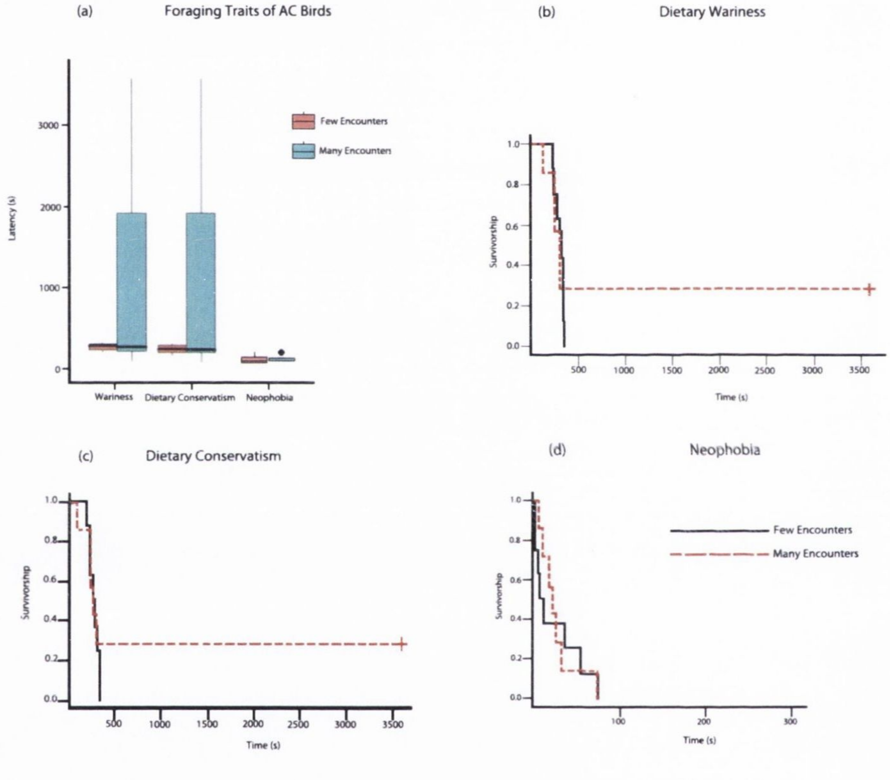


Figure 6.3.2 The boxplot (a) shows dietary wariness, dietary conservatism and neophobia for AC birds for both the "few encounters" and the "many encounters" treatments. Survival analysis for AC birds (b) overall dietary wariness which includes the neophobia and dietary conservatism latencies, (c) dietary conservatism and (d) neophobia. Crosses on (b) and (c) represent censored data; the solid line represents the "few encounters" treatment and dashed line represents the "many encounters" treatment.

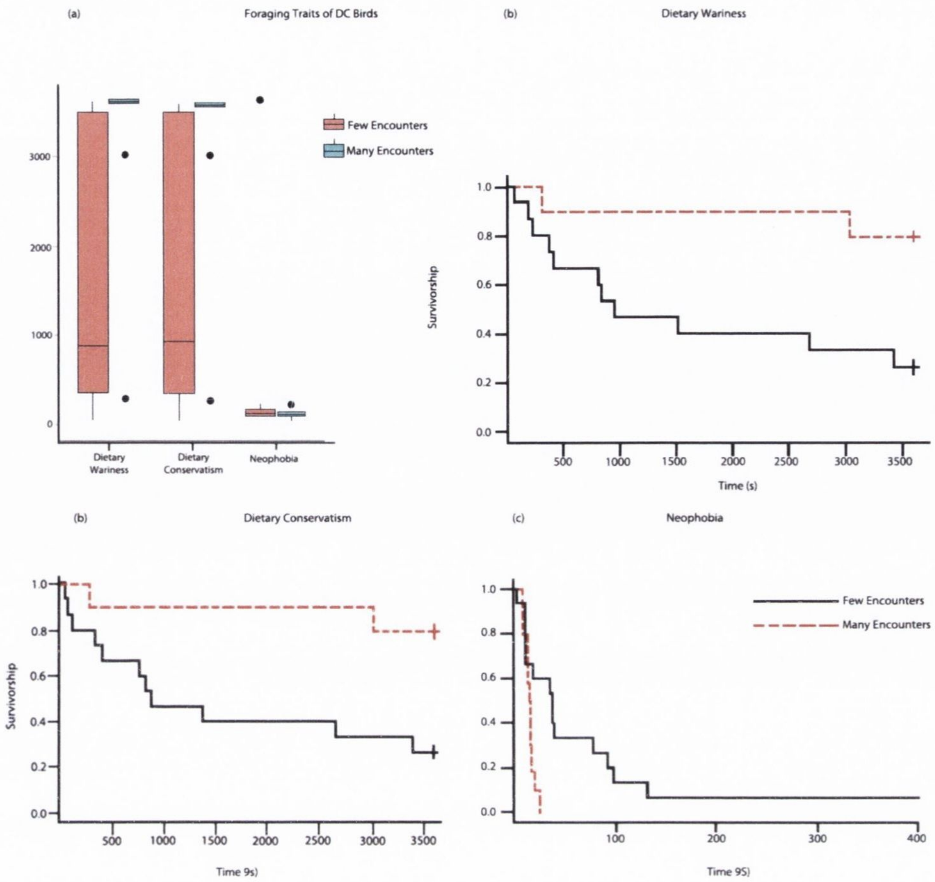


Figure 6.3.3 The boxplot (a) shows dietary wariness, dietary conservatism and neophobia for DC birds for both the "few encounters" and the "many encounters" treatments. Survival analysis for AC birds (b) overall dietary wariness which includes the neophobia and dietary conservatism latencies, (c) dietary conservatism and (d) neophobia. Crosses on (b) and (c) represent censored data; the solid line represents the "few encounters" treatment and dashed line represents the "many encounters" treatment.

6.4 Experiment 1 Part II

This experiment dealt with the same basic principle as the first experiment; the birds were offered a different novel coloured food in a different context. The novel colour used in this experiment was orange and was prepared as set out in section 2.1 and table 2.1.2. Not all of the birds used in the first experiment were used in these experiments but those that were used were kept in the same groups as they had been for the first experiment. There were 10 additional birds who took part in this experiment at a different time but conditions and training were identical. The total number of birds used across both batches was 23.

Instead of presenting food to the birds in their home boxes, it was presented to them from feeding dishes hanging from the ceiling of the main aviary. The birds were allowed to fly around the aviary, and as they did they encountered prey types at different rates.

Prior to beginning the experiment, the birds were trained to feed from the dishes hanging from the ceiling, using familiar food. This was achieved by first depriving the birds of food for one hour then allowing them to fly freely in the aviary where they could discover the food and feed on it. This was repeated until all of the birds were observed feeding from the dishes. There were a total of six feeding dishes, numbered 1-6, each containing two pieces of food. In group A there were two pieces of novel food and 10 pieces of familiar food. All the dishes contained at least one piece of familiar food. The novel food pieces were assigned to dishes randomly by drawing lots. In group B there were equal numbers of novel and familiar food, one piece of each in each dish.

As was the case in experiment 1 part I, birds were food deprived for one hour prior to involvement in an experimental trial. At the beginning of the trial, birds were released from their home boxes and allowed to move freely around the aviary for 20 minutes, where they could feed from the dishes. They were then placed back in their home box and food deprived for a further hour before a DC test was administered as described above. Data collection and analyses were the same as in part I. There was an additional interaction term included in the GLM to test for differences between the two different groups of birds used in this experiment.

6.4.1 Results

The total sample size used for this experiment was 23 birds. Table 6.4.1 below summarises the characteristics of these individuals. All of the individuals were wild birds, none were hand reared. Both treatment groups were evenly matched in terms of juveniles, adults and underlying foraging strategies. All the birds had similar experiences within the aviary.

Table 6.4.1 A summary of the characteristics of the individuals within each group, including method of rearing, age and under lying foraging strategy. The encounter rate refers to how many novel prey they encountered in their treatment.

Group	**Encounter rate**	**Total**	**Hand-reared**	**Wild caught**	**Juvenile**	**Adult**	**AC**	**DC**
A	Few	12	0	12	7	5	4	8
B	Many	11	0	11	7	4	4	7

Generalised linear models were once again employed to investigate the interaction between each of the measured foraging traits, underlying AC/DC foraging strategy, and experimental treatment (table 6.4.2 below). The two-way interaction between treatment and foraging strategy was found to be significant for dietary wariness and dietary conservatism but not for neophobia. Thus AC and DC birds were analysed separately.

Table 6.4.2 Summary of the results of generalised linear model analyses on the 3 foraging traits of interest, on the two-way interaction between foraging strategy and treatment. *indicates a significant interaction.

Foraging trait	GLM Results				
	F Value	Degrees of freedom	P value	Family	link
Dietary Wariness	8.205	3, 19	<0.01*	Gaussian	Log
Dietary Conservatism	7.86	3,19	<0.01*	Gaussian	Log
Neophobia	1.186	3,19	0.341	Gaussian	Log

A second GLM was employed to investigate the two-way interaction between treatment and the group to which the birds belonged. This experiment combined data from two separate batches of blue tits. The results of this analysis are shown in Table 6.4.3 below. There were no significant interactions for any of the foraging traits, it was therefore appropriate to group the results from both batches of blue tit together.

Table 6.4.3 Summary of the results of generalised linear model analyses on the 3 foraging traits of interest, on the two-way interaction between batch and treatment for both AC and DC birds.

Foraging Strategy	Foraging Trait	GLM Results				
		F Value	Degrees of freedom	P value	Family	link
AC	Dietary Wariness	0.028	3,4	0.875	Gaussian	Log
	Dietary Conservatism	0.074	3,4	0.799	Gaussian	Log
	Neophobia	0.442	3,4	0.542	Gaussian	Log
DC	Dietary Wariness	1.624	3,11	0.228	Gaussian	Log
	Dietary Conservatism	1.525	3,11	0.243	Gaussian	Log
	Neophobia	0.028	3,11	0.869	Gaussian	Log

Table 6.4.4 summarises the results of the analyses of both AC and DC birds. It shows that AC birds had lower dietary wariness and dietary conservatism when they experienced many encounters with the novel food compared to those in the few encounters treatment (fig. 6.4.1), but they were no different with respect to neophobia. The results for DC birds (fig. 6.4.2) reveal a different pattern of behaviour: there were no significant differences in dietary wariness and conservatism but neophobia was lower for those birds that encountered the novel prey many times (group B).

Table 6.4.4 Summary of the results of the survival analyses on both AC and DC birds for the difference in survival between the two treatments; low encounter rate with novel prey (Group A) and high encounter rate (Group B)

	Foraging Trait	Results of Survival analyses			Distribution
		Z	D.F.	P Value	
			(n = 8)		
AC birds	Dietary Wariness	-7.29	5	<0.001*	Weibull
	Dietary Conservatism	-7.26	5	<0.001*	Weibull
	Neophobia	-2.82	6	0.778	Exponential
			(n = 15)		
DC birds	Dietary Wariness	-1.64	13	0.101	Exponential
	Dietary Conservatism	-1.64	13	0.101	Exponential
	Neophobia	-4.05	13	<0.0001*	Exponential

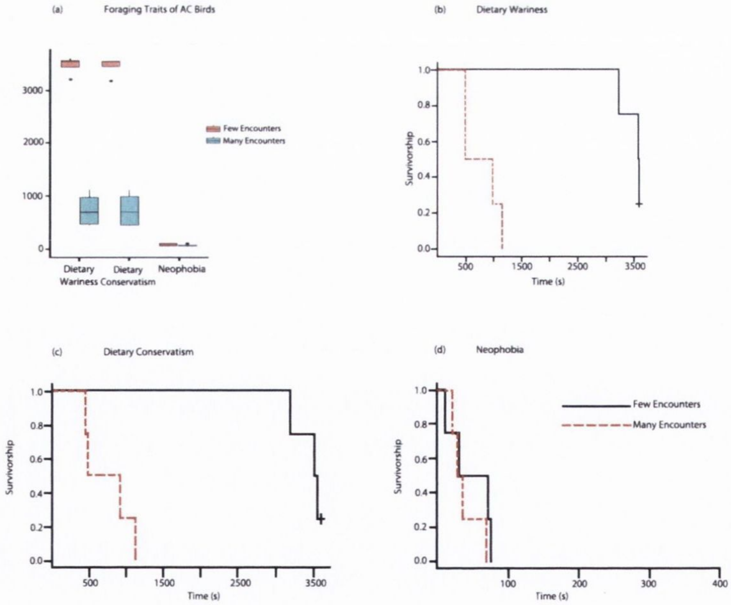


Figure 6.4.1 The boxplot (a) shows dietary conservatism, neophobia and overall dietary wariness for AC birds for both treatments. Summary of the survival analysis for both treatments (b) overall dietary wariness, (c) dietary conservatism, (d) neophobia Crosses on (a), (b) or (c) represent censored data In the survival plots the solid lines represent the few encounters treatment and dashed line represents the many encounters treatment.

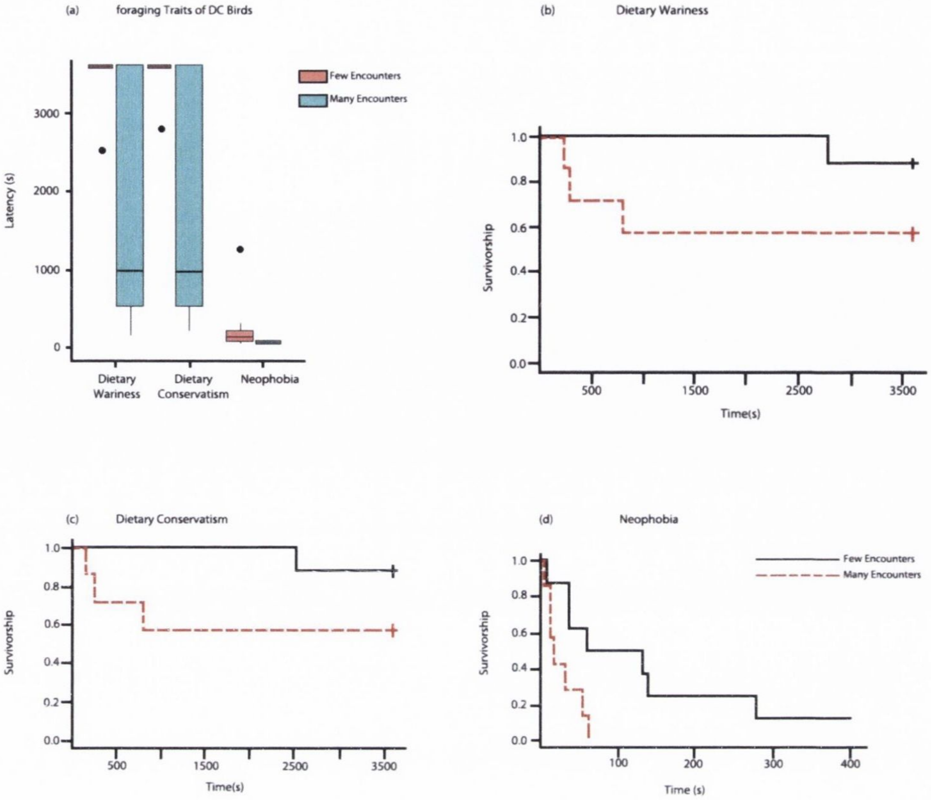


Figure 6.4.2 The boxplot (a) shows dietary conservatism, neophobia and overall dietary wariness for AC birds for both treatments. Summary of the survival analysis for both treatments (b) overall dietary wariness, (c) dietary conservatism, (d) neophobia Crosses on (a), (b) or (c) represent censored data In the survival plots the solid lines represent the few encounters treatment and dashed line represents the many encounters treatment

6.5 Experiment 2 Part I: How does varying the temporal distribution of novel food influence dietary conservatism in blue tits?

6.5.1 Methods

A new group of 10 blue tits were captured, held and trained as described in section 2.1. They were then randomly assigned to one of two treatment groups. Both groups were food deprived for one hour prior to treatment. The first group ('ten in one day' treatment) were offered ten consecutive pieces of novel food every minute over a ten minute period, while the second group ('ten in ten days' treatment) were given ten pieces of novel food spread over ten days, with only one piece of novel food offered each day. The colour of the novel food in this experiment was blue and was prepared as described in table 2.1.2. Food was presented to the birds in their feeding dishes, in their individual boxes. The day after each bird had received its final exposure to the novel food they were given a DC test (as described in section 2.1) with the same blue novel colour. The same latency data were collected from these DC tests and as it has been shown previously that AC and DC birds do not react in the same way to differently encountered novel food they were analysed separately.

6.5.2 Results

Table 6.5.1 below shows the main findings of the analyses. For all foraging traits there were no significant differences, with the exception of neophobia in the AC birds. Figure 6.5.1 below shows that those individuals who saw the novel food ten times in one day were less neophobic compared to those who saw the novel food ten times in ten days. Although dietary wariness and dietary conservatism were lower in the 'ten in ten days' treatment for AC birds it was not significant.

Table 6.5.1 Summary of the results of the survival analyses on both AC and DC birds for the difference in survival between the two treatments; 'ten in one day' and 'ten in ten days'.

	Foraging Trait	Results of Survival analyses			Distribution
		Z	D.F.	P Value	
			(n = 4)		
AC birds	Dietary Wariness	-0.952	1	>0.05	Weibull
	Dietary Conservatism	-1.82	1	>0.05	Weibull
	Neophobia	3.75	1	<0.001*	Weibull
			(n = 6)		
DC birds	Dietary Wariness	<0.001	4	>0.05	Exponential
	Dietary Conservatism	<0.001	4	>0.05	Exponential
	Neophobia	0.99	4	>0.05	Exponential

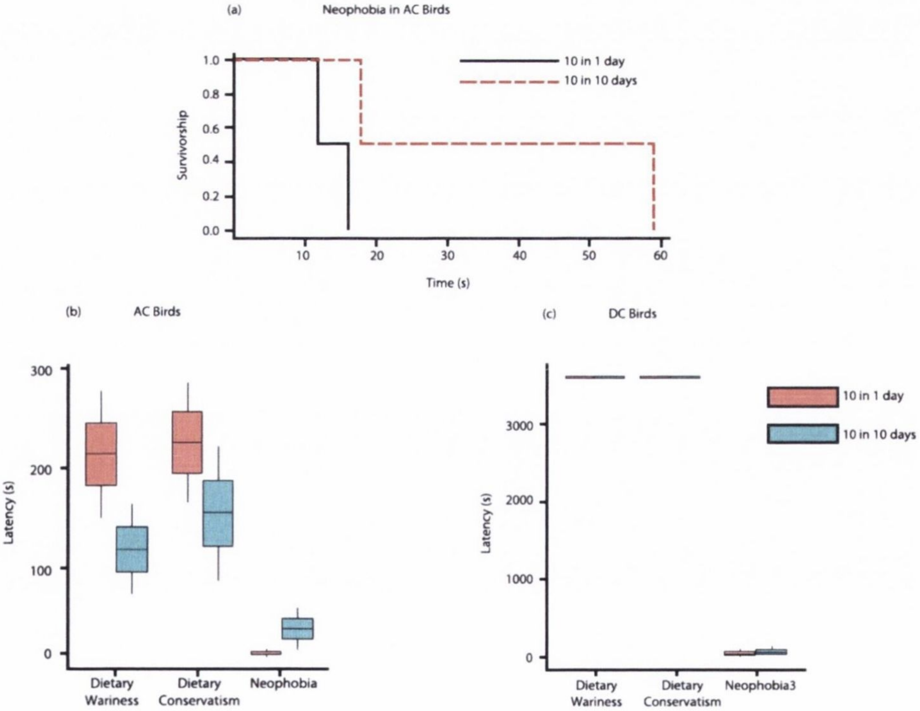


Figure 6.5.1 (a) Survival analysis for neophobia in AC birds in both the '10 in 1 day' and '10 in 10 days' treatments. Boxplots of the three foraging traits of (b) AC & (c) DC birds in both of the treatments.

6.6 Part II: How does varying the temporal distribution of novel food influence dietary conservatism in domestic chicks?

6.6.1 Methods

Thirty six chicks were obtained, housed and trained as described in section 2.2 and once they had been marked for identification, were randomly assigned to one of two groups of the same treatments as in part I of this experiment. Four chicks were designated as buddy chicks for the reasons given in section 2.2. The chicks in the treatment groups took part in a DC test as described in section 2.2.

When the chicks were two days old, they were familiarised with their respective foraging areas. Over the course of either four or five pre-training sessions, each chick was placed in the foraging area (fig 2.2.1) and offered familiar green food. The sessions began with four chicks in the foraging area at a time for two minutes, and each session contained progressively fewer chicks, so that the final round consisted of one lone chick foraging in the arena with two buddy chicks behind a barrier, present for two minutes. Familiarisation is an important aspect of the experimental training as it combats any contextual neophobia which may occur during the testing stage(Brigham & Sibley 1999a; Marples & Kelly 1999b; Richards *et al.* 2011b) . During the pre-training sessions it was important to ensure that all the chicks ate the food once in the foraging area.

Once chicks had become familiar with the green food and the foraging area to be used in a given experimental set up, they were ready to take part in the DC test to establish baseline levels of dietray conservatism. The procedure is outlined in section 2.1.4.

Chicks were deprived of food for one hour prior to receiving their respective treatments. Two foraging areas were set up for the chicks taking part in the 'ten in one day' treatment. Before a chick was placed into the foraging area a single piece of novel food, in this case yellow, was positioned on the floor of the arena next to the two buddy chicks. After a minute had elapsed the chick was transferred to the second foraging area, which had the same set up as the first and this continued until the chick had seen ten pieces of novel food. The chick was then placed back in its home pen were it was allowed to feed freely on familiar food. The following day the chicks took part in a second DC test using yellow as the novel colour. For chicks in the second treatment the procedure was similar. Chicks were again food deprived for an hour before being placed in the foraging arena for one minute. They were then placed in their home pen and allowed to feed. This continued for ten days, on the eleventh day chicks in this treatment took part in a DC test. AC and DC chicks were analysed separately. The data were analysed as described in section 2.3.

6.6.2 Results

Table 6.6.1 above shows the results of the survival analysis for both treatments, which were quite different compared to the previous experiment involving blue tits. There we saw no differences apart from reduced neophobia in the AC birds in the 'ten in one day' treatment whereas for the chicks we saw differences for the AC birds in all but neophobia.(fig 6.6.1) While the DC chicks showed significant differences in all foraging traits in the 'ten in one day' treatment, the DC blue tits showed no significant differences at all. There was one surprising result for DC chicks, which showed that those in the ten in ten days treatment had lower neophobia compared to those in the other treatment (fig. 6.6.2)

Table 6.6.1 Summary of the results of the survival analyses on both AC and DC birds for the difference in survival between the two treatments; ten encounters in one day and ten encounters in ten days

	Foraging Trait	Results of Survival analyses			Distribution
		Z	D.F.	P Value	
			(n = 24)		
AC birds	Dietary Wariness	4.93	21	<0.0001*	Weibull
	Dietary Conservatism	11.52	22	<0.0001*	Exponential
	Neophobia	-0.571	21	>0.05	Loggaussian
			(n = 8)		
DC birds	Dietary Wariness	2.10	6	<0.05*	Exponential
	Dietary Conservatism	2.56	6	<0.05*	Exponential
	Neophobia	-2.84	6	<0.01*	Exponential

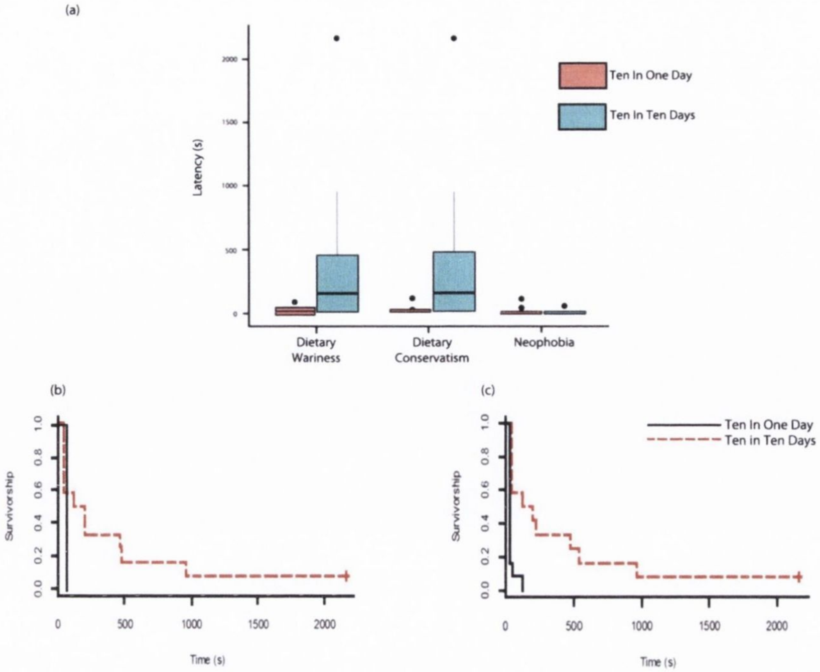


Figure 6.6.1 (a) Boxplots of the three foraging traits of AC birds in both of the treatments. Survival analysis for AC birds in both the '10 in 1 day' and '10 in 10 days' treatments, (b) neophobia and (c) dietary conservatism.

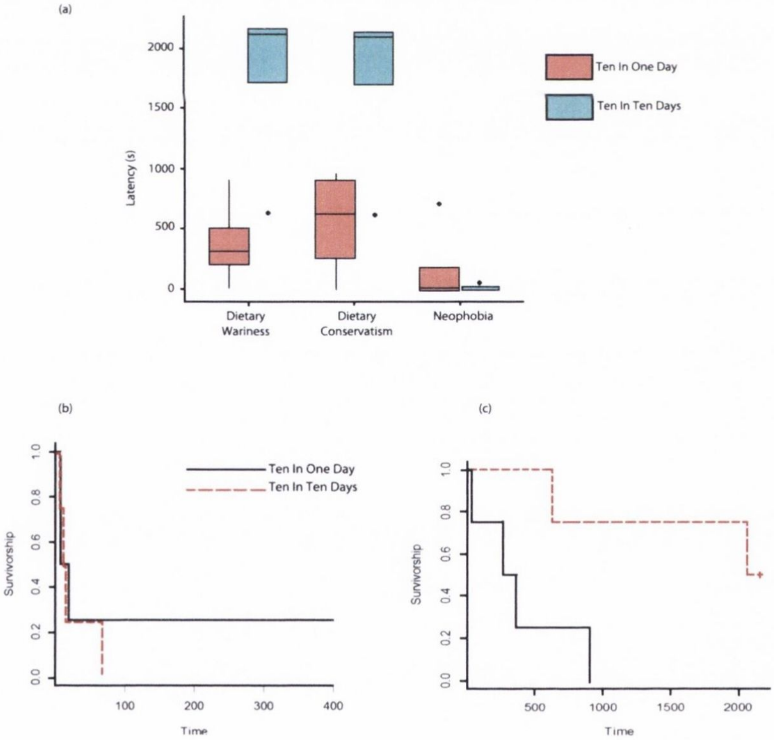


Figure 6.6.2 (a) Boxplots of the three foraging traits of DC birds in both of the treatments. Survival analysis for AC birds in both the '10 in 1 day' and '10 in 10 days' treatments, (b) neophobia and (c) dietary conservatism. The dots in (a) represent outliers.

6.7 Discussion

These experiments have shown that blue tits and chicks, encountering novel and familiar foods at different rates and temporal distributions, altered their behaviour in response, depending on how they encountered the food. We expected that the birds who encountered much more of the novel food would be faster to incorporate it into their diet but that was not the case in experiment 1 part I. Those individuals who experienced the fewest encounters with the novel food had the lowest levels of dietary conservatism and it is not quite clear why this might be the case, especially in light of the finding that the birds with the highest encounter rate were less neophobic towards the novel food when compared to those with fewer encounters. This trend was reversed in experiment 1 part II, where the individuals with the highest encounter rate displayed lower levels of dietary conservatism. As well as being less conservative they were also less neophobic (as they were also in part I).

Where the encounters with novel food were temporally varied, we saw that the blue tits were very resistant to change in their foraging strategies. DC individuals did not alter their behaviour when they encountered ten novel items in ten minutes, as we expected them to. Instead, they continued refusing to accept the novel food when they next encountered it. While AC individuals did react to the treatment, it was only the neophobic portion of their dietary wariness that was affected, with birds which encountered the ten novel items over a shorter period of time reducing their latency to approach them.

We also saw that deactivating the dietary wariness of the domestic chicks was much more straightforward when compared to the blue tits. Both AC and DC individuals showed significant differences in all aspects of dietary wariness, only the neophobia of the AC individuals unaffected by the treatments in experiment two part II (where chicks experienced 10 novel items in one day versus 10 in 10 days).

Looking at the behaviour of AC and DC birds separately revealed distinct differences between their foraging strategies, particularly when neophobia and was considered in experiments one and two. In experiment 1 part I, the AC birds showed no difference between treatment groups; they were no less neophobic in the 'many encounters' treatments than in the 'few encounters' treatments. This finding was somewhat surprising given that numerous studies have shown that exposure to novelty reduces neophobia (Jones 1986; Kelly & Marples 2004; Schlenoff 1984), suggesting that for AC blue tits it took relatively few encounters with novel food to deactivate neophobia. Conversely for DC individuals a reduction in neophobia came only in the many encounters treatment, suggesting that neophobic responses of AC and DC individuals are quite different. While in experiment 2 part I we only saw a reduction in neophobia by the AC blue tits, ten encounters over the course of ten minutes was not enough to reduce neophobia (or any aspect of wariness) in the DC blue tits. Meanwhile AC and DC chicks differed only in their neophobia experiment 2 part II.

In experiment 1 part II, when the novel foods were presented in a different context to part I of the experiment, some of the trends seen in part I were reversed. For AC birds there were significant differences in dietary wariness and conservatism between the treatments. Both of these measures were lower in the 'many encounters' treatment, which contrasts with part I where the result was reversed. However, the neophobic responses were the same, again suggesting that only a few encounters with novel foods are required to reduce neophobia in AC individuals. As was the case with part I, we saw a different reaction to the novel foods by DC individuals compared to the AC birds. There was no difference in wariness and dietary conservatism, but there was reduced neophobia in the 'many encounters' treatment. In this experiment, encountering many novel foods sequentially was not enough to deactivate DC in conservative foragers.

Similarly in experiment two, there was only a reduction in neophobia for AC blue tits in the 'ten in one day' treatment, while there were no reductions for any of the foraging traits in DC blue tits. This result suggests that deactivation of dietary conservatism is a more complex process compared to that of neophobia (Marples & Kelly 1999). In part II of the experiment, there were reductions in overall dietary wariness and dietary conservatism in AC chicks but no reduction in neophobia. Thus it seems that neophobia may have been deactivated in those chicks experiencing novel food just once a day for ten days, just as easily as it had been for chicks in the other treatment. This again hints as the ease with which neophobia can be deactivated compared to dietary conservatism. Although DC chicks had lower neophobia in the 'ten in ten days' treatment, there was an extreme outlier in these data which may have influenced the result, which, when removed gives the opposite result.

Marples and Kelly (1999) argued that neophobia and dietary conservatism were distinct processes owing to the ease with which neophobia could be deactivated and the complexity of dietary conservatism. The present study also illustrates the differences between behavioural responses to novelty, not only with regard to neophobia and dietary conservatism but also between adventurous and conservative individuals.

The differences between parts I and II of experiment one were perhaps most interesting of all. Why should those in the 'many encounters' treatment of part I refuse to accept the novel food while those in the 'many encounters' treatment of part II were prepared to accept it? Models of diet choice often predict that when resources are available in different frequencies, the most abundant resource should be the most exploited in order to maximise net rate of energy gain (Charnov 1976a; Emlen 1968; MacArthur & Pianka 1966; Pulliam 1974; Schoener 1971). Sherratt (2011) also suggests that sampling of novel items present in very low densities would not be beneficial, as the cost of obtaining the information about profitability would be too high, whereas if the prey are present in large numbers, then there is more to gain by sampling them because they may be profitable and therefore a resource worth exploiting. How an individual encounters these different food sources in a foraging patch is, therefore, likely to influence dietary decisions within that patch. (Shettleworth *et al.* 1988). The encounter rate informs the individual of the availability of the resources. Once this information has been gathered by the forager, it is assumed they will use this information to decide which foods they will eat. As stated, we expected that when individuals encountered more novel items they would more readily accept the novel food type into their diet, because this could be viewed as an indication that the novel food is in plentiful supply and should be exploited. Sherratt (2002) argued that visual foragers may have evolved a predisposition to react cautiously to novel conspicuous prey, since conspicuousness is likely to indicate that the prey are defended in some way. Perhaps sequential encounters with novel food items in part I of the experiment reinforced the idea that the prey were possibly defended, instead of deactivating their conservative strategy as we expected.

The novel food was presented alongside the familiar food in part I, in the 'many encounters' treatment, so there was no indication that the novel food was more abundant than the familiar food. If the birds were using encounter rate as an estimation of prey availability then they may have perceived that there was no cost in refusing the novel items (Shettleworth & Plowright 1992; Stephens & Krebs 1986). If the behaviour displayed in the lab translates to a real behaviour in the wild, then the way in which prey are encountered could have a profound effect on whether or not they are incorporated into an individual's diet and consequently on the fitness of those prey. The results of the first experiment suggest that if novel and familiar prey are present in equal numbers then familiar prey will continue to be the preferred resource for foragers whether they are adventurous or conservative.

This goes someway to explaining why novel food was ignored by the birds in part I of this experiment, but not why those in the 'few encounters' treatment decided to accept it. Allen (1988), in a review of frequency dependent predation, showed that apostatic selection occurs at low prey densities and anti-apostatic selection tends to occur at higher prey densities. As food was presented to the birds in their home boxes in an area a little under $1m^2$, the presentation of the food in this relatively small space could have indicated to the birds that food was present at relatively high densities. Some studies have suggested that at high prey densities foragers will switch from apostatic selection to anti-apostatic selection (Allen & Weale 2005; Horsley *et al.* 1979; Weale *et al.* 2000). This perceived high density of novel items may have influenced the birds to exploit the novel food resource.

Another possible interpretation of these results relates to aversion to aggregations. In the 'many encounters' treatment there can be no frequency dependent selection of prey because both prey types are present in equal numbers. The birds in the 'many encounters' treatment may have been treating the numbers of novel prey encountered as an aggregation and were therefore more fearful of it. Several authors have reported such a tendency among predators (Alatalo & Mappes 1996; Gagliardo & Guilford 1993; Riipi *et al.* 2001) and Fisher (1930) believed that it was not necessary for individual prey to be tightly clumped together in order to be perceived as an aggregation by predators. Rather, if large enough numbers were to be found in the territory of a predator, the predator may perceive this as an aggregation. The fact that aposematic organisms tend to distribute themselves in aggregations (Gagliardo & Guilford 1993) means that visual predators are likely to have an evolved predisposition to treat them with caution (Sherratt 2002) and this may have been the case here. The act of encountering a large number of novel prey in the small space of the home box was not enough to deactivate the DC of these birds, but seems to have increased it. It may also be the case that birds in the 'few encounter' treatment, having only encountered two of these novel prey, estimated there to be sufficiently high density of these prey items in the small foraging area they were occupying to warrant consuming them but not so high that they would consider them to be aggregated and therefore aversive.

In the experiment 1 part II, the birds have behaved as we first expected them to; birds in the treatment with the highest number of encounters had the lowest levels of DC. Part II differed from part I by taking place outside the home boxes of the birds and out in the aviary itself. This meant that the birds had to seek out the food actively and encounter it as they searched, as opposed to it being presented to them as in part I. In part II six feeding dishes were arranged in two rows of three, with each dish approximately one metre from the next nearest dish. This layout was somewhat similar to the design of Cowie (1977) in which the foraging behaviour of great tits was investigated. Unlike in part I, the birds did not preferentially select the novel food in the 'few encounters' treatment but continued to avoid it, having encountered it only twice within the aviary. This arrangement could indicate that the birds estimated a much lower density of novel items compared to in part I, and therefore they were not worth sampling (Sherratt 2011). Even in the many encounters treatment of experiment 1 part II, the novel prey were not likely to have been perceived as an aggregation as they may have been in part I of the experiment because of the large size of the aviary in which they were presented in part II.

The openness of the aviary may have played another part in the decision making process of the birds. In their boxes, food was presented to the birds and there was very little effort required on the birds' part to obtain the food. Out in the aviary, birds had to fly around, and, even though they had been trained to know where the food was likely to be, they had to expend energy to find it. Given that they had been without food for an hour already, they may have felt an added urgency to obtain food.

Experiment 1 Part II was a more realistic investigation of the foraging strategies wild birds would employ under varying encounter rates with novel and familiar foods. The less natural confinement of foraging bouts to within an individual's home box may possibly have confounded the results by artificially inflating the birds' estimations of prey densities. Yet the results were interesting nonetheless. Future studies into foraging behaviour in captivity should attempt to replicate real world conditions as far as possible. As was seen here, there were markedly different results obtained depending on where and how food was presented to the birds. It appears that the way in which food is encountered or presented to the birds is quite important. Many encounters with novel food in a small space appeared to deter individuals from consuming it, while the same number of encounters in more open spaces encourages exploitation of the resource.

If the results obtained here represent natural behaviours in the wild, then the way in which foraging individuals encounter their prey will profoundly influence their decision on whether to consume it or not (Stephens and Krebs 1986). Add to that the presence of AC and DC individuals and another layer of complexity reveals itself. Upon encountering equal numbers of novel and familiar prey, DC individuals ignored the novel prey and continued to prey on the familiar items, which could have a major impact on populations of novel prey, such as invasive prey species. Our results imply that if an invasive novel prey species could reach high enough numbers or arrived in large enough numbers then a proportion of the foraging population would simply refuse to predate them. Moreover if those prey were profitable it would represent a significant cost to DC foragers to ignore them for any length of time. Conversely, AC foragers encountering large numbers of novel prey may switch from familiar prey to these novel prey.

Additionally, the duration and time interval between encounters would appear to be quite important and the results here suggest that even relatively high encounter rates over a short period of time are not enough to encourage consumption of novel foods, even by AC individuals. Furthermore, the results highlight the many ways in which DC foragers, in particular, can behave sub-optimally when making decisions on whether or not to consume food items upon an encounter.

7 Handling time and prey profitability influence dietary conservatism in the domestic chick

7.1 Introduction

Classic models of prey choice show that individuals searching for food should attempt to maximise their net rate of energy intake by selecting the most profitable prey when available, and this choice is irrespective of the availability of the unprofitable prey types (Charnov 1976a, b; Elner & Hughes 1978; Emlen 1968; Pulliam 1974; Schoener 1971; Goss-Custard 1977). There have also been some empirical tests of these predictions, for example Krebs *et al.* (1977) found that great tits presented with a choice between large profitable and small unprofitable pieces of mealworm, behaved according to the predictions of these models. Similarly Elner and Hughes (1978) found that shore crabs, feeding on mussels, selectively preyed on mussels according to their relative handling times. Small mussels were ignored because the effort required to open them negated any nutritional gain, while intermediate sized prey were favoured because they were relatively easy to open and offered a greater energy reward.

In dietary choice situations, the decision by an individual to specialise on a particular prey type assumes that they are able to assess the current availability of alternatives in the environment and react accordingly (Elner & Hughes 1978). Diet choice models predict that animals should choose the most profitable options and the empirical evidence suggest that some animals can do this (Krebs *et al.* 1977; Krebs *et al.* 1978; Werner & Hall 1974). However, it is not known how individuals react in diet choice situations where the most profitable option is also the least preferred; more specifically, when the individual in question displays dietary conservatism.

The present study investigated dietary conservatism in the domestic chick and specifically whether altering the profitability of familiar foods influenced the level of DC shown by foraging birds. Optimal foraging theory dictates that when there are a number of food types available, foragers (in this case foraging chicks) should feed exclusively on the most profitable type. If the cost of foraging on this type increases relative to some alternative, a switch in preference should be made (Elner & Hughes 1978). If the handling time (time required to prepare the food for consumption) of one item is greater than that of another item of equal nutritional value, then it should be rejected, assuming both are present in equal amounts. In this study, the handling time of familiar food is increased by making it more difficult to obtain compared to novel food (the reasons for which are outlined in the methods below). In the absence of any underlying preference for novel or familiar food, the novel food should be chosen as predicted by the diet choice models, because the novel food is more profitable than the familiar food. However, it remains unknown at present how the profitability of the foods and the presence or absence of dietary conservatism will influence the food choice in birds. The present study uses foraging domestic chicks to investigate how DC and AC individuals change their foraging strategies when offered novel and familiar food which differs in its ease of handling.

7.2 Methods

A batch of 40 chicks were obtained, housed and cared for as described in section 2.2. Familiar food used in the experiments was green dyed chick crumbs while the novel colour used in the initial DC test was red and in the experimental treatments the novel colour was blue. These dyed foods were prepared as described in section 2.2 and table 2.2.1.

All of the chicks (including buddy chicks) underwent a DC test as described in section 2.2. In order to test the effect of altering the handling time of familiar food, the familiar food was presented in such a way that it was harder for the chicks to obtain. In the experimental treatments, food was offered to the chicks in feeding trays consisting of small wooden blocks, 6cm long, 3cm wide and 1.5 cm thick. Each block had two small depressions approximately 1.5cm in diameter and 1cm deep, into which food could be placed. In order to make the food harder to obtain, inedible plastic pellets, similar in size and shape (but not colour) to the chick crumbs, were placed into the depressions alongside the food. In order to obtain the food, chicks had to remove the pellets physically by pecking them out of the depression. The chicks did not eat the pellets but rather pecked at them until they bounced out of the hole or they simply lifted them out.

7.2.1 Pre-training

Chicks were randomly assigned to one of four treatment groups, outlined in table 7.2.1. A total of eight chicks were placed into each group with the remaining eight chicks designated as buddy chicks. Buddy chicks were necessary because solitary chicks tend to become agitated. These buddy chicks were present in pairs in a buddy holding area within the foraging arena (fig. 2.2.1). They were separated from the experimental chicks by a wire mesh, so that the experimental chick had auditory and visual contact with the buddy chicks, but the buddy chicks could not interfere with the foraging choices of the test bird.

The experimental treatments took place inside a small foraging arena, 84cm x 84cm with 21cm high walls with wooden floor (fig. 2.2.1). On the day of their arrival chicks were exposed to the test arena twice to train them to eat in this arena. They were placed into the arena in groups of four for five minutes. The floor of the arena was lightly covered with green-dyed chick crumbs, and a number of the wooden blocks were also present. This arena set up was used for the duration of training. On day two the chicks were placed into the foraging arena in groups of three for five minutes, repeated twice. On the third day chicks trained in pairs, with the majority of the chicks crumbs then present on or in the wooden block. Again, this was repeated twice. On the fourth day chicks were placed in the foraging arena to forage alone, with two buddy chicks present in the buddy holding area. On this occasion food was only present on or in the wooden blocks. This procedure was repeated until all the chicks were regularly taking food from the wooden blocks.

The chicks were then trained to remove food from the blocks, which had the plastic pellets inside. This was achieved by gradually increasing the ratio of pellets to chick crumbs until the chicks were successfully picking out the pellets to obtain access to the food. This method also ensured familiarity with the pellets, and avoidance of their ingestion. Once all the individuals were successfully removing the pellets to obtain food, they were ready to take part in the experiment.

Table 7.2.1 Summary of the treatments used, the number of pellets refers to how many plastic pellets were placed in the depression alongside one piece of familiar food.

Treatment	No. of Pellets	No. of chicks
Control	0	8
A	2	8
B	4	8
C	6	8

7.2.2Experimental treatments

Table 7.2.1 summarises the treatments used in the experiment. There were four treatments in all, a control and three experimental treatments which had two, four or six pellets in the wooden block as well as a single chick crumb. Tests carried out in training revealed that it was relatively easy for the chicks to remove the food with only two pellets present but more difficult when six were present.

After a period of food deprivation, a chick was placed into the foraging arena where two buddy chicks were already present. Buddy chicks were used in rotation and for no longer than 15 minutes. When they were not in use they were in their home pen where they could eat and drink freely. In the control treatment three wooden blocks were placed in front of the buddy "cage" (fig. 7.2.1). Chicks spent most of their time here and this positioning ensured they were able to perform the foraging task efficiently. A single piece of novel (blue-dyed chick crumbs, O'Brien's liquid blue) and familiar (green) food was placed into each depression in the wooden blocks, giving a total of three novel and three familiar pieces of food, one of each in each block. In other treatments the appropriate numbers of plastic pellets were placed into the depression with the familiar food, leaving the novel food unaffected. The following latencies were recorded; the latencies to peck first at both novel and familiar food; the latency to eat each piece of familiar and novel and food; the latency for three pieces of novel food to be eaten. From these data; the end of neophobia (first peck at the novel food) and the end of dietary conservatism (latency for three novel food crumbs to be eaten, minus neophobia) were calculated.

Figure 7.2.1 The experimental set up. This shows the set up for the control, with novel blue food and familiar green food placed in the depressions in the wooden blocks.

Each trial lasted two minutes and if a chick failed to eat three pieces of novel food they repeated the trial the following day up to a maximum of five trials. If they had still not eaten three novel food crumbs at this point they were awarded the maximum latency of ten minutes or 600 seconds. Data were analysed as described in section 2.3.

7.3 Results

Figure 7.3.1 above shows the results of the DC test. There were 19 AC chicks and 13 DC chicks in total. Table 7.3.1 shows their distribution within the experimental treatments. Those chicks which ate the novel food within the 960 seconds were classified as AC foragers and those that didn’t were classified as DC.

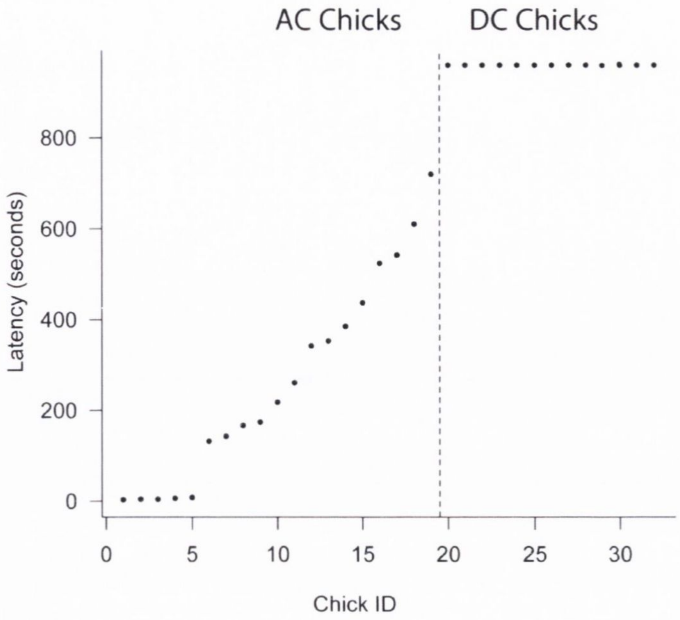


Figure 7.3.1 The results of the DC test, in which 19 chicks ate three pieces of novel food within the time of the DC test, while 13 did not and were thus designated as DC.

Table 7.3.1 The breakdown of AC and DC individuals and how they were distributed among the treatment groups.

Treatment	AC	DC	Total
Control	5	3	8
A	5	3	8
B	5	3	8
C	4	4	8
Totals	19	13	32

Table 7.3.2 shows the results of the GLMs carried out. They reveal that although there was no significant interaction between the levels of neophobia shown by AC or DC birds and the latencies displayed in response to the treatments, there was a significant interaction between the level of dietary conservatism of AC and DC birds and their responses to the treatments. This indicates that AC and DC birds reacted

differently to the treatments, therefore they were analysed separately.

Table 7.3.2 Summary of the results of generalised linear model analyses on the interaction between foraging trait (AC or DC) and treatment. *indicates significant differences.

Foraging trait	GLM Results				
	F	Degrees of freedom	P value	Family	link
Dietary Conservatism	9.911	2,29	<0.0001*	Gaussian	Log
Neophobia	0.319	2,29	0.729	Gaussian	Log

Table 7.3.3 outlines the results of the survival analyses carried out for both AC and DC birds. For AC birds there were no differences between the treatments for neophobia, but when dietary conservatism was considered, treatment C was significantly different from the control treatment. AC birds with familiar food covered by six plastic pellets ate the novel food more readily compared to the control (fig. 7.3.2(e)). Multiple pairwise comparisons with Bonferroni corrections revealed that there were no differences present among any of the other treatments (adjusted α= 0.008). DC birds showed no differences in the latency to eat three novel pieces of food: they continued to ignore the novel food in all treatments and there were also no differences among the treatments, fig 7.3.2. There was however a reduction in neophobia in treatment C compared to the control.

Table 7.3.3 The results of the survival analysis for both AC and DC birds comparing the treatments with the control group. *indicates a significant difference.

		Treatment								
	Trait	A			B			C		
		Z	d.f.	P	Z	d.f.	P	Z	d.f.	P
AC	Dietary Conservatism	-0.811	15	>0.05	-0.727	15	>0.05	-3.142	15	<0.01*
	Neophobia	-1.207	15	>0.05	0.506	15	>0.05	0.460	15	>0.05
DC	Dietary Conservatism	-0.174	9	>0.05	0.688	9	>0.05	-0.142	9	>0.05
	Neophobia	-0.888	9	>0.05	-1.058	9	>0.05	--2.43	9	<0.05*

The latency to eat the first three pieces of food (either novel or familiar) could be indicative of the cost of the foraging exercise, if individuals took longer to eat three pieces of food it would point to longer handling times. This measure was chosen because all individuals in the treatments ate at least three pieces of food; although six pieces were available, not all of the birds ate six pieces. For that reason a further survival analysis investigating the latency to eat the first three pieces of food, whatever their familiarity, was carried out. For DC birds in treatments B and C, the time to consume three pieces of food was significantly different from the control treatment (table 7.3.4). Additionally treatment A was significantly different from treatments B and C, while there was no difference between treatments B and C, (figure 7.3.3 (a)). AC birds however showed no differences between any of the treatments, for any of the foraging traits, (figure 7.3.3(b)).

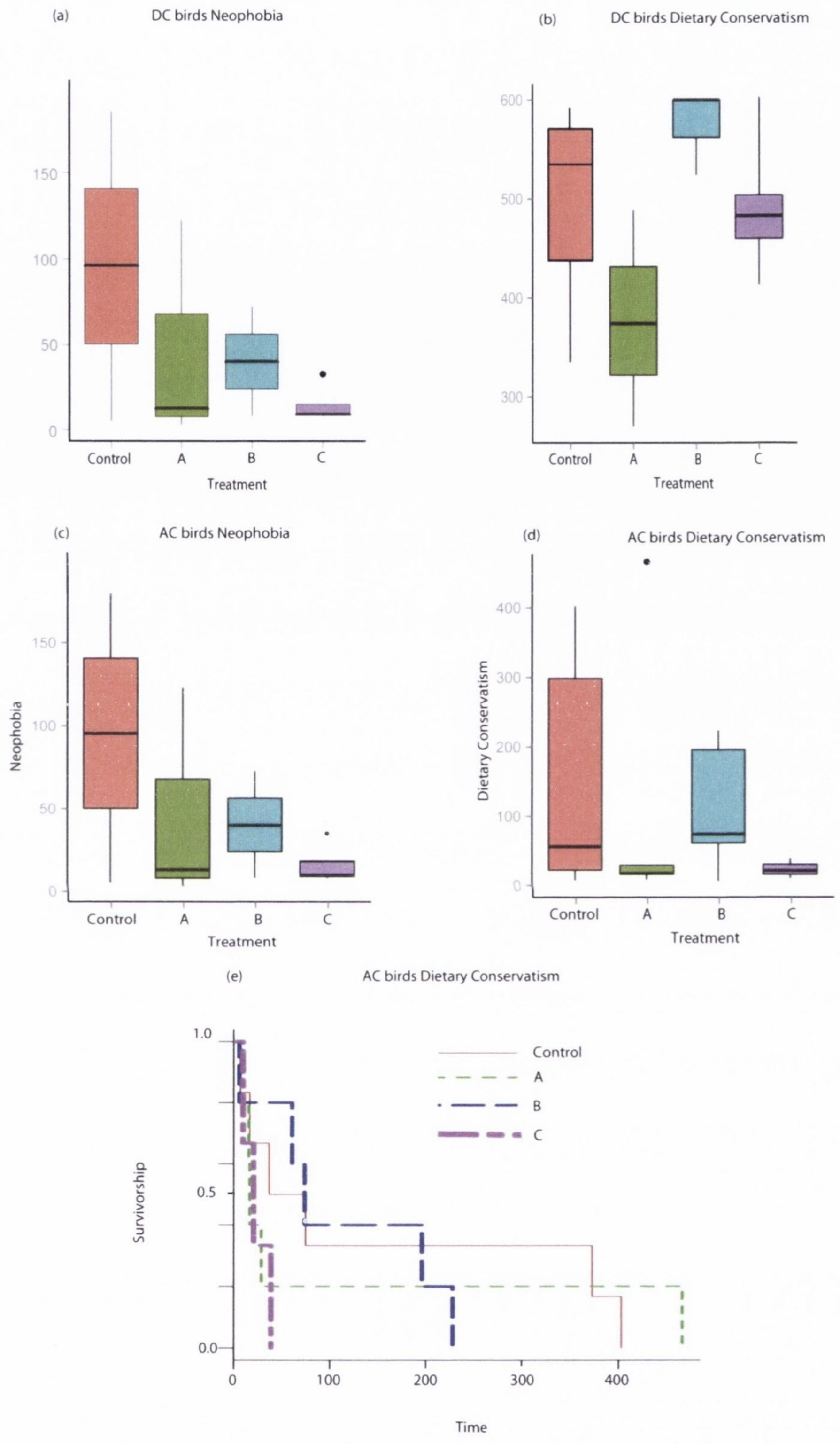
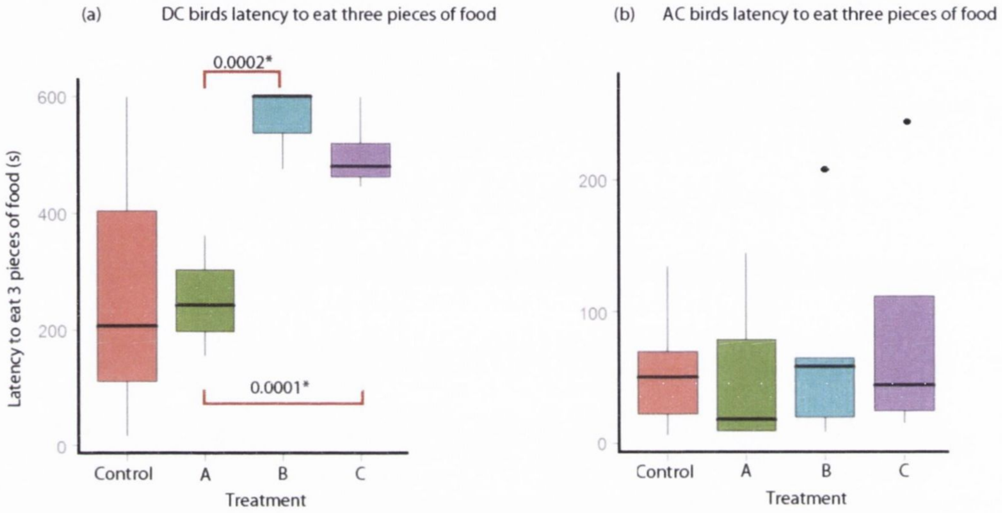


Figure 7.3.2 (a) Neophobia scores for DC birds, (b) dietary conservatism scores for DC birds, (c) neophobia scores for AC birds, (d) dietary conservatism for AC birds and (e) survival curves for dietary conservatism in AC birds.

Table 7.3.4 The results of the survival analysis for the latency to eat the first three pieces of food.

	Treatment								
	A			B			C		
	z	d.f.	P	z	d.f.	P	z	d.f.	P
AC	-0.122	15	>0.05	0.437	15	>0.05	0.732	15	>0.05
DC	0.109	8	>0.05	2.583	8	<0.01*	2.041	8	<0.05*


(a) DC birds latency to eat three pieces of food

(b) AC birds latency to eat three pieces of food

Figure 7.3.3 The latency for both (a) DC and (b) AC birds to eat the first three pieces of food (novel or familiar) in each treatment. Numbers on the boxplots are P-values from the multiple pairwise comparisons with * indicating a significant difference (adjusted α = 0.008).

7.4 Discussion

DC chicks did not alter their food preferences despite the fact that familiar food was more costly to pursue. In order to consume familiar food, DC chicks significantly increased their foraging time. Compared to the control treatment, DC chicks in treatments B and C took significantly longer to eat three pieces of food, which was also the case for treatments B and C compared to treatment A. The addition of the plastic pellets added a significant cost to ignoring novel food. There was, however, a significant difference in neophobia between treatment C and the control, perhaps indicating a temptation to begin sampling the novel food in these conditions. Yet this reduction in neophobia was not enough to trigger eating of the food, and so full acceptance into the diet.

There was no such cost of the treatments for AC chicks because there was no difference in the latency to eat three pieces of food in any of the treatments. When the cost of choosing familiar food became too high due to the presence of the plastic pellets, the AC chicks switched from familiar to novel food. When the cost of foraging on a particular resource increases foraging, optimal foraging theory predicts that there will be a switch to more profitable resources (Charnov 1976a; Emlen 1968; Pulliam 1974; Schoener 1971) and this is what was observed for AC chicks. Krebs *et al.* (1977) and Elner and Hughes (1978) found similar results in great tits and common shore crabs, *Carcinus maenas*, respectively.

All models of optimal foraging include the assumption that individuals are capable of judging the profitability of a given food item and acting accordingly (Charnov 1976a; Emlen 1968; Pulliam 1974; Schoener 1971) and the results presented here would suggest that the AC chicks were able to do that. It would be fair to assume that DC chicks would also be capable of doing this, yet they chose to ignore the novel food even though it was more profitable in some of the treatments. Clearly then, their propensity to behave in a conservative manner can be costly in certain foraging situations, causing them to behave in a sub-optimal manner. It is possible, of course, that DC chicks have a higher threshold of foraging cost, compared to AC chicks, above which they will switch from familiar to novel foods and that this higher threshold was not reached in these experiments. However, even if this were the case, their strategy of eating only familiar food is clearly somewhat costly. This cost must be compensated by some benefit for the trait to persist in the population.

In an early discussion of foraging theory, Schoener (1971) described the characteristics of a number of forager types. These included energy maximisers, (individuals whose fitness is maximised when net rate of energy gain is maximised), and time minimisers, (those whose fitness is maximised when net energy gain is maximised for a given time spent foraging). Our results would suggest that AC chicks both maximised energy and minimised time by switching to the novel food when the profitability of the familiar food was decreased by the presence of the pellets. On the other hand, DC foragers were neither energy maximisers nor time minimisers. They could, perhaps, be classified as risk minimisers, gaining an increase in fitness by minimising their risk of eating toxic or defended prey. The profitability of the novel food is unknown to the chicks and perhaps it was not present in large enough numbers to warrant sampling by the DC chicks (Sherratt 2011), even though the AC chicks' sampling threshold was reached. Novel items encountered in the wild may well be defended, and if present in low numbers there is little to gain from sampling; rather this could incur a significant cost (Sherratt 2011).

An alternative reason why DC chicks would concentrate their foraging effort exclusively on one prey type is that they might become more efficient at finding and handling that one type, than if they searched for more than one type, in a manner similar to search image (Tinbergen 1960). However, in this experiment, the food was offered in a depression in a feeding block, so locating it was not a problem. The response of the DC birds, therefore, suggests that this food location reason for specialising in the familiar food is unlikely to be the full explanation for their behaviour.

The strategy employed by the AC chicks was not only optimal in the sense that they ate the more profitable of the resources available, but doing so in a relatively short space of time afforded them more time for other activities, which in a real world setting could translate to a considerable fitness advantage. On the other hand, it could be argued that such a strategy could turn out to be quite costly if the novel food was chemically defended (Sherratt 2011), though research suggests that sampling unprofitable novel foods helps foragers learn to avoid them more quickly (Shettleworth 1972).

Shettleworth and Plowright (1989) demonstrated that pigeons, subjected to foraging bouts of different lengths, were able to assess the amount of time available for foraging (the time horizon) and adjust their preferences accordingly. So, when pigeons were coming to the end of a short foraging bout, they tended to choose the less profitable prey more often than birds which had more time available. A similar result was also demonstrated by Lucas (1987a) in great tits. Many of the DC birds took part in a number of trials due to their failure to eat the novel food, so it is interesting that they never behaved in the way that Shettleworth and Plowright's pigeons did. This finding highlights how strong the chicks' urge to forage conservatively actually is.

It is not known to what extent the behaviour reported here would be exhibited by populations of wild birds, although there are AC and DC foragers present in wild populations (Marples *et al.* 1998). The AC/DC foraging strategies are known to exist in wild bird populations and it is therefore likely that the behaviours reported here could occur in at least some situations. As highlighted above, the costs and benefits of these strategies depend ultimately on the nature of the novel food encountered by the foragers. If the prey are defended, then clearly a conservative approach is favourable; conversely if the prey are profitable, to ignore them could be considerably costly for DC foragers. AC foragers may incur large costs if novel prey are chemically defended, though by sampling novel prey they gain valuable information (Sherratt 2011) about future encounters.

This study highlights the difference between AC and DC foragers. On the one hand, AC foragers behaved in a manner predicted by optimal foraging models. They accepted novel food when to reject it would have been costly. DC foragers, in contrast, continued to eat only familiar prey even though doing so was potentially decreasing their net rate of energy intake. This could have a profound effect on the fitness of individuals in the current climate of large scale habitat change. An increasing number of species are faced with novel ecological conditions, and how they adapt to those conditions will ultimately decide their fate. An understanding of the foraging choices made by both types of forager is needed if we are to know and effectively manage the changes in their foraging conditions.

8 General Discussion

8.1 Blue tits and the level of dietary conservatism observed

This population of blue tits had by far the greatest proportion of DC individuals compared to all other species and populations studied so far (Marples *et al.* 2007; Marples *et al.* 1998; Richards *et al.* 2011; Thomas *et al.* 2004; Thomas *et al.* 2010). Figure 8.1.1 shows the total number of DC birds within those used for this study. There may be a number of reasons why this was the case. The way in which the birds were captured may have been one reason. In order to maximise our catch of birds at any given site, we placed feeders with food at the site for a number of days before mist netting at the site. Most of the mist netting occurred in relatively suburban areas of the city. It would therefore be fair to assume that many of the individuals would have been familiar with bird feeders and the food contained within them. We generally used peanut and wild bird seed mix. Therefore we may have been artificially attracting those individuals to the feeders that were not prepared to eat other sources of food and were generally of a DC nature. However other studies, including Marples and Mappes (2010), which got very few DC birds, also caught the birds by mist netting at feeders, so it may just be a feature of this population.

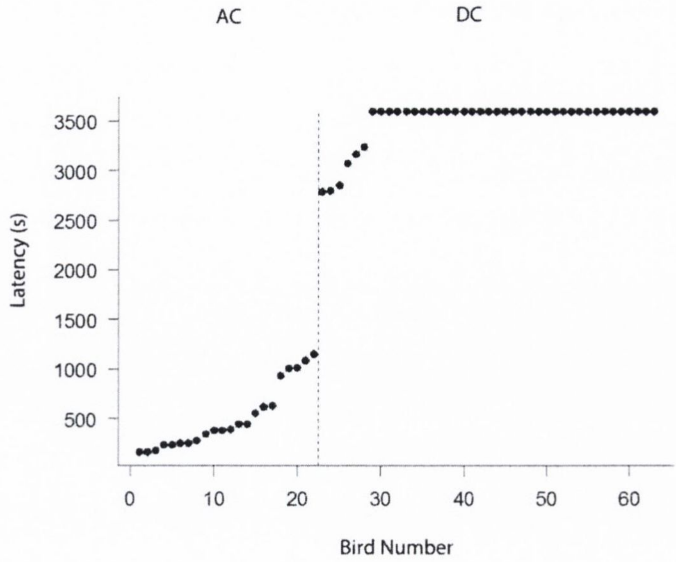


Figure 8.1.1 The total number of AC and DC blue tits found in this study. The y-axis represents the latency (in seconds) for the birds to eat three pieces of novel food.

The majority of the birds used in this study were from one of two sites: the botanical gardens in Dartry, and a small wooded area in Santry, both in Dublin. While mist netting for the birds at both these sites I observed a relatively high number of predatory species. In Dartry there were a number of cats present all year round, both belonging to the botanical gardens and neighbouring houses. In Santry there were at least one pair of buzzards, *Buteo buteo* nesting at the site, which can occasionally prey on blue tits (Dare 1961). Additionally on the majority of mornings I saw at least one sparrowhawk, *Accipiter nisus*. The results of chapter five on the effect of predation threat on the level of dietary conservatism displayed, indicated that when there was a threat, birds became more conservative. Thus the presence of feeders in these predator rich areas gives birds a quick and relatively safe way to obtain food, and once again this may have attracted more DC individuals than AC. If it is an advantage to be conservative in the presence of a predator then perhaps the majority of birds in these areas are already DC, hence the high proportion that we caught. While being a feature of those populations, it may not be a trend for the species as a whole. Studies of the balance of the two foraging strategies among blue tit populations of other areas would therefore be of great interest.

8.2 Behavioural plasticity in dietary conservatism

8.2.1 Adapting to a changing environment

The ability of individuals to adapt to changing or unstable environments and conditions is crucial for their survival, as it enables them to feed and reproduce more efficiently. The greatest threats to populations at present are habitat destruction, climate change and the introduction of exotic species (Lande & Shannon 1996). Habitat destruction and fragmentation decrease biodiversity (Wilcox & Murphy 1985), reducing the size of suitable habitats for predators and prey alike. Climate change can alter the characteristics of the landscape, changing conditions to such an extent that they are no longer compatible with the physiological needs of some species (Davis & Shaw 2001; Parmesan *et al.* 1999). It can also affect the phenology of important events, such as migration (Altwegg *et al.* 2012), reproduction (Visser *et al.* 2004) and the emergence of plants and insects (Walther *et al.* 2002). The introduction of exotic invasive species, which can be linked to both habitat destruction and climate change, can occur through intentional or accidental release of species outside their natural range (Mack *et al.* 2000). The presence of invasive species can seriously alter the ecosystem into which they have been introduced.

A degree of phenotypic plasticity can help alleviate the effects of the changes mentioned above (De Witt & Scheiner

2004). Adapting behaviour is just one way that animals can adjust to the changing environment, particularly when it comes to diet choice. The results of the experiments carried out here reveal just how plastic the DC response can be. The presence of competitors persuaded DC foragers to incorporate novel foods into their diets, something that they did not do when there was no pressure to do so.

8.2.2 Plasticity in foraging strategies in response to environmental conditions

The threat of predation meant that AC foragers, who would normally eat novel food with little or no hesitation, ignored novel food in favour of familiar food. Thus it seems that there might be some cost to evaluating novel food before consuming it. It has been demonstrated that dividing attention between foraging and predator detection can lead to increased mortality from predators (Dukas 2004; Godin & Smith 1988), thus it seems likely that judging the value of a novel resource might require additional attention, which might otherwise be directed towards predator detection.

When encounter rates indicated that a novel resource was plentiful in the environment, both AC and DC foragers generally accepted that resource more readily. However, the results of these experiments indicated that the manner in which the resource was encountered greatly influenced the decision of whether to consume it or not. It seems that there was an element of density dependence (Cook & Miller 1977) in the decision making process. If the birds gauged there to be a very high density of novel prey they may have actually regarded it as an aggregation (Fisher 1930), and instead of accepting the novel food in this instance, the aggregated nature of the food may have been aversive (Gamberale &

Tullberg 1996; Roper & Marples 1996; Sillén-Tullberg 1990; Speed 2000).

There were, nonetheless, some occasions where some individuals stuck rigidly to their foraging strategy despite the apparent high cost of doing so. In chapter seven, the handling time of familiar food was increased, and here we saw that although the AC chicks were willing to accept the more profitable novel food, the DC chicks were not. This experiment was not carried out on wild birds but if the results apply to wild birds, which seems plausible given the apparent ease with which DC can be deactivated in chicks compared to blue tits (chapter six), then this rigidity in foraging strategy when applied to handling time, could represent a significant cost to the DC forager.

Looking at the results overall, they were generally, at least somewhat, intuitive. When the cost of ignoring novel foods was high, we saw a tendency for both AC and DC birds to accept them. When the cost of acceptance was deemed too high, they were refused. The results suggest that, like classical empirical work on optimal foraging (for example Milinski and Heller 1978 and Elner & Hughes 1978), the birds were able to use the information they gathered during the experimental treatments and alter their behaviour to either forage more efficiently (chapters 4 & 6) or to divert attention to where it needed to be (chapter 5).

8.3 Factors which might influence the ratio of AC/DC foragers

8.3.1 Predation

Some of the results reported here suggest that there are conditions that are more suitable for AC birds and some which are more suitable for DC birds. Looking at predation pressure for example, birds living in a territory or environment that contains high numbers of top predators (e.g. raptor species) might do better if they are DC. The results from chapter five indicate there may be some cost for AC birds in processing the decision whether or not to eat novel food (Dukas & Kamil 2000), which distracts them from detecting predators. The experiment carried out here revealed the location of the predator to the foraging bird, so that they could adjust their behaviour accordingly, which may not happen in the natural environment. Animals wishing to prey on foraging birds would be more successful if they remained hidden from their intended victims, giving them little time to react (Kenward 1978).

Studies have revealed that individuals, engaged in activities which reduce vigilance, suffer higher mortality (Godin & Smith 1988). Consequently AC birds may be at a greater risk from unseen predators than their DC counterparts, DC birds being able to direct some of their attention to predator detection. The fact that AC birds began to behave more like DC birds in the predation threat experiments supports this argument. Therefore a greater selective pressure on AC individuals, driven by top predators, might lead to populations which are more DC in nature, where there is a greater risk from predation.

This selection pressure for a greater proportion of DC foragers may also have implications for the species that the birds themselves prey upon. A novel morph of a prey species of the foraging birds would stand a better chance of surviving in an environment that contained predators of its predator. This would occur for two reasons. Firstly, because the presence of top predators might reduce the numbers of foraging birds, and secondly, because of the selective pressure for birds in that environment to adopt a more conservative foraging strategy, or for those birds which are genetically DC to become more numerous. Even if AC birds were present in the area, they might be at greater risk of predation (Dukas 2004; Godin & Smith 1988), and therefore might not survive long enough to encounter the novel prey, allowing it to reach fixation within the local environment (Thomas *et al.* 2003). For these reasons, dietary conservatism may have facilitated the initial evolution of aposematism as has been argued before (Marples *et al.* 2005; Thomas *et al.* 2003). This, of course, assumes that AC birds devote less attention to predators in general, not only when they encounter novel prey.

It might be tempting to suggest that dietary conservatism originated as a response to chemically defended prey, however it has been proposed that this does not have to be the case (Marples *et al.* 1998; Thomas *et al.* 2003). I have shown here that DC could have evolved as a response to predation threat. Simply put, those birds that refuse to incorporate novel food into their diet may suffer less predation because they would be better able to detect an imminent attack. While AC birds, by dividing their attention between assessing the novel food and detecting a predator, might suffer greater predation.

8.3.2 Intraspecific competition

There is a suggestion that intraspecific competition, in combination with DC, could contribute to how individuals are distributed. In highly competitive environments or in areas where there are high densities of individuals, AC birds might be better competitors and exclude DC foragers from these areas. AC foragers may be better at exploiting novel resources, therefore better at expanding their diets to alleviate the effects of competition. Even though the results of the experiments in chapter four suggest that DC birds are prepared to accept novel food in these kinds of conditions, they may prefer to seek out territories containing fewer competitors and more familiar food.

8.4 Neophobia and Dietary Conservatism: distinct processes?

8.4.1 Deactivation of neophobia and dietary conservatism

In their paper addressing the differences between dietary conservatism and neophobia, Marples and Kelly (1999) revealed that dietary conservatism was a much more complex behaviour than neophobia. Neophobia could be deactivated with relative ease, whereas dietary conservatism seemed to be a much more robust trait comprised of several stages (see section 1.1). The results reported here lend weight to these claims. In many of the experiments, neophobia was reduced by the treatments while dietary conservatism remained unaffected.

The experiments that dealt with encounter rates (chapter six), more than any of the other experiments, revealed distinct differences between the deactivation of neophobia and dietary conservatism, particularly for DC birds. In the first set of experiments the numbers of novel food items that the birds saw were different between the treatment groups. The results showed that when the food was presented to the DC birds in a small space, those in the 'many encounters' treatment were more averse to consuming the novel food, i.e. their level of dietary conservatism was higher than the birds in the 'few encounters' treatment. However these same DC birds that experienced more novel foods in the treatment were less neophobic. Even though the DC birds were less willing to consume the novel foods in this treatment, they were more willing to approach the food. These results suggest that deactivating neophobia is a relatively simple process, as has been reported before (Marples & Kelly 1999; Roper & Marples 1996; Schlenoff 1984). It seems that deactivating the dietary conservatism component of their dietary wariness is somewhat more complex. Furthermore how it is deactivated differs depending on whether the individual is AC or DC.

Similarly, in the experiments dealing with handling time and prey profitability (chapter seven), there were different responses to the treatments by DC birds in terms of the neophobic and DC response. Making the familiar prey unprofitable compared to the novel prey was not enough to deactivate dietary conservatism, but it was enough to deactivate neophobia. The birds were willing to approach and peck at the novel food but not consume it. Following from Marples and Kelly (1999) this was perhaps a sign that the birds were approaching acceptance or at least a willingness to begin to assess and sample the novel food. As mentioned in the discussion in chapter seven, we may not have reached the point in the experimental treatment at which the cost of handling the familiar food persuaded DC birds to abandon their conservative strategy.

The second set of experiments in chapter six demonstrated the ease with which DC could be deactivated in chicks compared to blue tits. Ten exposures to the novel food were enough to deactivate DC in both AC and DC chicks, whereas the same treatment had no effect on either type of blue tit. Only neophobia in AC blue tits was affected. Thus, even though the chicks from the first set of experiments seemed to be on the path to acceptance (i.e. they were willing to begin sampling the novel food), the results from the second set of experiments suggest that it would be much more difficult to achieve this feat in blue tits by similar methods. All of this further highlights the difference between neophobia and dietary conservatism.

8.4.2 Differences between AC and DC birds.

There were distinct differences in behaviour between AC and DC birds in virtually all the experiments, particularly in relation to neophobia and the ease with which it could be deactivated. In the first set of experiments dealing with encounter rate (experiment one part I, p.78), there was no difference in the neophobic reaction of the AC birds between the treatments. Thus it seems that it took relatively few encounters with novel foods to deactivate their neophobia. In contrast the DC birds only reduced their neophobia when they encountered the novel food many times.

In the second part of these experiments there were different behavioural responses between the two forager types again. When AC birds encountered many novel foods they showed reduced dietary conservatism but not neophobia, while DC birds showed no reduction in dietary conservatism but a reduction in neophobia. This again highlights the contrasting ways birds with different foraging strategies react to novelty.

Upon encountering a predator (chapter five), there was again distinct differences between the reactions of AC and DC birds, not only in relation to the novel food on offer but to the predator itself. DC birds were much slower to return to feeding after seeing a predator, while AC birds returned just as quickly as those birds that had seen a pigeon. While it was not explicitly examined in the experiment, there is a suggestion that this reaction may be related to boldness (Wilson *et al.* 1994), thus there may be a tendency for AC birds to be bolder than DC birds under threat of predation. This also suggests that there may be some AC/DC and Bold/shy behavioural syndrome that exists, though again I would emphasise that it was not the purpose of these experiments to determine the existence of such a syndrome and more research in this area would help to clear this matter up.

The experiments dealing with handling time and profitability of novel prey (chapter seven), revealed that AC birds were perhaps more sensitive to the relative cost of preferentially selecting familiar food when it was more difficult to obtain. While DC birds continued to ignore novel food even when it was clearly a more profitable choice, they did, however, show reduced neophobia in the treatment where familiar food was most difficult to obtain. AC birds foraged efficiently in all treatments, while DC birds were significantly slower in the treatments compared to the control. If the behaviour displayed in the lab by domestic chicks is applicable to wild birds, the reduced efficiency in feeding could be very costly.

8.5 The maintenance of adventurous and conservative foragers

The difference between AC and DC foragers and their response to novelty under different ecological conditions suggests a mechanism for the maintenance of this resource polyphenism (West-Eberhard 1989). There are sets of ecological conditions that can favour either the AC or the DC strategy. When a situation such as this exists, there is likely to be selection for alternative phenotypes under different conditions (Moran 1992).

As can be seen from the results reported here, some environmental conditions elicit different responses from AC and DC birds, some of which may result in differential fitness levels between the two alternative foraging strategies. For example, AC foragers in an environment containing a high number of top predators may be more susceptible to predation than their DC counterparts (see chapter five and Godin & Smith 1988). Thus there will be a selective pressure to be DC in this ecological scenario. Conversely, when familiar food becomes costly to handle compared to a more profitable but novel alternative there is pressure to forage using the AC strategy.

Conditions such as this should also select for a level of plasticity among alternative foraging strategies, particularly if the environment is variable and the conditions switch between favouring one strategy over the other (Moran 1992). Plasticity was evident in many of the experiments, particularly among

DC birds; when faced with competition, they were willing to consume novel food in these circumstances.

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