PHOBIC FINCHES: INVESTIGATING NEOPHOBIA REACTIONS IN A COLOUR POLYMORPHIC SPECIALIST, THE GOULDIAN FINCH, ERYTHRURA GOULDIAE

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Abstract

Unpredictable changes to familiar environmental conditions, owing to Human Induced Rapid Environmental Change (HIREC), are increasingly presenting novel stimuli and creating strong selection pressures on specialist species to adapt to these changes. Neophobia is an ecologically relevant and adaptive fear behaviour, functioning to allow animals to avoid danger. However, cognitive mechanisms such as neophobia are seldom investigated within conservation research. This thesis examines the neophobic responses of a food and habitat specialist, the Gouldian finch, *Erythrura gouldiae,* within captive conditions across two experimental trial conditions. Dietary wariness was investigated to determine how this food specialist will respond to the novel appearance of food (neophobia) which deviates from in-situ habitat preferences. Furthermore, investigation into the attenuation to novel food was conducted to determine changes in the acceptance of novel food over time and the existence of dietary conservatism within this species. Gouldian finches were also exposed to novel environments in separate testing conditions. I investigated spatial neophobia to determine how this habitat specialist will respond to ecologically relevant habitat types, which replicate and deviate from in-situ habitat preferences. I interpret Gouldian finch responses to novel food and novel environments into the ecological consequences dietary wariness (food neophobia and dietary conservatism) and spatial neophobia may have on wild populations. Furthermore, Gouldian finches are colour polymorphic in both sexes and previous research has shown head colour signals personality within this species; red-headed birds are more aggressive, yet less explorative and risk taking than black-headed birds. This offers the opportunity to further investigate head colour in food and spatial neophobia contexts and investigate dietary conservatism in addition to food neophobia. The effects of age and sex were also investigated as previous research has shown age and sex effects are inconclusive in other species and only object neophobia has been investigated in the Gouldian finch to date. Throughout this thesis, I provide evidence that Gouldian finches consistently elicit greater strengths of neophobia to novelty, which deviates the most from in-situ food and habitat preferences.

Gouldian finches were more hesitant to approach and feed on novel food than familiar food (Chapter Two). Moreover, finches consistently discriminated between food types, showing continual preference for the familiar food and highlighting this specialist evidences high proportions of dietary conservatism within the population (Chapter Two). Further, I found these attenuation responses to novel food were consistent between trials (Chapter Two). An effect of age was identified showing younger birds fed on the novel food faster than older birds (Chapter Two). Gouldian finches were more hesitant to approach and enter open habitats than dense habitats in both trial conditions (Chapter Three). Males demonstrate more hesitancy than females to approach novel habitats and younger birds entered novel habitats sooner than older birds within the first trial condition (Chapter Three). Finch responses to habitats differed with social contexts as birds partnered with black-headed finches demonstrated greater conflict to approach habitats but entered sooner in comparison to birds partnered with red-headed finches (Chapter Three). Entry latencies into novel habitats were significantly correlated within both trial conditions, demonstrating consistent responses in both trial conditions (Chapter Three). I found evidence that food and spatial neophobia were correlated in one trial condition only, representing inverse relationships on feeding latencies to novel food and entry latencies into open habitats and a positive relationship in the conflict to approach novel food and dense habitats (Chapter Three). I provide further evidence that neophobia is an effective cognitive mechanism to augment conservation research and supplement previous research, which highlights Gouldian finches are particularly vulnerable to changing environmental conditions. Specifically, I propose Gouldian finches will not incorporate new food types into the diet and deliver the first evidence to show the faster assessment and entry into novel environments is facilitated by the presence of a black-headed finch. These findings evidence the effect of head colour should no longer be overlooked in conservation research on this species.

Acknowledgements

What an unusual feeling this is having finally made it to this stage of submitting a thesis. Now that I am here I am not entirely sure what to say! I certainly do feel mixed emotions about this as it's the end of a two year slog, which is great as I have made it but also a bit depressing because it is the end of another chapter in my life.

But what an whirlwind adventure this has been!

When starting out on this MPhil programme as a rookie researcher (which I still know I am), I was under the impression it would be a joint venture between myself and my three supervisors. Nope! These last two years have been an uphill struggle that have produced some incredibly exciting research findings and has helped me develop considerably on a personal and professional level. I cannot thank the people involved in this research enough but will do my best to express my eternal gratitude here.

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Chapter One

Introduction to the thesis

1.1 Conservation issues and the current role of behaviour and cognition theory

Organisms are increasingly challenged to adapt to changed conditions owing to anthropogenic practices, which can ultimately determine survival (Sih et al 2011; Greggor et al 2014). Tackling this ever increasing effect of Human Induced Rapid Environmental Change (HIREC) on animal species is proving extremely challenging for conservationists globally. Efforts of implementing achievable solutions to decelerate population growth, for example managing invasive species and increase or stabilise declining populations of near threatened and endangered species, have so far had limited success (Phillips 2007; Reaser et al 2007; Moseby et al 2011; Olden 2011; Pearce-Higgins et al 2012), with some cases amplifying non target species decline. A well-known example of this unanticipated effect of non-target species decline through invasive species management is the case of the rosy wolf snail, *Euglandia rosea.* Introduced to Hawaii as a biological pest control to tackle the invasive giant African snail, *Achatina fulica,* the rosy wolf snail had minimal success in reducing populations of the target giant African snail and heavily predated on native species, causing the extinction of 15 endemic Hawaiian tree snails (Reaser et al 2007). Although this is a rare example of a conservation tragedy, it is not unreasonable to question the underlying management decisions that led to the determination of implementing a novel predator to Hawaii as a feasible management solution to tackling an invasive species, particularly as this had a direct consequence on invertebrate species that are now no longer extant. In addition to managing invasive species, other conservation priorities include tackling human-animal conflict (Dickman 2010), reducing the impact of windfarm implementation on bird population declines (Marques et al 2014), conservation breeding (Witzenberger & Hochkirch 2011), reintroduction (Seddon 2010; Sutherland et al 2010) and reducing adverse responses to novel cues (Greggor et al 2014). Coupled with the ever-growing effect of continually changing habitats owing to HIREC (Clavel et al 2011), this highlights the need for interdisciplinary approaches to be implemented within conservation management to gauge the mechanisms that are impacting specific conservation issues, not only at a species level but on an ecological level, thus aiding conservationists to preserve biodiversity (Roth & Krochmal 2015).

The studies of animal behaviour and animal cognition are important components within conservation, but to date are underutilised within conservation practices, particularly cognitive theory (Greggor et al 2014). Behaviour is an interaction with the animals' environment that is driven by the cognitive mechanisms of an individual (Shettleworth 2001). Cognition is a complex psychological process encompassing perception, learning, memory and decision-making (Mettke-Hofmann 2014). Information perceived from environmental stimuli is acquired from the animals' environment, processed and retained which is later utilised to make decisions in future situations, thus encompassing cognition in its broadest sense (Shettleworth 2001; Greggor et al 2014; Mettke-Hofmann 2014). Cognition drives behaviour, which in turn influences species interactions, species distributions, ecological patterns and affects ecosystem functioning (Greggor et al 2014). Tackling current conservation issues from a behavioural and cognition based approach could improve conservation efforts, particularly as species management often depends upon manipulating behaviour (Greggor et al 2014). Given that HIREC is altering habitats at an accelerating rate and is creating great selection pressures on species to respond to unpredictable changes in the environment (Mettke-Hofmann 2017), it is essential to identify the cognitive and perceptual biases that govern specific behaviours, particularly towards novel cues.

1.2 Neophobia, a short history

Neophobia (the fear of the novel; Greenberg & Mettke-Hofmann 2001) is an adaptive and ecologically relevant fear behaviour (Greggor et al 2015), functioning to assist animals to avoid danger. Neophobia was first described by psychologists in the 1950s (Berlyne 1950) following the implementation of comparative psychology tests using albino rats (*Rattus* spp.) and quantifying non-human animal fear, anxiety and memory (Berlyne 1950). Since then, psychologists and more recently, behavioural ecologists have intensely researched the function of neophobia, yet from different approaches. Psychologists are generally concerned with the cognitive mechanisms underlying neophobia (Greggor et al 2015). Moreover, psychologists endeavour to strengthen the understanding of the organisation of brain circuitry and the roles of the hippocampus (responsible for perception, learning and memory; Miller et al 1986) and the amygdala (responsible for emotions such as fear and subsequent fear responses; Davis 1992). Both the hippocampus and amygdala are major brain regions that govern cognitive mechanisms, which in turn govern neophobia (Sutherland & McDonald 1990; Knight et al 2005; Magal & Mintz 2014; Ramos 2015). Most neophobia research conducted by psychologists use laboratory animals, particularly rats. Subject species are often manipulated through surgical means (damaging regions of the brain; Rollins et al 2001; Magal & Mintz 2014; Ramos 2015), induced with drugs (Palsson et al 2005; Lin et al 2012), or a combination of the two (Sutherland & McDonald 1990; Fernandez et al 2004) and exposed to novelty to assess whether perception, memory and decision making are affected for example. Behavioural ecologists are generally concerned with the ultimate causes of neophobia as oppose to the proximate causes underlying neophobic responses and are not restricted to captive animal studies. Most behavioural studies on neophobia are conducted within the laboratory setting, however ex-situ research has shown neophobia has direct effects on fitness costs (Vrublevska et al 2015) and effects on adaptive abilities (Atwell et al 2012) within wild populations, thus has significant relevance to wild population functioning. Greggor et al (2015) has emphasised, psychologists and behavioural ecologists generally focus on either the proximate or the ultimate causes of neophobia; psychologists often overlook ecological validity of neophobia and behavioural ecologists seldom consider the cognitive mechanisms underlying neophobic responses. However, recent research has shown there is overlap between psychology and behavioural ecology (Roth et al 2010; Kozlovsky et al 2014; Al-Shawaf et al 2015), which is encouraging as these disciplines share a common research interest and augment neophobia research from different approaches. Although the convergence of psychology and behavioural ecology is relatively limited, neophobia testing has advanced substantially within both psychology and behavioural ecology research since its first description in the 1950's and has become a common research method to determine species' initial responses to novelty.

1.3 Cognitive processes and behavioural responses to novelty

Neophobia is currently categorised into object neophobia, food neophobia (Chapter Two), spatial neophobia (Chapter Three) and predator neophobia (Greggor et al 2015). But how does neophobia function (Fig 1.1)? From encountering the stimulus, the individual will assess whether to exploit the resource or avoid it. This determination is centred on previous experience of a known resource or through categorisation in which the individual classifies the stimulus as familiar through perceptual similarity (Greggor et al 2014; Fig 1.1).

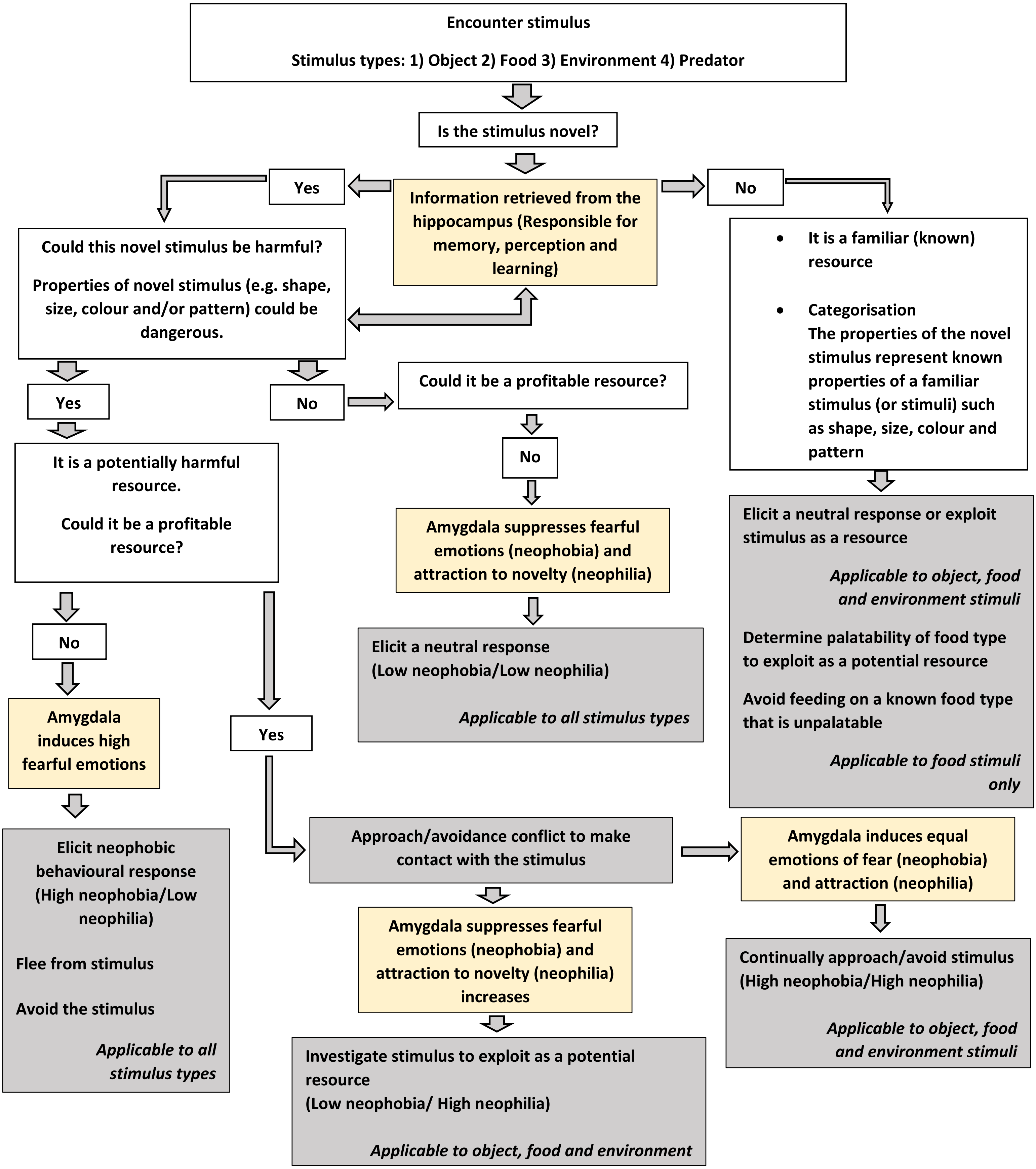


Fig 1.1. Proposed scenario of the cognitive and behavioural processes which take place when an organism encounters novel stimuli. Neophobia begins when an individual encounters the novel stimulus (object, food, environment, predator) and influences the behavioural response to flee from or avoid the novel cue. Categorisation and the proposed process of neophilia (Greenberg & Mettke-Hofmann 2001) are also included to represent alternative decision-making and behavioural responses to the novel stimulus. The brain regions responsible for these cognitive and behavioural processes are described within the yellow text boxes. Behavioural responses to novelty are within the grey text boxes.

The perception of whether the stimulus is a known resource, appears to be similar to a known resource (categorisation), or is a completely novel stimulus takes place within the hippocampus of the brain, responsible for memory, perception and learning (Miller et al 1986; Fig 1.1). Neutral behavioural responses are elicited following the determination the resource is familiar or alternatively, an individual will exploit or sample the stimulus based on the perception the stimulus represents an optimal resource (Fig 1.1). Avoidance of familiar resources is governed by the perception the stimulus is not beneficial, for example unpalatable food types (Fig 1.1).

A stimulus is novel when an individual encounters a stimulus which deviates from what they have already experienced before (Greenberg & Mettke-Hofmann 2001; Greggor et al 2015). The crucial determination when encountering novelty is whether the stimulus could be harmful to the individual (Fig 1.1). Whilst the hippocampus provides no specific experience information on the novelty type itself, information is relayed from other previous experiences in order to assess the potential threat the stimulus poses to the individual (Miller et al 1986). Moreover, exposure to this novelty allows the individual to obtain information from the stimulus and is processed and retained within the hippocampus to deal with similar experiences later in life (Miller et al 1986; Greenberg & Mettke-Hofmann 2001). In its broadest sense neophobia is elicited when an individual perceives the novelty type is likely to be harmful and responds to avoid or flee from the stimulus, but neophobia does not an operate as a singular decision making process. Neophilia is the attraction to novelty (Greenberg & Mettke-Hofmann 2001) and contrary to neophobia, elicits exploration of a resource as oppose to avoidance because it is a means to gather information from the stimulus to exploit as a potentially profitable resource (Mettke-Hofmann 2014). Neophobia and neophilia are independent of one another because they are modulated by different gene expressions (Powell et al 2003; Weisstaub et al 2006) however they do occur simultaneously and govern whether an individual will avoid or exploit novel stimuli (Greenberg & Mettke-Hofmann 2001; Mettke-Hofmann et al 2002; Mettke-Hofmann et al 2009;Mettke-Hofmann 2014).

Emotional responses of fear (neophobia) and attraction (neophilia) are induced by the brain's amygdala (Davis 1992) following the decision of whether the stimulus is possibly harmful and whether it is a potentially profitable resource to exploit (Fig 1.1). Individuals that demonstrate high levels of neophobia and low levels of neophilia will flee or avoid the resource following the determination the stimulus is likely to be harmful and unprofitable (Fig.1.1). Alternatively, novel stimuli can be perceived as unthreatening and unprofitable, demonstrating low neophobia and low neophilia, resulting in a neutral behavioural response to novelty (Fig 1.1). These behavioural responses both elicit low levels of neophilia, as the novelty is not perceived as a stimulus that can offer information to the benefit of the individual, therefore avoidance or neutral responses will always be favoured. Individuals eliciting high levels of neophilia can respond to novelty in two ways. Whilst the novelty type is attractive in that it may be profitable (inducing neophilia), the individual is in conflict with the costs and benefits of exposing themselves to potential danger to gain a potentially valuable resource. Approach/avoidance conflict is a behavioural response to novelty that can be quantified and demonstrates neophobia and neophilia do operate simultaneously (Mettke-Hofmann et al 2009). If the potential profitability of accessing the resource outweighs the cost of exposure to potential danger, an individual will investigate the stimulus as high levels of neophilia drive exploration responses to make contact with the novelt stimulus (Greenberg & Mettke-Hofmann 2001). Continual conflict between avoiding potential danger through fear (neophobia) and approaching potential danger at the benefit of information gathering to obtain a profitable resource (neophilia) can be elicited and demonstrates high levels of neophobia and neophilia.

1.4 Neophobia varies within and between species and is context specific

Behavioural flexibility in the face of environmental change such as food availability, competition for resources and responses to novel resources is the most important attribute of ecological plasticity when considering a species ability to adapt to predictable and unpredictable environmental conditions within behavioural and conservation contexts (Greenberg 1990b). Ecological plasticity refers to the variability found in organisms within the same (or similar) genotype and is expressed through development pattern, phenotypes or in behaviour according to varying environmental conditions (Greenberg 1990b).

Animals occupy different life styles depending upon diet, the habitat occupied, the harshness of the environment and predictable and unpredictable variation within environmental conditions (Mettke-Hofmann 2014; 2017). Organisms occupy either specialist or generalist life-styles and these are applicable to both diet and habitat selection (Mettke-Hofmann 2014). Food specialists are indeed specialised in their dietary requirements, as this foraging strategy refers to species that exploit one or very few food types whilst food generalists exploit several resources available to them within the environment (Webster & Lefebvre 2001). Whilst food specialists occupy a much narrower ecological niche than generalists, behaviours of specialists have adapted to exploit few food resources efficiently whilst generalists have behaviourally adapted to exploit many resources less efficiently (Clavel et al 2011). Habitat specialists thrive in a narrow range of environmental conditions and occupy a much narrower habitat niche than generalists who exploit a greater range of habitats than specialists, thus the distinction between habitat specialists and generalists (Webster & Lefebvre 2001). Both specialists and generalists do co-exist within overlapping ecological niches because both strategies can do well in predictable environmental conditions, such as seasonal variability within environmental conditions and food availability for example (Mettke-Hofmann 2014).

Neophobia varies between species (Cowan 1977; Mettke-Hofmann et al 2013) because it is dependent upon ecological plasticity (McKinney 1997; Wilson & Lefebrve 2000; Greenberg & Mettke-Hofmann 2001; Mettke-Hofmann et al 2002; Biesmeijer et al 2006; Colles et al 2009; Mettke-Hofmann 2014) and migratory strategy for example (Mettke-Hofmann et al 2004; Mettke-Hofmann et al 2005; Mettke-Hofmann et al 2009; Mettke-Hofmann et al 2013). Moreover, neophobia varies within a species (Mettke-Hofmann 2012; Greggor et al 2016a) because it is dependent upon an individual’s temperament (McDougall et al 2006), developmental stage (Reale et al 2007), and experience (Greenberg & Mettke-Hofmann 2001; Mettke-Hofmann 2012; Greggor et al 2014; Greggor et al 2016a). More recently, neophobia types have been shown to be context-specific, because neophobic responses are dependent upon the type of novel stimuli an individual is exposed to (Verbeek et al 1994; Boogert et al 2006; Ruuskanen & Laaksonen 2010; Greggor et al 2016a).

Given the rate HIREC is affecting animal species globally, organisms are increasingly faced with unpredictable changes in the environments they encounter (Mettke-Hofmann 2014). Consequently, changes to what were previously familiar environments could have significant and detrimental effects on behavioural adaptations of species (McKinney 1997). There is a wealth of research focussing on object neophobia in non-human animals (Richard et al 2008; Biondi et al 2010; Mettke-Hofmann 2012; Williams et al 2012; Greggor et al 2015). This involves placing a novel object in close proximity to familiar food and measuring the latencies to feed on the familiar food. Previous research has shown object neophobia varies within species (Fox & Millam 2007; David et al 2011; Greenberg & Holekamp 2017), between species

(Mettke-Hofmann et al 2004; Mettke-Hofmann et al 2005; Mettke-Hofmann et al 2013) and is dependent upon migratory strategy and on ecological plasticity (Greenberg 1990a & b; McKinney 1997; Biesmeijer et al 2006; Colles et al 2009). More specifically, migratory species have been shown to demonstrate greater object neophobia than closely related residents in warbler species (*Sylvia spp*; Mettke-Hofmann et al 2005), new world blackbirds (*Icterids*; Mettke-Hofmann et al 2013) and in parrot species (*Psittacidae*; Mettke-Hofmann et al 2004). Furthermore, specialist species have been shown to be more neophobic than generalists when exposed to novel objects (Greenberg 1983; 1984; 1990b; Webster & Lefebrve 2001) which demonstrates generalists are more behaviourally flexible (or plastic) to deal with changes to familiar environmental conditions than specialists.

Food and spatial neophobia research is much more limited than object neophobia, particularly in regards to animal life-styles and ecological plasticity. Food neophobia is a behavioural strategy to hesitate eating unfamiliar (novel) food (Marples et al 1998; Marples & Kelly 1999; Johnson 2000; Faith et al 2013). Previous research has shown food neophobia is demonstrated by a range of animal species, particularly primates (Johnson 2000; Visalberghi et al 2003; Gustafsson et al 2014), rats (Hall et al 1997; Lin et al 2009; Modlinska et al 2015) and birds (Turro-Vincent et al 1995; Marples & Roper 1996; Kelly & Marples 2004; Liebl & Martin 2014). Food neophobia can inform behavioural ecologists and conservations of the effects of avoidance to novel food has upon species ecology and extinction risk (McKinney 1997), particularly in regards to foraging strategies. Food generalists explore more habitats and food resources than specialist species (Mettke-Hofmann 2014), which supports the neophobia threshold hypothesis (Greenberg 1990a) as they learn early on in life what foods are safe to consume and are protected later on in life by neophobia to avoid harmful foods (Mettke-Hofmann 2014). Specialist species could be particularly vulnerable to extinction as their specialised foraging strategy impedes the opportunity to exploit new resources and respond to unpredictable changes in the environment such as habitat fragmentation (McKinney 1997; Biesmeijer et al 2006; Colles et al 2009).

Whilst food neophobia has been beneficial in determining species initial responses to novel food, it doesn't tell us about foraging activities beyond the initial response to novelty. Food neophobia is one component of dietary wariness, which also encompasses dietary conservatism (Marples et al 1998; Marples & Kelly 1999; Kelly & Marples 2004). The stages of dietary wariness are grouped into the time to initial contact (neophobia) and the time from initial contact to full incorporation into the diet (dietary conservatism; Marples & Kelly 1999; Kelly & Marples 2004) which are independent and ecologically relevant behavioural processes but presently categorised in some studies as one process, usually termed neophobia (Martin & Fitzgerald 2005) . Dietary wariness (neophobia and dietary conservatism) can inform behavioural ecologists of species acceptance of novel food over time, providing greater insight into specialist and generalist responses to novel food in greater depth. Dietary conservatism will be further discussed in Chapter Two.

Spatial neophobia is the adverse response to enter new environments (Mettke-Hofmann et al 2009). Whilst migrants have been shown to be more neophobic to novel objects than residents (Mettke-Hofmann et al 2004; Mettke-Hofmann et al 2005; Mettke-Hofmann et al 2013), spatial neophobia has been shown to be reduced in migratory species in comparison to residents (Mettke-Hofmann et al 2009). Migratory species are continuously faced with unfamiliar situations in comparison to residents (Mettke-Hofmann 2014) therefore, should be less neophobic to enter novel environments than residents.

Nomadic species track superabundant resources, residing in one location for short periods before moving onto the next location (Davies 1982; Mettke-Hofmann 2014). Unlike migration, nomadic movement is irregular and destinations differ year on year because they have adapted to the conditions they inhabit where resources (food and/or water) are patchy and unpredictable in space and time (Dean 1997). Whilst nomads are wide-ranging, they are rarely generalist species and specialise in habitat and food resources (Runge et al 2014). Nomads are not restricted to directional cues as migrants are and pay attention to environmental changes in order to track resources, suggesting they are behaviourally flexible to environmental change (Mettke-Hofmann 2017). However, unpredictable environmental change such as habitat fragmentation reduces resources patches and tracking food patches could become increasingly unpredictable and energetically demanding. With this in mind, it is essential to investigate neophobic responses towards novel food and habitats to provide greater insight into the conservation implications this has on a species, particularly those highly susceptible to habitat modification such as specialists.

1.5 Neophobia is only the initial response to novelty

To date, most studies on neophobia have been conducted within the laboratory and are currently at the stage where the focus of experimentation is on the initial reaction to novelty only (Sih & Del Guidice 2012), where frequency and latency to make contact with the novel cue are used as measures to quantify neophobic responses. The investigation of how attenuation (reduction in a response to a cue) factors into different types of neophobia is rare (Ensminger & Westneat 2012; Mettke-Hofmann 2012) and is often not investigated alongside neophobia experimentation. Attenuation is dependent upon predictable and repeatable cues therefore eliciting a neutral response to this stimuli (Travaini et al 2013; Greggor et al 2014). A greater focus on attenuation for conservation can be crucial for improving conservation practices because this reflects the species' ability of how they adapt to changed conditions beyond the initial response to novelty (Greggor et al 2014). This could allow for more accurate predictions to be made on how animals will respond to other forms of novel stimuli and how this has a knock on effect on species dispersal. Furthering our understanding into neophobic responses to ecologically relevant stimuli such as food and spatial neophobia, as well as pairing neophobia testing with attenuation and dietary conservatism could further our understanding on behavioural adaptation to novel cues and assist conservationists to tackle existing cues, which are impeding species' opportunities to exploit potential resources.

1.6 The Gouldian finch, *Erythrura gouldiae*

The Gouldian finch is a small granivorous, songbird endemic to Northern Australia (Brazill-Boast et al 2011a, Figs 1.2 & 1.3). This nomadic species is both a habitat and a food specialist, inhabiting open savannah grasslands and heavily relying upon grass seeds, particularly *Sorghum* species (Tidemann et al 1992; Brazill-Boast et al 2011a).

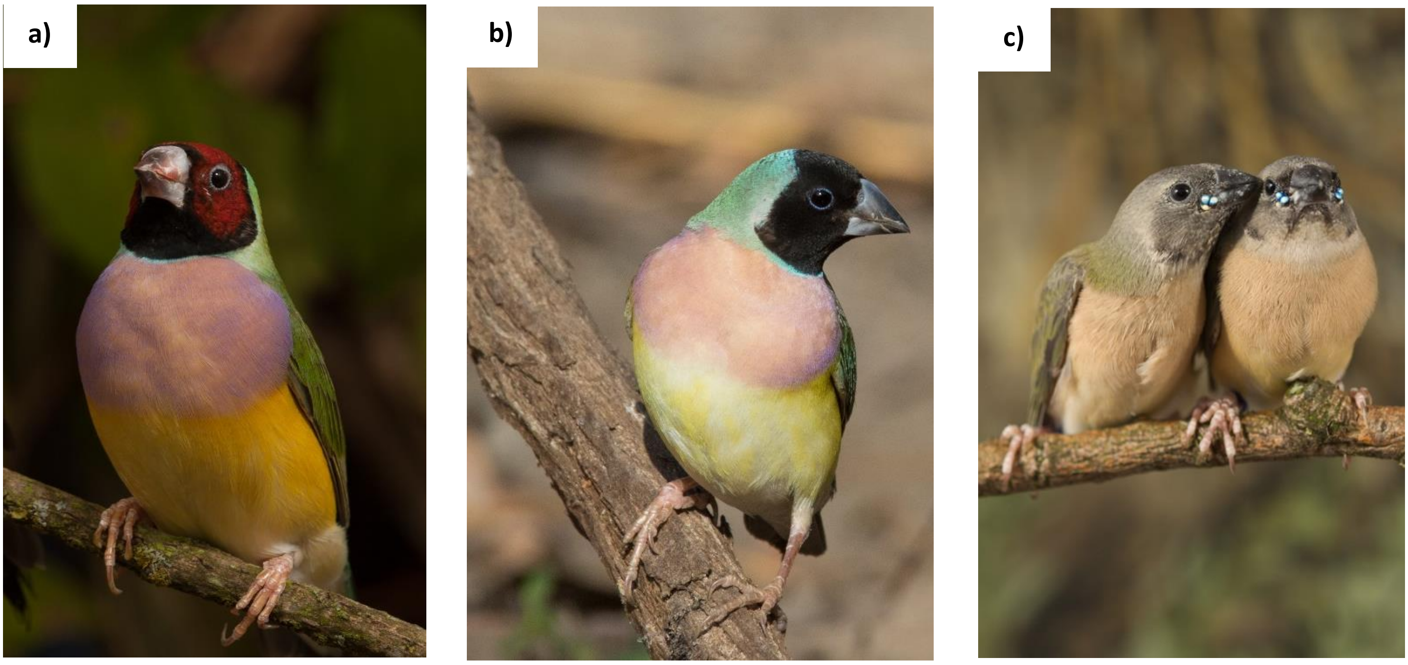
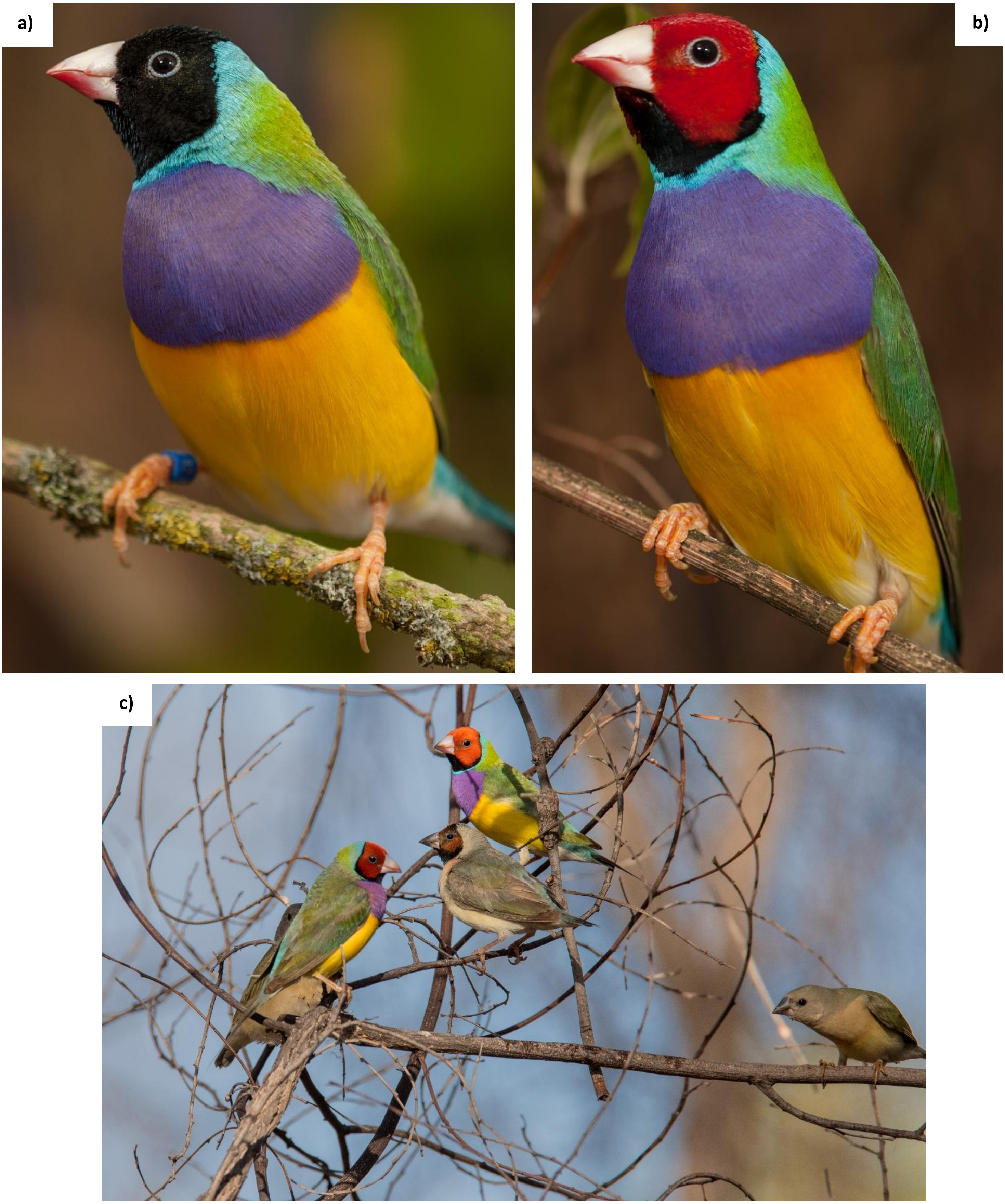


Fig 1.2a) Adult red-headed female **1.2b)** adult black-headed female and **1.2c)** juvenile Gouldian finches. Images courtesy of Gerhard Hofmann and Dr Claudia Mettke-Hofmann.



Figs 1.3a) Adult black-headed male Gouldian finch, **1.3b)** Adult red-headed male Gouldian finch. **1.3c)** Adult and juvenile Gouldian finches located within open savannah grassland habitat. Images courtesy of Gerhard Hofmann and Dr Claudia Mettke-Hofmann.

Currently categorised as near threatened (Birdlife International, 2018), Gouldian finch populations have declined over the past four decades in size and distribution, resulting in a small number of isolated populations that remain (Legge et al 2015; Weier et al 2016). A stronghold of the species is located within the Kimberleys, Northern Australia where most research on this species has been conducted (Brazill-Boast et al 2011a & b; 2013; Legge et al 2015; Maute et al 2015). It is understood habitat fragmentation through farming practices, such as cattle implementation onto Gouldian finch habitat and frequent and intense fire regimes are the principal causes of decline (Maute et al 2015; Weier et al 2016). Such practices create seasonal food bottlenecks for the dietary specialised finch generating increased stress hormone levels, particularly within the wet season (December to March) when food is limited (Maute et al 2015). Furthermore, competition for food and nesting sites with the generalist and more competitive Long-tailed finch, *Poephila acuticauda* (Fig 1.4a & b), within overlapping niches has resulted in the Gouldian finch being susceptible to competitive exclusion (Brazill-Boast et al 2011b). As such, the Gouldian finch is particularly vulnerable to further population decline given anthropogenic practices and intraspecific competition are operating simultaneously. Coupled with the specialist nature of this species, an inability to adapt to changing habitat conditions could determine whether the Gouldian finch can persist in the wild.

Fig 1.4a) Black-headed male Gouldian finch and two long tailed finches at a watering hole and **1.4b)** Group of male and female Gouldian finches and one long tailed finch located at a watering hole. Images courtesy of Gerhard Hofmann and Dr Claudia Mettke-Hofmann.

Gouldian finches are a highly social species (Brush & Seifried 1968) and a unique example of non-melanin based colour polymorphism, which is expressed through head colour in both sexes (Brush & Seifried 1968; Mettke-Hofmann 2012). Within the same population, 70% black-headed, 30% red-headed and <1% yellow-headed birds exist in stable frequencies (Brush & Seifried 1968, Fig 1.5).

Fig 1.5 Three male Gouldian finches of the red, yellow and black headed colour morphs. Images courtesy of Gerhard Hofmann and Dr Claudia Mettke-Hofmann.

Previous laboratory studies have shown head colour signals personality in the Gouldian finch (Williams et al 2012); red-headed birds are more aggressive yet less explorative and take fewer risks than black-headed birds in perceived dangerous situations (Williams et al 2012). Signalling behavioural traits such as aggression through phenotypic expression is advantageous, particularly for social species to reduce the occurrence of aggressive interactions (Pryke 2009). Colour morphs face different selection pressures, such as predation, therefore behaviours have adapted in response to morph-specific pressures (Galeotti et al 2003; Mettke-Hofmann 2012).

A study conducted by Mettke-Hofmann (2012) tested same sex, mixed head colour finch pairs (one black-headed and one red headed bird) in object neophobia and neophilia (the attraction to novelty; Greenberg & Mettke-Hofmann 2001) testing conditions as well as testing capture rank and dominance relationships. Mettke-Hofmann (2012) found behaviours were correlated as birds that approached the novel object for exploration were the ones captured first and were also less neophobic. Black-headed birds were more likely to be captured sooner than red-headed birds. Neophilia rank was related to head colour as black-headed birds approached the novel object sooner than red-headed birds. No relationship between head colour and dominance were found within this study but this is likely because this research did not stage contests for a limited resource as was implemented in previous dominance research on the Gouldian finch (Pryke & Griffith 2006; Pryke 2007). Whilst red-headed birds are the most dominant, they could be more susceptible to predation because they are more conspicuous than the other two head colour morphs in natural backgrounds (Mettke-Hofmann 2012). It is likely red-headed birds allocate more time to information gathering in potentially dangerous conditions to reduce the costs of conspicuousness (Mettke-Hofmann 2012), paying more attention to other birds to respond to potentially dangerous situations. This has been shown in an earlier study by King et al (2015) demonstrating Gouldian finches demonstrate social conformity; when shyer birds were partnered with a bolder partner, they themselves became bolder and bolder birds became shyer when partners with a shy bird. Food shortages are likely to affect red-headed finches in particular because of their reduced exploration capacity, influenced by their conspicuousness and the costs of exposure.

In addition to head colour, it is also important to assess the effect of age on novelty responses. Mettke-Hofmann (2012) found very interesting results in regards to age. Older birds within a pair were more neophilic to touch a novel object at a neutral location and less neophobic than younger birds as they fed sooner by a novel object positioned next to the feeder. However, absolute age analyses revealed older birds were slower to touch a neutral object than younger birds. Effects of age on neophobic responses could be essential particular for social species as individuals use social cues to overcome their own fear of novelty (Bouchard et al 2007; Fu et al 2013; Krueger et al 2014; Greggor et al 2016b). Research findings are inconclusive with regards to age on responses to novelty with studies showing older individuals are less neophobic than younger individuals (Fu et al 2013), younger individuals are less neophobic than older individuals (Biondi et al 2010) and showing both outcomes dependent on relative and absolute age (Mettke-Hofmann 2012). Given older individuals are more experienced, they could be deemed more neophobic than younger individuals, but perhaps this is older birds exhibiting less interest in the novel stimuli (low neophilia; Mettke-Hofmann 2012), whereas younger birds are less experienced and are therefore more explorative by exhibiting more interest to novel stimuli (high neophilia; Mettke-Hofmann 2012). Whichever the outcome, the role age classes play in the social network could be essential, especially for specialist species like the Gouldian finch as they track suitable food locations, (Tidemann et al 1992) which could be led by older more experienced birds, therefore facilitating movement and dispersal. Given the wealth of research focussing on the conservation of this species (Brazill-Boast et al 2011 a & b; 2013; Legge et al 2015; Maute et al 2015, Weier et al 2016), the effect of changed conditions on head colour morphs and age has not yet been assessed. Adaptation to changed conditions could be different between head colour morphs and age groups because of the selection pressures they experience and the knowledge they possess about locating resources. Moreover, augmenting research on specialist species responses to novelty could be beneficial to inform conservationists of the ecological implications specific to this species. This provides a unique opportunity to investigate how a specialist, colour polymorphic, near threatened species adapts to changed conditions through exposure to ecologically relevant forms of novelty.

1.7 Thesis outline & aims

The overarching goal of this research was to investigate different types of neophobia in relation to age, sex, head colour and partner head colour in Gouldian finches. The three main objectives were as follows:

> **Objective 1**: Determine the effect of age, sex, head colour and partner head colour to novel food, attenuation to novel food and the existence of dietary conservatism.
>
> **Objective 2**: Investigate the effect of age, sex, head colour and partner head colour of Gouldian finches to novel environments.
>
> **Objective 3**: Determine whether responses to food and spatial neophobia are consistent and correlated to one another.

Chapter Two

Food neophobia and the existence of dietary conservatism in a colour polymorphic specialist, the Gouldian finch, *Erythrura gouldiae*.

2.1 Introduction

Animal foraging strategies are identified depending upon an animal's diet, the habitat occupied and harshness of environment in which a forager inhabits (Mettke-Hofmann 2014). Organisms occupy either specialist or generalist life-styles and these are applicable to both diet and habitat selection (Mettke-Hofmann 2014). Food specialists are indeed specialised in their dietary requirements, as this foraging strategy refers to species that exploit one or very few food types (Webster & Lefebvre 2001). Food generalists are much less restricted in their dietary requirements than specialists as these foragers exploit several resources available to them within their environment, demonstrating much less discrimination in food choice than specialists do (Webster & Lefebvre 2001). Whilst specialists occupy a much narrower dietary niche than generalists, behaviours of food specialists have adapted to exploit few food resources efficiently whilst generalists have behaviourally adapted to exploit many resources less efficiently (Clavel et al 2011). Both foragers do co-exist within overlapping ecological niches because both strategies can do well in predictable environmental conditions, such as seasonal variability in food availability for example (Mettke-Hofmann 2014).

Shifts in plant seasonality and their geographical range (Dieleman et al 2015; Leishman & Gallagher 2015), owing to Human Induced Rapid Environmental Change (HIREC) is having significant conservation implications on the specialist species which rely on them particularly for food acquisition (Hodgson et al 2010; Mortelliti et al 2010; Clavel et al 2011). Rapid and unpredictable environmental change reduces the optimal resources available to specialist species more so than generalist species (Cody 1981; Day et al 2016) because generalists exploit a greater variety of food resources within their habitat (Webster & Lefebvre 2001). As optimal resources diminish with habitat modifications, specialist species are increasingly confronted with novel resources and challenged to locate familiar food, whilst simultaneously competing for these resources with generalists, ultimately affecting survival rates (Tylianakis et al 2008). Whilst specialist species' trade-off for reduced resource availability with more efficient resource exploitation

(Eeley & Foley 1999; Webster & Lefebvre 2001; Zayed et al 2005; Hardy et al 2007; Clavel et al 2011; Maute et al 2013; Legge et al 2015), a reduced dietary niche and capacity to exploit new resources within changing environmental conditions could determine whether specialists will continue to persist in the wild (McKinney 1997; Biesmeijer et al 2006; Colles et al 2009).

Dietary wariness encompasses two behavioural processes in response to novel food, food neophobia and dietary conservatism (Fig 2.1). Food neophobia is the behavioural hesitancy to approach novel food attributed to its novel appearance (Marples & Kelly 1999; Greggor et al 2015). Food neophobia is measured from the time an individual initially encounters the novel food to the time initial contact is made with novel food, at which point food neophobia ceases (Fig 2.1). When an individual is faced with a novel food (or any other novel situation), two behavioural processes occur simultaneously but act independently of one another, approach and avoidance (Mettke-Hofmann et al 2009). This process occurs during the latency period from initial encounter to initial contact and measures the conflict between approach and avoidance on novel food (Fig 2.1). Individuals can be neophobic and simultaneously neophilic (attraction to novelty; Greenberg & Mettke-Hofmann 2001) to novel food. Approach/avoidance conflict can be quantified by measuring the frequencies in which an individual approaches novel food and subsequently moves away before initial contact; increasing approach/avoidance demonstrates greater conflict to novel food.

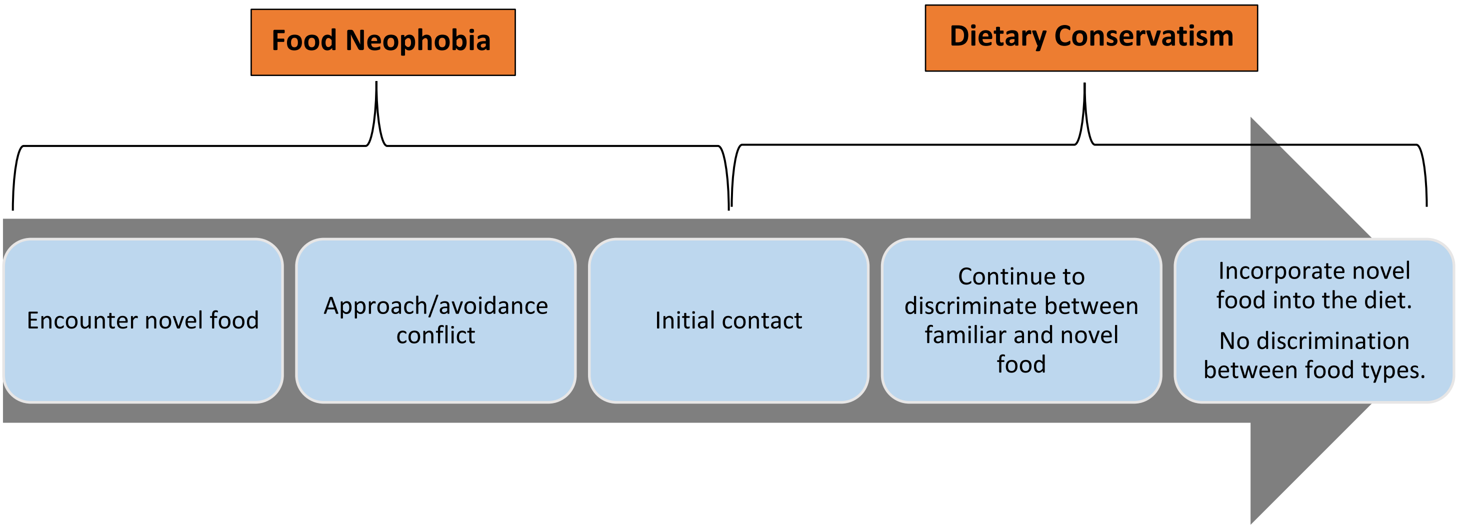


Fig 2.1 After Marples & Kelly (1999) Proposed process of dietary wariness. Food neophobia begins when an individual encounters the novel food and ceases when the individual makes contact with the novel food. Dietary conservatism proceeds neophobia and begins when the individual makes contact with the food and ends when the individual fully incorporates the novel food into the diet.

Dietary conservatism is the aversion to feeding on novel food and adding new foods into the diet, which is attributed to the risk of being poisoned (Marples et al 1998; Marples & Kelly 1999; Kelly & Marples 2004). Dietary conservatism is measured as the time from initial contact (food neophobia ceases) to the time novel food is fully incorporated into the diet (Kelly & Marples 2004; Fig 2.1). Dietary wariness studies often comprise of changing food types or altering food types in some way (such as colour) to compare the study species' hesitancy and the conflict between approach and avoidance of novel food in comparison to familiar (control) food items (Kelly & Marples 2004; Martin & Fitzgerald 2005; Marples et al 2007). Previous research has shown dietary wariness is demonstrated by a range of non-human animal species, particularly primates (Johnson 2000; Visalberghi et al 2000; Gustafsson et al 2014), rats (Hall et al 1997; Lin et al 2009; Modlinska et al 2015) and birds (Turro-Vincent et al 1995; Marples & Roper 1996; Kelly & Marples 2004; Liebl & Martin 2014).

Adverse responses to novel food can inform behavioural ecologists of the effects behavioural plasticity (generalist/specialist forager) has on species' ecology and extinction risk (McKinney 1997). Given generalist species explore more habitats and food resources than specialists (Mettke-Hofmann 2014), this supports the neophobia threshold hypothesis (Greenberg 1990a) as they learn early on in life what foods are safe to consume and are protected later on in life by neophobia to avoid harmful foods (Mettke-Hofmann 2014). Neophobia is a heritable trait (Heath et al 2011) that is associated with behavioural plasticity (Greenberg 1990b) and food neophobia is thought to be an adaptive behavioural trait, influenced by experience and social facilitation, whereby an individual's fear of novel food is overcome sooner by watching others feed on unfamiliar food. This has been shown in Capuchin monkeys, *Cebus apella,* as focal capuchins' fear of novel food were overcome sooner in the presence of group members regardless of whether group members were eating the novel food or familiar food (Visalberghi & Addessi 2000).

Differences in the response to novel food have also been shown to be dependent upon an individual's temperament (Coleman & Wilson 1998; Biondi et al 2010). For example, a study by Coleman & Wilson (1998) investigated the responses of Pumpkinseed sunfish, *Lepomis gibbosus,* to novel food and before testing were categorised into three temperament groups (bold, intermediate and shy) dependent on the behavioural responses to a potential threat. Fish within each temperament category were exposed to novel food and the researchers found intermediate individuals consistently took more bites from novel food in open space testing conditions and the shy individuals consistently took the least bites.

Whilst these previous studies in primates and fish have been beneficial to understand species initial reactions to novel food, these studies focus on food neophobia only, overlooking the responses of individuals beyond the initial contact with the novel food. Investigation into dietary conservatism in addition to food neophobia can determine individual and species level attenuation/acceptance of food over time; that is with increasing intake of novel food, dietary conservatism wanes through attenuation (Burešová & Bureš 1980). Both stages of dietary wariness are independent and ecologically relevant behavioural processes and have been mostly reported in birds. For example, research in captive Japanese quail, *Coturnix japonica* and later in wild European blackbirds, *Turdus merula,* and European robins, *Erithacus rubecula*, discovered individual differences in the responses to novel food (Marples et al 1994; Marples et al 1998). In particular, research conducted by Marples et al (1998) investigated feeding rates of wild blackbirds and robins to familiar and novel food (dyed pastry baits) over successive presentations and found birds differed considerably from one another to contact the novel food (neophobia) and eat the food regularly (dietary conservatism ends). One third of blackbirds showed reduced food neophobia in comparison to other blackbirds, contacting the novel food the first time they saw it whilst none of the robins contacted the novel bait on the first presentation but did show large variability as individual food neophobia ceased from two to 68 trials. Great variation was also found in dietary conservatism as two thirds of blackbirds had fully accepted the novel food into the diet by the third day whilst others demonstrated a prolonged aversion to novel food, with one individual taking more than 125 plus presentations before acceptance. Robins accepted the novel food between 18 to 68 trials depending on the individual. This research has highlighted that food neophobia and dietary conservatism are distinct processes and are governed by species and individual differences in response to novel food. Moreover, this research provided the first evidence that not all individuals are dietary conservative and that proportions of the population consume and accept novel food as soon as neophobia has waned, which was later labelled adventurous consumerism (Marples & Brakefield 1995; Marples et al 1998; Marples et al 2007; Thomas et al 2003, 2004). Further research into these two foraging strategies of adventurous consumerism and dietary conservatism is mostly restricted to birds but has recently been shown in fish (Thomas et al 2010; Richards et al 2014).

Research into dietary wariness can inform behavioural ecologists of species initial responses to novel food (neophobia) and the speed at which individuals accept novel food and incorporate this into the diet (dietary conservatism/adventurous consumerism) but often food neophobia and dietary conservatism are categorised as one process, usually termed neophobia (Johnson 2000; Martin & Fitzgerald 2005; An et al 2011). Investigating food neophobia and dietary conservatism as separate processes provides greater insight into feeding activities over time and the existence of dietary conservatism and adventurous consumerism within populations. This approach has particularly importance for considering the conservation implications of specialist species' initial responses to novel food and whether repeated exposure will increase acceptance of novel food over time, given that HIREC is increasingly changing habitats and exposing specialists to novel food resources.

The Gouldian finch is a near-threatened songbird, endemic to northern Australia (Brazill-Boast et al 2011a; Birdlife International, 2018). This species is a habitat and a food specialist and is adapted to open savannah grasslands (Brazill-Boast et al 2011a). Gouldian finches predominantly forage on grass seeds, particularly *Sorghum* species (Brazill-Boast et al 2011a) and are particularly susceptible to food shortages in the wet season (December to March) when the abundance of preferred grass seeds are depleted (Dostine et al 2001). Principle causes of decline are believed to be cattle implementation and frequent and intense fire regimes, which fragment Gouldian finch habitat and reduce optimal resource availability (Maute et al 2015; Legge et al 2015; Weier et al 2016). Additionally, competition for food and nesting sites with the generalist and more competitive Long-tailed finch, *Poephila acuticauda,* has resulted in the Gouldian finch being susceptible to competitive exclusion (Brazill-Boast et al 2011b). Given these current threats the Gouldian finch is exposed to, an inability to adapt to changing habitat conditions could ultimately determine whether the Gouldian finch can persist in the wild. In-situ research has shown personality is signalled through head colour in this species; red-headed birds are more aggressive yet less explorative and take fewer risks than black-headed birds in perceived dangerous situations (Williams et al 2012; King et al 2015). Object neophobia and neophilia testing conditions have shown older birds demonstrate less object neophobia than younger birds (Mettke-Hofmann 2012) and males are more neophilic to approach novel objects than females (Williams et al 2012).

There are no known studies which have investigated the effects of novel food on neophobic responses and the existence of dietary conservatism in this food specialist. This provides a unique opportunity to investigate how a food specialist responds to unfamiliar food, which is novel in colour and quantify neophobia and determine the existence of dietary conservatism. Additionally, further investigation into the effects of personality (head colour; Williams et al 2012); age (Mettke-Hofmann 2012) and social conformity (partner head colour; King et al 2015) can be implemented within a dietary wariness context.

2.1.1 Aims

The aim of this research was to investigate the effect of seed type, age, sex, head colour and partner head colour on food neophobia and the existence of dietary conservatism in Gouldian finches. The following predictions were made:

1) Gouldian finches will approach and feed on familiar food sooner than novel food.
    - Gouldian finches are food specialists (Brazill-Boast et al 2011a) and will hesitate longer to approach and feed on novel food because the novel food deviates from in-situ food preferences.
2) Gouldian finch approach/avoidance conflict will be greater to novel food than familiar food.
    - Gouldian finches will approach familiar food less often before feeding for the first time in comparison to feeding for the first time on novel food as the bird is in conflict to approach and sample novel food to avoid a possibly harmful substance.
3) Gouldian finches will be dietary conservative.
    - Gouldian finches are food specialists (Brazill-Boast et al 2011a) and will continually discriminate between familiar and novel food. It is expected Gouldian finches will not incorporate novel food into the diet.
4) Age.
    - Older birds have demonstrated less object neophobia in this species than younger birds (Mettke-Hofmann 2012), but there are no other neophobia studies on this species to make predictions on the effect of age on dietary wariness. Furthermore, previous research in other species have not found

consistency of the effects of age on dietary wariness (Mirza & Provenza 1990; Biondi et al 2010; Gustafsson et al 2014) and on this basis no specific prediction can be made.

5) Sex.
    - Although males have been shown to demonstrate more object neophilia than females (Williams et al 2012), there are no known neophobia studies identifying an effect of sex in this species, therefore a specific prediction on dietary wariness cannot be made.
6) Black headed birds will demonstrate less hesitancy to approach and feed on novel food than red-headed birds.
    - Although head colour effects on neophobia have not been identified in this species (Mettke-Hofmann 2012), previous research has shown black-headed birds are more explorative and risk-taking than red-headed birds (Williams et al 2012). The actual sampling of novel food may be closely linked to exploration (Inglis & Ferguson 1986) and on this basis it is predicted black-headed birds demonstrate reduced dietary wariness in comparison to reed-headed birds.
7) Birds partnered with a black-headed finch will demonstrate less hesitancy to approach and feed on novel food than birds partnered with red-headed finches.
    - Changes in behaviour according to partner head colour (social conformity; King et al 2015) have not been tested in neophobia testing conditions, but we predict black-headed birds will be less hesitant to approach and feed on novel food than red-headed birds (Prediction 6). Therefore, it is expected birds partnered with a black-headed finch will demonstrate reduced dietary wariness in accordance with black-headed partner responses.

2.2 Methods

2.2.1 Study group

Thirty two Gouldian finches obtained from 12 private breeders were used. All birds were wild type, parent reared, and ages ranged from one to six years (information derived from closed rings and breeder information). Sex ratios were equal with 16 males (eight red-head: eight black-head) and 16 females (seven red-head: nine black-head). All birds were housed together within six 'free-flight' cages (1.20m long x 80 cm deep x 1.00 m high) in groups of five to six individuals. All birds were grouped in mixed sexes, ages and head colours with the exception of the one year old individuals (10 birds) who were housed in same sex groups throughout the study period. Birds were fed 2:1 mixture of Astriliden Spezial: Amadinen-Zucht Spezial, red sibirica millet, grit (all purchased from Blattner-Hiemtierfutter, Ermengurst, Germany) and egg shells within feeders located at the front of the cage and French red spray millet (Blattner-Hiemtierfutter) located next to the feeders. Water was available from water dispensers located at the front of the cage and within the bird baths located on the cage floor for bathing. Once per week Blattner's vitamins (Blattner-Hiemtierfutter) were supplemented in the drinking water. Birds were kept at a temperature of 24°C and provided with a full spectrum light source with a light:dark cycle of 13:11 hours. In addition to the two wooden perches located within each cage, natural branches and twigs were positioned within each cage.

The weights and fat scores of all birds were recorded before each trial of food neophobia testing (Kaiser 1996) and birds were categorised into two age classes: one year old (10 birds hatched in 2016) and older than one year (22 hatched before 2016). The age of each bird was known and age classes were categorised for experimentation and analyses purposes. All finches were tested within same sex pairs and matched for size and weight (grams) to control for sex and size effects (Table 2.1). King et al (2015) found Gouldian finches adjusted their behaviour to novel objects (neophilia testing) and simulated predator attacks (risk-taking) according to the head colour (personality) of the partner bird, demonstrating social conformity. To test the effect of head colour within food neophobia testing conditions, two trials of food neophobia were implemented. Within a counterbalanced design, finches were either paired with a partner of the same head colour (same head colour pair) or a partner with a different head colour (mixed head colour pair, one red-headed finch and one black-headed finch) in trial one experimentation conditions (Table 2.1). The head colour of the partner experienced within trial one conditions was then swapped for the opposing head colour with the second trial conditions to ensure each finch had experienced both head colour combinations (Table 2.1). This was to assess whether the head colour (personality) of the partner had an effect on the responses to novelty of the other bird. Furthermore, testing in pairs represents a more realistic setting as Gouldian finches are a social species (Brush & Seifried 1968). Finches were also paired by age, with one partner finch from the one year old group (n=10) and one partner from the older than one year group (n=22). In the instance pairings from each age category could not be made (due to the smaller number of one year old birds), finches were paired based on the greatest difference in age. All birds were first tested in food neophobia conditions and in the following week, were tested in spatial neophobia conditions. As birds were testing in two head colour combinations, it was not possible to counterbalance food and spatial neophobia testing. 16 pairs of finches were tested within trial one conditions (nine same head colour and seven mixed head colour pairs) and within trial two conditions (seven same head colour and nine mixed head colour pairs (Table 2.1). The number of birds was reduced to 31 individuals within trial two conditions as one red-headed female died before testing within trial two conditions (Bird I.D. 09/2627/11/15; Table 2.1).

Table 2.1 Pair allocation of Gouldian finches within trial one (n=32) and trial two conditions (n=31). Within the sex column, M refers to males and F refers to females. Within the head colour column, BH denotes black-headed finches and RH denotes red-headed finches. Four female birds were retested within trial two conditions (denoted as **(partner bird number)) due to other female birds requiring same or mixed head colour partners. Retested females were tested within the allocated head colour combination within trial two conditions first, then retested as a supplementary partner. Data from the first exposure to novelty was used for analyses for the retested females.

Bird Number	Bird I.D.	Sex	Head Colour	Age	Weight (grams)	Head Colour Combination (Trial One)	Partner Bird number (Trial Two)	Head Colour Combination (Trial Two)
1	**12680/12/41**	M	BH	5	31.2	Same	14	Mixed
2	**26056/14/99**	M	BH	3	26.4		13	Mixed
3	**PB/16/98**	M	BH	1	20.2	Mixed	23	Same
4	**GREEN**	M	RH	4	22.9		16	Same
5	**PB/16/137**	F	RH	1	19.9	Same	11 (**10)	Mixed
6	**GREY**	F	RH	4	19.8		12	Mixed
7	**GREEN-WHITE**	F	BH	3	21.3	Mixed	27	Same
8	**PB/16/35**	F	RH	1	21.2		28 (**31)	Same
9	**12680/11/37**	F	BH	6	19.3	Mixed	30	Same
10	**GREEN 72**	F	RH	5	16.6		5 (**32)	Same
11	**26056/14/59**	F	BH	3	18.9	Same	5	Mixed
12	**26056/12/117**	F	BH	5	20		6	Mixed
13	**GREY**	M	RH	4	21.3	Same	2	Mixed
14	**CMH20**	M	RH	1	22.4		1	Mixed
15	**A3F/365/50**	M	BH	4	18		17	Same

16	**PB/16/39**	M	RH	1	16.8	Mixed	4	Same
17	**BLUE/ORANGE**	M	BH	3	16.8	Mixed	15	Same
18	**PB/16/78**	M	RH	1	17.3		24	Same
19	**39026/11/60**	M	BH	6	17.1	Same	25	Mixed
20	**26056/13/95**	M	BH	4	16.1		26	Mixed
21	**BLACK/13/17**	F	RH	4	17.1	Same	30	Mixed
22	**09/2627/11/15**	F	RH	6	15.8		Died before trial two	
23	**BLACK/13/12**	M	BH	4	24	Mixed	3	Same
24	**BLACK 73**	M	RH	3	22.6		18	Same
25	**WHITE**	M	RH	4	19	Same	19	Mixed
26	**PB/16/108**	M	RH	1	17.9		20	Mixed
27	**CMH/21**	F	BH	1	21	Mixed	7	Same
28	**CGH/12/32**	F	RH	5	21.2		8	Same
29	**BLACK/13/3**	F	BH	4	17.9	Same	10	Mixed
30	**PB/16/19**	F	BH	1	17.7		21 (**9)	Mixed
31	**BLACK/13/6**	F	BH	4	19.9	Same	8	Mixed
32	**PB/16/9**	F	BH	1	22.7		10	Mixed

2.2.2 Experimental set up

Tests were conducted within four experimental cages (1.2m long x 0.7m deep x 1.00m high) each containing three perches (Fig 2.2). Cages comprised of three wooden walls and the front and top of the cages were wire mesh walls. Finch pairs were not in visual contact with other finch pairs but could hear each other. Food and water was always available throughout testing conditions. Data collection was recorded using video cameras positioned one metre from the allocated testing cages.

Fig 2.2 Experimental cage set up of one food neophobia testing cage. This shows the locations of drinkers on the left and right sides of the cage and the positions of the feeders located between the two drinkers. The birdbath is located on the cage floor. The video cameras were positioned one metre from the cage.

Plastic plant pot saucers (14cm diameter x 2.5 cm depth) were used as feeders throughout experimentation and two were fixed to the wire mesh wall of each cage (Fig 2.3). Within the testing cages, one perch ran parallel to the front mesh wire wall (front perch) and the further two perches were positioned at 90^{o} angles to the front perch at each end of the cage (Fig 2.3).

Fig 2.3 Feeder positions and perch formations within food neophobia testing conditions

The front perch was marked at a distance of 7.5cm away from each feeder as this is the average body length of a Gouldian finch and was used to assess distance within the data collection sessions. Four finch pairs were moved into the experimental cages simultaneously and allowed three days (Friday to Sunday) to habituate to the cages, feeders, partners and the video cameras positioned at front of each cage. To identify individuals within a pair during data collection, one bird was fitted with two white leg bands (one per leg) before transfer to the experimental cage. Weights and fat scores of each bird were recorded before and after each trial condition. Two trials of food neophobia experimentation were conducted because each finch was tested twice, to investigate the effect of head colour.

Novel food was produced by dying the Amadinen-Zucht Spezial seed mixture (familiar seed) a different colour. Familiar seed was dyed green for testing in trial one conditions and dyed red for trial two conditions (Fig 2.4).

Fig 2.4 Food neophobia seed types. Familiar food is shown within the two feeders on the left. Trial one novel seed (green seed) is within the top right feeder and trial two novel seed (red seed) is within the bottom right feeder.

Food dye was purchased from Sugarflair Colours Limited (Essex, United Kingdom) and the products implemented for dying the seed were peppermint green pastel paste gel edible concentrated food colouring (trial one) and scarlet pastel paste gel edible concentrated food colouring (trial two). The seed was dyed either green or red by boiling 50 parts seed (g) in a solution of 1 part dye (milliletres) with 100 parts water (millilitres) for 20 minutes at a low heat. Dyed seed was dried at room temperature for 24 hours then separated into 20g portions and frozen at a temperature of -21°C. Food neophobia testing lasted one week for each finch pair to investigate attenuation and dietary conservatism.

2.2.3 Data collection

Four pairs of Gouldian finches were tested simultaneously and on consecutive days from Monday to Friday. Feeders within the cages were removed for one hour (08:00hrs to 09:00hrs) to allow for standardised hunger levels to take place within the finch pair. Water was not removed and accessible at all times. Food neophobia testing took place from 09:00hrs to 12:30hrs each day when the feeders were returned to the cages, this time one feeder contained familiar food and one feeder contained novel food. The position of the familiar and novel seed were counterbalanced within and between cages each day. All data collection was conducted using digital video cameras using GeoVision 1480 for later analyses. During the recording the experimenters (G.E and C.M.H) were not in the experimentation room. Once the three and a half hour experimentation period was complete, the novel food was removed from the experimental cage and replaced with familiar food. Food neophobia testing was conducted over a four week period to ensure all birds had been tested. Once the experiments were completed within trial one conditions, the experiments were repeated, this time with birds paired in a different head colour combination than in the previous trial. The time between testing conditions (trial one and trial two) for each individual bird ranged between three to four weeks with the exception of one bird (Bird I.D. PB/16/9) which was tested in trial two conditions two weeks after trial one conditions.

Ethical note

Holding and experimental aviaries conformed to Home Office codes of practice and were carried out in approved facilities within the University. All experiments are non-regulated by the Home Office and complied with the ethical and welfare guidelines for animals and the legal requirements of the University and the United Kingdom (Ethical approval ID number CMH_GE/2016-5).

2.2.4 Data extraction

All data were transcribed from the video recordings from GeoVision 1480 and all statistical analyses were performed within SPSS 23.

Once feeders containing familiar and novel food were positioned within the cages the following measures for each finch within a pair were recorded: (1) approach latencies, measured as the time elapsed from the beginning of the recording session to the time in seconds (s) each finch was within reaching distance (one body length away) from each food type, (2) the frequencies in which each bird approached the food type (one body length away or less) then subsequently moved away (either in flight or by locomotion along the perch) before feeding on the food type. This was a measure of the conflict between approach and avoidance to the food item. (3) initial feeding latencies, the first time (s) each bird fed on each food type (head down within the feeder). This measure was considered as the ending point of neophobia and starting point of attenuation. (4) feeding visits following initial feeding, measured as the number of times each finch fed on each food type after the first time each finch fed on each food type. This measure was implemented to determine whether the number of feeding visits to familiar and novel food converged and would be the ending point of dietary conservatism.

All birds ate the familiar food on the first day of presentation within both trials and had eaten the novel food in both trials by the third day. As some birds did not eat the novel food on the first day of presentation, the approach frequencies of the focal bird to novel food were added on each experimentation day until the individual fed for the first time on novel food. This generated exact approach frequencies for each bird and produced accurate measures of the approach/avoidance conflict to food types for each bird. Frequencies of approach following initial feeding were not included in the analyses as the frequencies following initial feeding were analysed for the investigation into attenuation and dietary conservatism. The initial feeding latencies were treated in the same manner as the approach frequencies. As some birds did not eat the novel food on the first day of presentation, the total time per experimentation day (12,600 seconds/210 minutes) for the focal bird was added to the time the bird first fed on the novel food in the subsequent testing day(s). All latency measurements were recorded in seconds and converted to minutes for analyses. Once birds had eaten the familiar food the frequencies of feeding visits were recorded as the number of times each finch fed on this food type per experimentation day. This was repeated for the novel food.

2.2.4.1 Food neophobia data manipulation and statistical analyses

For each dependent variable, the minute values were rounded to the closest whole values and a constant value was added. Log transformations revealed the presence of negative integers in the data and rounding values to whole numbers and adding a constant value prevented data points from being excluded from the GLMM as was experienced before data were manipulated in this way. None of the dependent variables within either trial were normally distributed. Spearman rank order correlations were performed on the dependent variables (Approach latencies, approach frequencies and initial feeding latencies) to each food type within each trial. Positive and significant correlations were found within trial one conditions to familiar food (Familiar food; Approach latencies vs Initial feeding latencies $rs(32)=0.952$, $p<0.001$) and trial two conditions to novel food (Approach latencies vs approach frequencies $rs(31)=0.481$, $p=0.007$). Approach latencies were excluded from the analyses.

Data within trial conditions were analysed separately. The analyses of the approach frequencies and initial feeding latencies within trial one conditions were conducted using GLMMs (Generalized Linear Mixed Models). The seed types (familiar and novel) were compared as within factors along with the other independent variables as between factors (age, sex, head colour and partner head colour) for each dependent variable. Bird I.D was included as a random effect. As response variables were not normally distributed, a Poisson distribution and a Log-link function was used for all analyses. A step-wise removal of variables was conducted to determine only the significant effects on the dependent variables. This was performed by removal of the variable representing the highest *p*-value until only significant effects were present in the model. Interaction analyses were included within the model to determine potentially useful and significant interactions. Interaction analyses were performed only when more than one fixed effect was significant to determine whether a significant interaction was present between these variables. Technical issues were experienced when two fixed factors and the interaction between these factors were included in the model as the coefficient effect table (post-hoc tests) results had missing values within rows of the results table. This was applicable to only one test result, which included a significant interaction within the food neophobia results (Trial two initial feeding latencies).

To work around this, results for the main effects of the model results were obtained by inclusion of single factors and the interaction between factors. To obtain coefficient results, the single factors were analysed within one separate model and the interaction between these factors were analysed within another separate model to obtain completed coefficient results.

The same analyses were performed within trial two conditions following repetition of the experiments with the new pairings (head colour combination change). Further, to assess correlations of food neophobia between trials, the initial feeding latency to feed on familiar food was subtracted from the latency to feed on the novel food for each bird within trial one conditions to generate a value which quantified the neophobic response of each individual (Mettke-Hofmann et al 2002; Perkovic & Mettke-Hofmann 2018). This was repeated with trial two data and the difference scores generated from trial one and trial two conditions were correlated using Spearman’s Rank Order correlations.

2.2.4.2 Attenuation and dietary conservatism data manipulation and statistical analyses

To determine attenuation and the existence of dietary conservatism, the feeding visit frequencies to novel food were subtracted from the feeding visits to familiar food for each bird on each day of testing. This was implemented to determine whether feeding visits to familiar and novel food converged. Birds fed on familiar food more often than novel food, therefore this approach produced more positive values as oppose to subtracting familiar food feeding visit frequencies from novel food frequencies. This approach generated a difference score between the two food types for each bird. This was conducted on data from both trial conditions. Some values were negative because birds ate the novel food more often than familiar food. The greatest negative value was -13 (within trial two). A value of 13 was added to each data point in both trial conditions to produce positive values and ensure data within each trial was treated equally. None of the dependent variables within either trial were normally distributed. All analyses were conducted using GLMMs. Seed type was not compared within this measure because the difference score generated one value to represent changes to in feeding visits to both seed types. The days (Monday to Friday) were compared as within factors along with the other independent variables as between factors (age, sex, head colour and partner head colour) for each dependent variable. Bird I.D was included as a random effect. As response variables were not normally distributed, a Poisson distribution and a Log-link function were used for all analyses. A step-wise removal of variables was conducted to determine only the significant effects on the dependent variables by removing the factor with the greatest *p*-value until only significant effects were present within the model. Interaction analyses were included within the model to determine potentially useful and significant interactions. Spearman Rank Order correlations were performed on the difference scores to determine the relationship between trials for each day of presentation and investigate consistency in behaviour in response to familiar and novel food.

2.2.4.3 Proportions of adventurous consumerism and dietary conservatism within trial conditions

To determine the proportions of adventurous consumerism within trial one conditions, the number of individual birds that fed on the novel food at the same frequency as the familiar food on one or more days were recorded. The remaining number of birds within the group were also recorded. These individuals did not eat the novel food at the same frequency as the familiar food on any day of presentation, demonstrating dietary conservatism. The number of birds within each foraging strategy category (adventurous consumerism and dietary conservatism) were converted into percentages of the total population (n=32) to produce population proportions. Following the repetition of experimentation, the proportions of adventurous consumerism and dietary conservatism were calculated within trial two conditions (n=31).

2.3 Results

2.3.1 *Trial One Conditions*

Approach frequencies

The final model showed seed type was the only significant effect on the approach frequencies before first feeding of Gouldian finches (n=32) within trial one conditions (Table 2.2).

Table 2.2 Final GLMM model results representing significant and non-significant fixed effects on the approach frequencies of Gouldian finches (n=32) to seed types within trial one conditions. Significant effects are highlighted in bold. Interactions are not present within the model as only one fixed effect was significant.

Source	F-Value	Significance value
Corrected Model	**7.659**	***p*<0.001**
Seed Type	**35.933**	***p*<0.001**
Head Colour	0.674	*p*=0.415
Age	0.147	*p*=0.703
Partner Head Colour	0.007	*p*=0.933
Sex	1.664	*p*=0.202

Gouldian finches approached the novel food (9.336±3.851) significantly more often than familiar food (3.195±1.188) before eating it for the first time (GLMM t-test; t=-5.994, *p*<0.001; Fig 2.5). No other variable had a significant effect on the approach frequencies of Gouldian finches within trial one conditions.

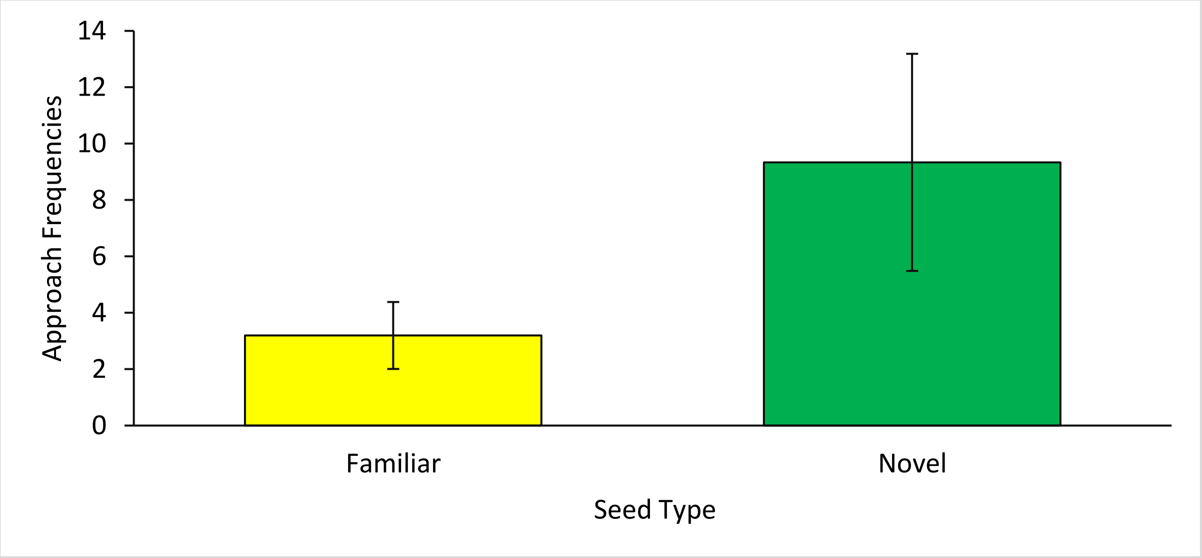


Fig 2.5 Mean (SE) approach frequencies of Gouldian finches (n=32) to familiar and novel food within trial one conditions.

The random effect of Bird I.D was significant. The individual explained 1.7% of the variation in the approach frequencies within trial one conditions, irrespective of seed type (Random effect results; Estimate 0.018±0.006, Z=3.220, *p*=0.001).

2.3.2 *Initial feeding latencies*

Corresponding to the approach frequencies, the final model showed seed type was the only significant effect on the initial feeding latencies of Gouldian finches within trial one conditions (Table 2.3).

Table 2.3 Final GLMM model results representing significant and non-significant fixed effects on the initial feeding latencies (minutes) of Gouldian finches (n=32) to seed types within trial one conditions. Significant effects are highlighted in bold. Interactions are not present within the model as only one fixed effect was significant.

Source	F-Value	Significance value
Corrected Model	**15.522**	***p*<0.001**
Seed Type	**74.354**	***p*<0.001**
Head Colour	1.132	*p*=0.292
Age	0.806	*p*=0.373
Partner Head Colour	0.582	*p*=0.448
Sex	0.041	*p*=0.839

Gouldian finches fed on the familiar food (4.77±0.485 minutes) significantly sooner than the novel food (70.850±21.764 minutes; GLMM t-test, t=2.238, *p*<0.001; Fig 2.6).

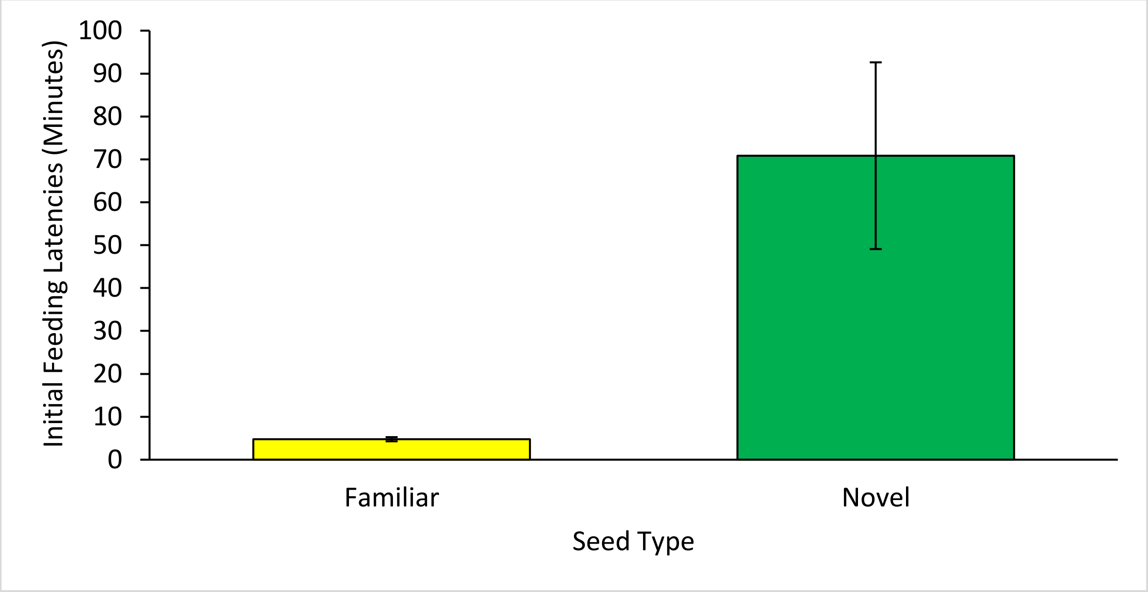


Fig 2.6 Mean (SE) initial feeding latencies (minutes) of Gouldian finches (n=32) to familiar and novel seed types within trial one conditions.

No other variable had a significant effect on the initial feeding latencies of Gouldian finches within trial one conditions. The random effect of Bird I.D was significant on the initial feeding latencies of Gouldian finches. The individual explained 44% of the variation in the initial feeding latencies within trial one conditions, irrespective of seed type (Random effect results; Estimate 0.439±0.133, Z=3.303, *p*=0.001).

2.3.3 *Attenuation-How does acceptance of novel food into the diet change over time?*

The final model showed the effect of day was the only significant factor effecting the difference scores between familiar and novel food within trial one conditions (Table 2.4).

Table 2.4 Final GLMM model representing the significant and non-significant fixed effects on the difference scores between familiar and novel food within trial one conditions. Significant effects are highlighted in bold. Interactions are not present within the model as only one fixed effect was significant.

Source	F-Value	Significance value
Corrected Model	**3.164**	***p*=0.002**
Day	**2.843**	***p*=0.026**
Head Colour	0.150	*p*=0.695
Age	0.214	*p*=0.644
Partner Head Colour	0.808	*p*=0.370
Sex	0.205	*p*=0.651

The greatest difference score between feeding visits to familiar and novel food was demonstrated on the first day of presentation (Monday 23.929±5.970; Fig 2.7) and was significant against Friday (GLMM t-test; t=3.034, *p*=0.003).

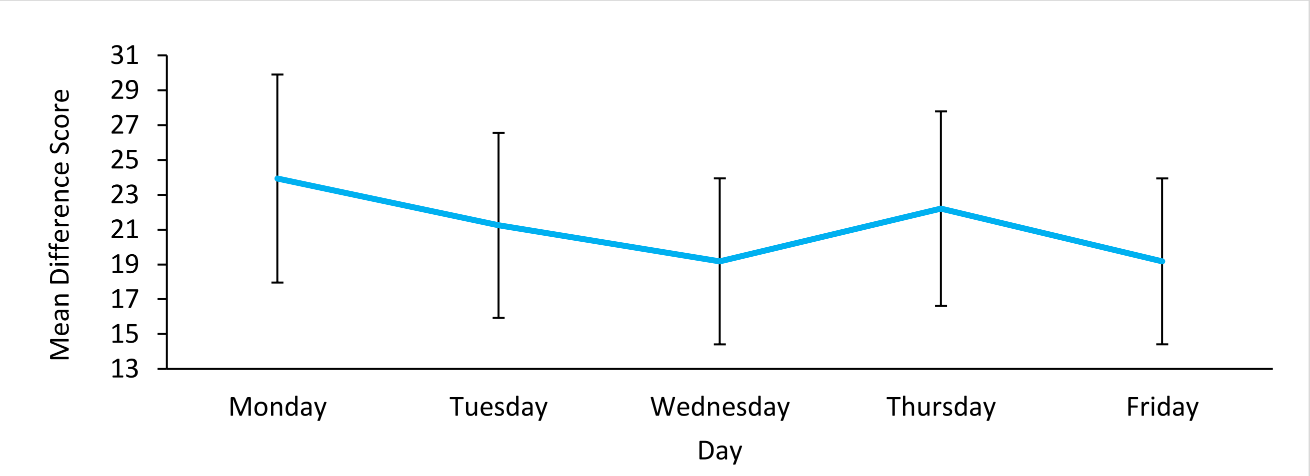


Fig 2.7 Mean (SE) difference scores between the feeding visits to familiar and novel food within trial one conditions. The lowest possible difference score value is 13, which would represent complete convergence of food types.

No other day was significant (GLMM t-tests; Tuesday t=1.365, *p*=0.174, Wednesday 1.953, *p*=0.165, Thursday t=1.844, *p*=0.067). As the week progressed the difference score between familiar and novel food decreased slightly demonstrating some increase in the convergence of feeding visits to familiar and novel food with repeated presentations (Tuesday 21.242±5.312, Wednesday 19.174±4.763, Thursday 22.200±5.582, Friday 19.174±4.761; Fig 2.7).

No other variable had a significant effect on the difference scores within trial one conditions. The random effect of Bird I.D was significant and showed the individual explained 4% of the variance in the difference scores of Gouldian finches within trial one conditions (Random effect results; Estimate 0.040±0.018, Z=2.18, *p*=0.031).

2.3.4 *Proportions of adventurous consumerism and dietary conservatism within trial one conditions*

Within trial one conditions, we found eight Gouldian finches ate the novel food at the same frequency as familiar food on one or more days, showing adventurous consumerism is demonstrated by 25% of this captive population (Table 2.5). The remaining 24 birds within this study continuously discriminated between food types and did not eat the novel food at the same frequency as the familiar food on any day of presentation, demonstrating dietary conservatism is present within 75% of this captive population (Table 2.5).

Table 2.5 Population Proportions (%) of adventurous consumerism and dietary conservatism in Gouldian finches (n=32) within trial one conditions

	No discrimination between food types	**Discriminated between food types. Continuously opted for familiar food.**
Number of individuals	8	24
Total percentage (%)	25%	75%
Population proportions (%) of adventurous consumerism and dietary conservatism	**Adventurous Consumerism=25%**	**Dietary Conservatism=75%**

2.3.5 *Trial Two Conditions*

Approach frequencies

The final model showed seed type was the only significant effect on the approach frequencies before first feeding of Gouldian finches (n=31) within trial two conditions (Table 2.6).

Table 2.6 Final GLMM model results representing the significant and non-significant fixed effects on the approach frequencies of Gouldian finches (n=31) to seed types within trial two conditions. Significant effects are highlighted in bold. Interactions are not present within the model as only one fixed effect was significant.

Source	F-Value	Significance value
Corrected Model	**7.508**	***p*<0.001**
Seed Type	**34.157**	***p*<0.001**
Head Colour	0.594	*p*=0.444
Age	0.651	*p*=0.423
Partner Head Colour	0.941	*p*=0.336
Sex	1.041	*p*=0.312

Corresponding to trial one conditions, Gouldian finches approached the novel food (5.559±1.774) significantly more often than familiar food (2.592±; 0.792) before eating it for the first time (GLMM t-test, t=-5.844, *p*<0.001; Fig 2.8). No other variables or the random effect of Bird I.D had a significant effect on the approach frequencies of Gouldian finches within trial two conditions.

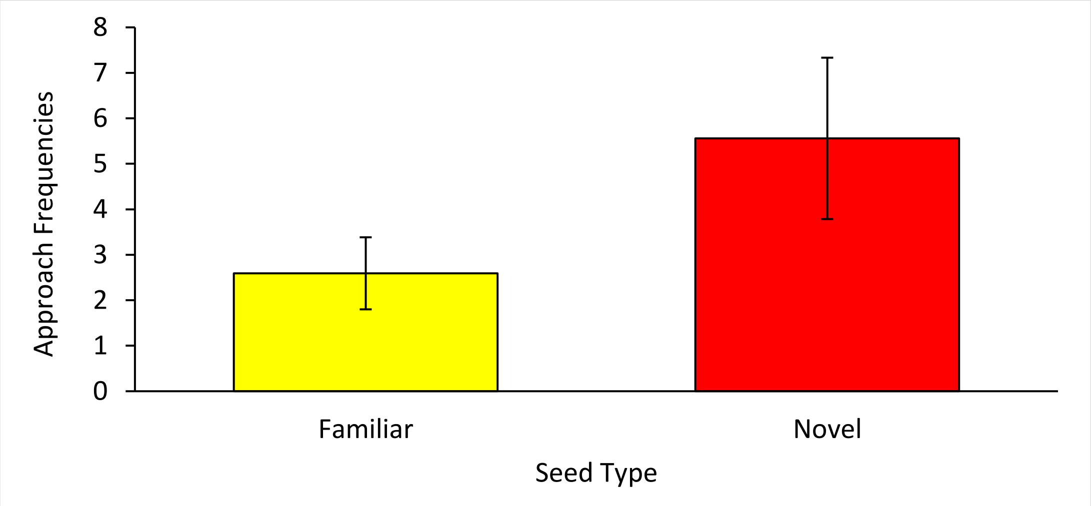


Fig 2.8 Mean (SE) approach frequencies of Gouldian finches (n=31) to familiar and novel food within trial two conditions.

2.3.6 *Initial feeding latencies*

The final model showed seed type, age and the interaction between age and seed type were significant on the initial feeding latencies of Gouldian finches (n=31) within trial two conditions (Table 2.7).

Table 2.7 Final GLMM model representing the significant and non-significant fixed effects on the initial feeding latencies (minutes) of Gouldian finches (n=31) to familiar and novel food within trial two conditions. Significant effects are highlighted in bold. The significant interaction between Seed Type and Age is denoted as *.

Source	**F-Value**	**Significance value**
Corrected Model	**37.334**	***p*<0.001**
Seed Type	**177.175**	***p*<0.001**
Head Colour	0.059	*p*=0.809
Age	22.912	*p*<0.001
Partner Head Colour	0.087	*p*=0.770
Sex	0.014	*p*=0.906
Seed Type*Age	**11.118**	***p*=0.002**

Corresponding to trial one conditions, Gouldian finches fed on the familiar food (6.833±1.054 minutes) significantly sooner than novel food (58.234±8.001 minutes; GLMM t-test; t=-2.680, *p*<0.001; Fig 2.9).

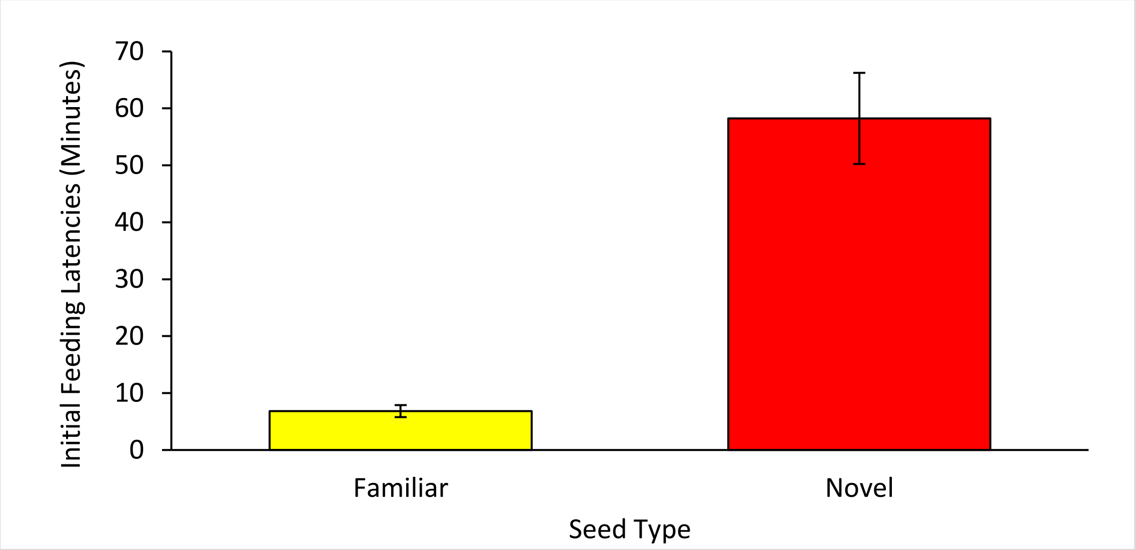


Fig 2.9 Mean (SE) initial feeding latencies (minutes) of Gouldian finches (n=31) to familiar and novel food within trial two conditions.

Overall, the initial feeding latencies of one year old birds to both food types were faster in comparison to older birds. The outcome of the interaction showed there was no significant difference on the initial feeding latencies to familiar food between the age classes (GLMM t-test; t=-1.689, *p*=0.102). One year old birds (24.351±3.957 minutes) fed on the novel food for the first time significantly sooner than older birds (141.13±30.435; GLMM t-test; t=-3.363, *p*<0.001; Fig 2.10).

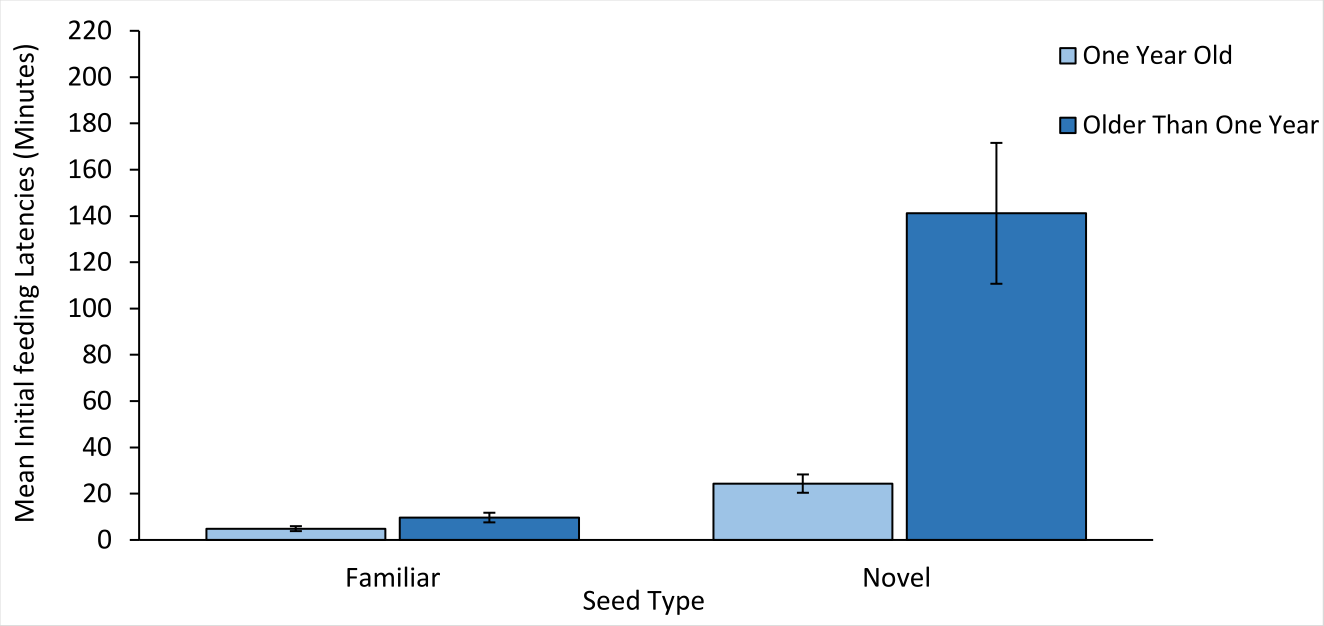


Fig 2.10 Mean (SE) initial feeding latencies (minutes) of one year old birds (n=10) and older than one year old birds (n=21) to familiar and novel food within trial two conditions.

No other variable had a significant effect on the initial feeding latencies of Gouldian finches within trial two conditions. The random effect of Bird I.D was significant and showed the individual explained 46% of the variation in the initial feeding latencies within trial two conditions, irrespective of seed type (Random effect results; Estimate 0.459±0.211, Z=2.177, *p*=0.029).

The relationship between the initial feeding latencies of Gouldian finches within trial one and trial two conditions were found not to be correlated (Spearman correlation test: $r_S(31)=0.238$, *p*=0.197).

2.3.7 *Attenuation-How does acceptance of novel food into the diet change over time?*

The final model showed the effect of day was the only significant factor effecting the difference scores between familiar and novel food within trial two conditions (Table 2.8).

Table 2.8 Final GLMM model representing the significant and non-significant fixed effects on the difference scores between familiar and novel food within trial two conditions. Significant effects are highlighted in bold. Interactions are not present within the model as only one fixed effect was significant.

Source	F-Value	Significance value
Corrected Model	**3.635**	***p*=0.001**
Day	**5.327**	***p*<0.001**
Head Colour	0.153	*p*=0.697
Age	1.018	*p*=0.315
Partner Head Colour	0.478	*p*=0.491
Sex	1.664	*p*=0.202

The greatest difference score between feeding visits to familiar and novel food was demonstrated on the first day of presentation (Monday 24.79±6.589; Fig 2.11) and was significant when compared to Friday (GLMM t-test; t=3.768, *p*<0.001). The difference scores on other presentation days were not significant (GLMM t-tests; Tuesday t=0.071, *p*=0.943, Wednesday 0.628, *p*=0.531, Thursday t=0.321, *p*=0.748). As the week progressed the difference scores remained relatively unchanged (Tuesday 18.735±5.128, Wednesday 19.596±5.300, Thursday 19.227±5.324, Friday 18.612±5.039; Fig 2.11).

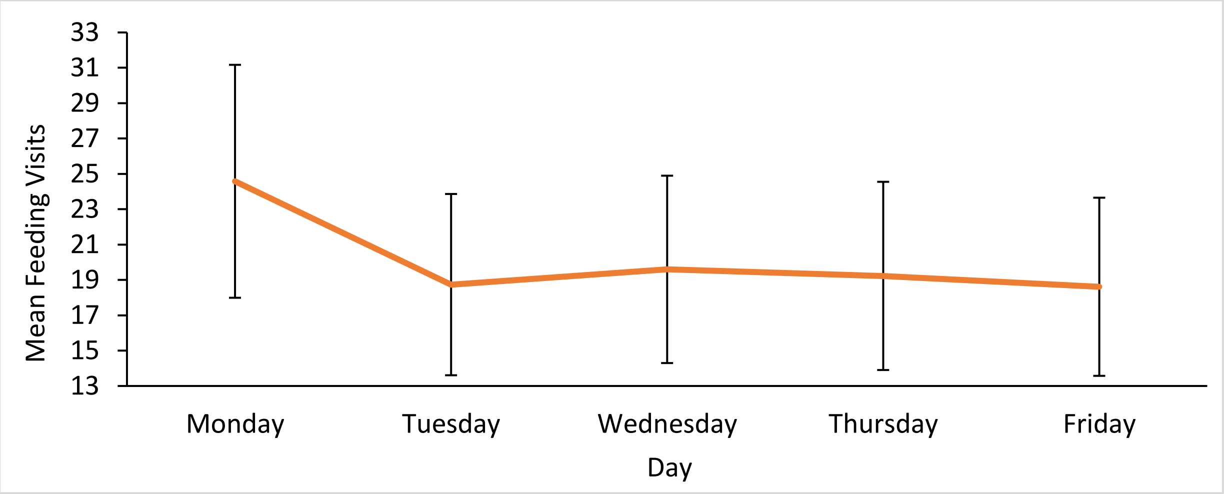


Fig 2.11 Mean (SE) difference scores between the feeding visits to familiar and novel food. The lowest possible difference score value is 13, which would represent complete convergence of food types.

The individual explained 10% of the variation in the difference scores to food types within trial two conditions as the random effect of Bird I.D was significant (Random effect results; Estimate 0.10±0.038, Z=2.623, p=0.009). No other variable had a significant effect on the difference scores between familiar and novel food within trial two conditions. When scores were correlated on each day, there were significant correlations on Monday only (Spearman correlation tests: Monday $r_s(31)=0.423$, p=0.018; Tuesday $r_s(31)=0.022$, p=0.906; Wednesday $r_s(31)=-0.100$, p=0.594, Thursday $r_s(31)=-0.157$, p=0.398, Friday $r_s(31)=0.140$, p=0.454).

2.3.8 *Proportions of adventurous consumerism and dietary conservatism within trial two conditions*

Within trial two conditions, we found nine Gouldian finches ate the novel food at the same frequency as familiar food on one or more days, showing adventurous consumerism is demonstrated by 29% of this captive population (Table 2.9). The remaining 22 birds within this study continuously discriminated between food types and did not eat the novel food at the same frequency as the familiar food on any day of presentation, demonstrating dietary conservatism is present within 71% of this captive population (Table 2.9).

Table 2.9 Population Proportions (%) of adventurous consumerism and dietary conservatism in Gouldian finches (n=31) within trial one conditions

	No discrimination between food types	**Discriminated between food types. Continuously opted for familiar food.**
Number of individuals	9	22
Total percentage (%)	29%	71%
Population proportions (%) of adventurous consumerism and dietary conservatism	**Adventurous Consumerism=29%**	**Dietary Conservatism=71%**

2.4 Discussion

This study investigated the responses of mixed and same head colour pairs of Gouldian finches to novel food to determine whether head colour, age, sex and partner head colour affected food neophobia, changes in responses to food types with repeated presentations and the existence of dietary conservatism. Exposing Gouldian finches to novel food elicited strong neophobic responses in both trial conditions as approach frequencies and feeding latencies were greater to novel food in comparison to familiar food. The only significant effect on the approach frequencies to familiar and novel food type was seed type. The initial feeding latencies of Gouldian finches were significantly influenced by seed type and younger birds ate novel food sooner than older birds within the second trial condition only. No other variable had a significant effect on the initial feeding latencies within either trial condition. The effects of sex, head colour and partner head colour did not influence neophobic responses of Gouldian finches to food types within either trial condition. The only significant effect on the difference scores between familiar and novel food (attenuation) within both trial conditions was the effect of day. The difference scores were greater on Monday within both trial conditions in comparison to Friday and as the week progressed from Monday, the difference scores remained relatively unchanged. The difference scores were significantly correlated on Monday only.

Gouldian finches are specialist granivores, heavily relying upon *Sorghum* species within in-situ habitats (Brazill-Boast et al 2011a). We found Gouldian finches fed on the familiar food sooner than novel food and that this effect was repeatable within both trial conditions, thus confirming prediction 1. Moreover, we found finches demonstrated significantly greater approach/avoidance conflict to novel food in both trial conditions when compared to responses to familiar food, confirming prediction 2. Encountering novel food brings rise to two important assessments. Firstly the assessment of whether this food type is completely novel or whether properties of this food resembles a known food, and secondly, the assessment of whether this food is safe to ingest and incorporate into the diet. Given finches within this study were food deprived for one hour, naturally they will feed on familiar food much sooner, firstly because they are motivated to feed and secondly because they are familiar with this food type, thus determining safe consumption. This is in line with a previous study by Inglis & Ferguson (1986) finding an inverse relationship between hunger and explorative behaviours in European Starlings, *Sturnus vulgaris*. They found food deprivation influenced starlings to feed from a dish with readily available mealworms first then increasingly investigate experimental holes containing hidden mealworms later on in the trial and feed from the dish less often. What is particularly interesting within the initial feeding latencies is that the random effect of Bird I.D showed the individual explained 43% and 45% of variation in the initial feeding latencies to food types within trial one and trial two conditions respectively. Such variation attributed to the individual suggests that these two assessments of food quality vary considerably in Gouldian finches. Individual differences in the responses to make contact with novel food (neophobia ceases) and the latency to incorporate novel food into the diet (dietary conservatism ceases) has been found in a variety of wild populations of animal groups including primates (Visalberghi et al 2000), birds (Marples et al 1998), rats and mice (Kronenberger & Medioni 1985; Inglis et al 1996). This variation within a species could have detrimental consequences for more food neophobic and dietary conservative individuals. Changing environmental conditions owing to HIREC depletes familiar resources and present more novel resources that will unlikely be exploited by hesitant and dietary conservative individuals. This has specific consequences to the Gouldian finch as we found that Gouldian finches are dietary conservative. The attenuation to novel food (difference scores) was affected by day and found to be consistent between trials, however we found that overall the convergence of familiar and novel food remained relatively unchanged across the week within both trial conditions. This shows finches consistently discriminated between food types and evidences dietary conservatism exists in this species, therefore confirming prediction 3. Research into dietary conservatism and adventurous consumerism foraging strategies have shown approximately 30% to 50% of individuals within a population are dietary conservative whilst the remaining population are adventurous consumers (Marples et al 1994; Marples et al 1998; Marples & Kelly 1999; Kelly & Marples 2004; Marples et al 2005). Within this study, we found the proportion of dietary conservatism foragers within trial one and trial two conditions were 75% and 71% respectively and adventurous consumerism was present within 25% and 29% of the population. The existence of dietary conservatism within this captive population is much greater than proportions identified in previous studies (Marples et al 1994; Marples et al 1998; Marples & Kelly 1999; Kelly & Marples 2004; Marples et al 2005) and this is likely attributed to their food specialism. These findings strongly indicate Gouldian finches are particularly vulnerable to habitat change as we have shown the majority of Gouldian finches will not incorporate novel food into the diet. High proportions of dietary conservatism in wild populations of Gouldian finch could have concerning conservation implications on this species. Gouldian finches are particularly susceptible to food shortages in the wet season (December to March) when the abundance of preferred grass seeds are depleted (Dostine et al 2001). Hormonal stress responses have been quantified in wild populations of Gouldian finch and showed residual corticosterone (CORT) concentrations were significantly elevated in the wet season in comparison to the dry season, when food is plentiful (Maute et al 2015). Furthermore, these CORT concentrations were contradictory to the two other sympatric grass finch species implemented within this study, as long-tailed finch, *Poephila acuticauda*, and masked finch, *P. personata,* CORT concentrations were greater in the dry season when breeding is at its peak (Maute et al 2015). This study highlights that Gouldian finches are extremely sensitive to changes in food availability within in-situ environments, as it does not appear that any other driver would have such an effect on seasonal stress responses. Ultimately, depleting familiar food resources and the presence of novel food with habitat change will have significant detrimental effects on this dietary conservative specialist as we have shown here that Gouldian finches will unlikely incorporate novel food into the diet, subsequently affecting survival rates and the determination of whether this species can persist in the wild.

Our study showed younger birds ate the novel food within trial two conditions significantly sooner than older birds. These findings contradict those of object neophobia in this species as older birds were found to demonstrate less object neophobia than younger birds (Mettke-Hofmann 2012). Species responses to types of novelty are not always correlated (Verbeek et al 1994; Boogert et al 2006; Ruuskanen & Laaksonen 2010; Greggor et al 2016a) and this could well be the case for Gouldian finches. Interestingly, younger birds have been shown to be more explorative than older birds in object neophilia testing conditions, touching a novel object in a neutral location first (Mettke-Hofmann 2012). Greater object neophilia in younger birds demonstrates these individuals are more explorative and this may explain why younger birds were faster to sample novel food in comparison to older individuals. These findings are interesting because younger individuals are expected to be more neophobic than older birds because they have less experience in new situations to compare with previous experiences (Nilsson et al 2016). The age effect within this study was not consistent as younger birds were faster within the second trial condition only. Perhaps greater exploration in younger birds does influence these age effects to the responses on novel food, however there are alternative explanations to these findings, which could be attributed to the sample size in the younger bird age class. Within this study, ten birds of the total population were one year old birds and our study design consistently paired one year old birds with an older bird within both trial conditions. Responses of younger birds to novel food could be a direct effect of increased risk taking to access food due the presence of an older, more dominant partner. The relationship between age and dominance within animal groups is well documented in primates (Fischer et al 2004; Robbins et al 2005), birds (Holberton et al 1990; Smith et al 2001), and pack animals (Mech 1999; de Villiers et al 2003). Given younger birds had already been tested with an older bird within the first trial condition, faster responses to feed on novel food in the second trial could well be an effect of increased risk taking due to the presence of an older, more dominant bird to access this resource quickly. However, it is currently unknown whether younger birds respond similarly or differently to novel food when partnered with another one year old bird of the same and opposing head colours. The assemblage of head colours and age within this study does show age biases as ten birds of the total study group were one year old. Of the ten birds within the one year old category, four birds were black-headed morphs (one male and three female). Given previous research has shown black-headed morphs are more explorative and risk-taking (Wlliams et al 2012), it is more likely that our results are more strongly influenced by age as oppose to head colour because of the reduced number of black-headed birds within this younger age category. It is possible to further investigate whether head colour or age had a stronger effect on responses to novel food by incorporating a more balanced design, which would require a greater sample size of birds to ensure head colours and ages are equal within testing conditions. Another interesting consideration for the future is to investigate colour preferences in Gouldian finches. Seed colours (green and red) were implemented depending on the trial condition therefore we cannot determine whether younger birds may in fact have an intrinsic colour preference for red food, which could have driven younger individuals to feed on the novel food sooner within the second trial condition. Investigating colour preferences would be certainly interesting in the future to determine whether Gouldian finches do opt for certain coloured food. There may well be an effect of age within this response to novel food, yet it is currently unclear whether other factors are driving these responses. It would be beneficial to further investigate age effects in more detail to determine whether it is indeed exploration or dominance effecting younger bird responses to novel food or whether other factors such as head colour, partner head colour and intrinsic colour preferences contribute to food neophobia in Gouldian finch age groups. This does provide exciting opportunities to identify potential variation in novelty responses in regards to age and disentangle any other effects on responses to food types.

We did not find an effect of head colour on the dietary wariness responses of Gouldian finches to novel food within any trial condition. Previous research has shown no effects of head colour in object neophobia testing conditions (Mettke-Hofmann 2012), which demonstrates neophobic responses are not dependent upon the head colour morph of the focal bird within object and food neophobia contexts. Moreover, we did not find any effect of partner head colour on the responses to novel food of the other bird within a pair, therefore it does not appear that birds are responding to novel food in accordance to their partners' responses.

Given these findings of food neophobia and dietary conservatism in the Gouldian finch, these provide insight into how wild populations may respond to novel foods and suggests that once neophobia has ceased, this species will not incorporate novel food into the diet, mostly comprise of dietary conservative individuals and the majority of the populations will unlikely become adventurous consumers. Future research should investigate whether wild populations incorporate novel seeds into the diet to validate the findings within this study and determine if novel food is accepted in order to aid survival in this specialist bird.

Chapter Three

Black-headed Gouldian finches, *Erythrura gouldiae,* facilitate the faster assessment and subsequent cross over of social partners into unfamiliar environmental conditions.

3.1 Introduction

Organisms occupy either specialist or generalist life-styles and these are applicable to both diet and habitat selection (Mettke-Hofmann 2014). Habitat specialists thrive in a narrow range of environmental conditions and occupy a much narrower habitat niche than generalists, who exploit a greater range of habitats than specialists (Webster & Lefebvre 2001). Both habitat specialists and generalists do co-exist within overlapping ecological niches because both strategies can do well in predictable environmental conditions, such as seasonal variability within environmental conditions and food availability for example (Mettke-Hofmann 2014).

Increasingly, research is showing that non-human animals are not equally at risk of population decline when faced with the effects of anthropogenic practices, such as habitat fragmentation (Krauss et al 2003; Devictor et al 2008; Brückmann et al 2010; Reino et al 2013; Carrara et al 2015). These previous studies have consistently found evidence that specialist species are particularly sensitive and vulnerable to habitat fragmentation compared to sympatric generalists. These findings are not restricted to animals and have been shown to affect specific plant species and communities as well (Lienart & Fischer 2003; Brückmann et al 2010).

Habitat fragmentation reduces habitat size and isolates plant and animal species, which has a knock on effect on the entire ecosystem, cascading up the trophic levels (Lienart & Fischer 2003). These effects of habitat fragmentation on ecological plasticity have been evidenced in depth in butterfly (*Lepidoptera*), species which have been shown to be a good model to test the effects of habitat fragmentation, given that these pollinators are usually restricted to specific habitats (Brückmann et al 2010). Krauss et al (2003) found habitat area was the most influential effect on butterfly communities and influenced specialists more than generalists and Brückmann et al (2010) found the reduction in habitat connectivity reduced species richness of specialist butterflies by up to 70%. The link between habitat fragmentation and population decline in specialist species also expands into vertebrate research. Vergara & Armesto

(2009) investigated the responses of Chilean bird species to habitat fragmentation and found habitat and food specialists were particularly affected across spatial scales as optimal food and nesting sites were compromised with decreasing habitat suitability. These findings on specialists are concerning and highlight that modifications to previously known environmental conditions result in increasing uncertainty of the distribution and the quality of optimal resources available to specialist species and compel them to cross into unsuitable habitats, hence fragmentation (Mettke-Hofmann et al 2009). Moreover, isolation effects on specialists not only reduce resource availability but also increase competition with generalist species. As habitat size shrinks, the relative proportion of generalists is expected to increase (Matthews et al 2014) because they are able to exploit more resources and are more behaviourally flexible to variable environments (Mettke-Hofmann 2014). Because generalists are more behaviourally flexible when presented with altered environments they become more competitive and are likely to outcompete specialists for resources within increasing overlapping niches. The importance of environmental or spatial familiarity is essential particularly for specialist species to locate valuable resources, such as food, mates and territories (Mettke-Hofmann et al 2009). However, species responses to environmental familiarity and the cognitive processes which govern their dispersal and settlement decisions has not been widely researched (Pusenius et al 2000; Wolf et al 2009; Merkle et al 2014).

Spatial neophobia and neophilia are two essential decision making motivations, which govern whether an individual will avoid or exploit novel environments (Mettke-Hofmann et al 2002; Mettke-Hofmann et al 2009; Mettke-Hofmann 2014). Spatial neophobia is a fearful behavioural response, eliciting avoidance of novel environments whilst spatial neophilia is the attraction to novel environments, eliciting exploration (Mettke-Hofmann, 2014). These two motivations are independent of one another because they are modulated by different gene expressions (Powell et al 2003; Weisstaub et al 2006) however they do occur simultaneously (Mettke-Hofmann et al 2009;Mettke-Hofmann 2014). This has been shown in a relatively recent study in resident and migratory Warbler species (*Sylvia;* Mettke-Hofmann et al 2009) where approach frequencies before entering were measured and latencies to enter the novel space were recorded. Resident Warblers were more hesitant than migrants to enter the novel space. In comparison to migrants, resident Warblers approached the novel space more often, demonstrating greater approach/avoidance conflict to enter the novel space, thus greater neophobia. Further, residents entered the novel space later than migrants, demonstrating greater neophilia is elicited in migrants. Interestingly, an earlier study focussing on object neophobia found resident Warblers demonstrated less object neophobia than migratory species (Mettke-Hofmann et al 2005), which highlights neophobia is context specific and influenced by life history. As well as ecological plasticity in terms of the migratory-resident continuum, habitat and food specialists have been shown to be less spatially explorative than generalists (Leimar et al 2003). Foraging strategies result in lower dispersal in specialists compared to generalists, however the cognitive mechanisms underlying neophobia are unexplored in this research which limits predictions about how unfamiliarity may compromise specialist resource exploitation and dispersal. More recently, research is increasingly evidencing spatial neophobia is demonstrated on an individual level, not just the species level, evidencing consistent individual differences within a species, termed personality, influence responses to novel environments (Fox et al 2009; Schuett et al 2011; Kluen & Brommer 2013).

The Gouldian finch is a near-threatened songbird, endemic to northern Australia (Brazill-Boast et al 2011a; Birdlife International, 2018). This species is a habitat and a food specialist adapted to open savannah grasslands (Brazill-Boast et al 2011a) and is highly mobile because they are nomadic and track superabundant resources within their geographical range (Tidemann et al 1992; Dostine et al 2001). Gouldian finches inhabit simple, open habitats, characterised by widely spaced *Eucalyptus* trees with a seasonal grassy understorey and bare soil patches (Hutley et al 2000). Habitat preference is especially important for this specialist species as Gouldian finches are the only Australian finch that nest exclusively in tree hollows of *Eucalyptus* trees (Tidemann et al 1992). Previous habitat preference studies have shown Gouldian finches select nesting sites within areas dominated by grasses, particularly their preferred food type, *Sorghum* species (Tidemann et al 1992; Brazill-Boast et al 2011). Principle causes of decline are believed to be cattle implementation and frequent and intense fire regimes, which fragment Gouldian finch habitat and reduce optimal resource availability (Maute et al 2015; Legge et al 2015; Weier et al 2016). Overlapping niches with the generalist and more competitive Long-tailed finch, *Poephila acuticauda,* has resulted in the Gouldian finch being susceptible to competitive exclusion (Brazill-Boast et al 2011b). Food neophobia testing conditions have shown Gouldian finches are hesitant to feed on novel food and discriminate between familiar and novel food consistently, demonstrating dietary conservatism (Chapter Two). Habitat preference and site selection is well documented in wild populations but currently the effects of how altered habitat conditions affects Gouldian finch dispersal remains unknown because Gouldian finches are nomadic and are difficult to track because of emigration, predation or both (Woinarski & Tidemann 1992; Tidemann & Woinarski 1994). Unpredictable habitat modification, such as habitat fragmentation creates novel scenarios and unfamiliar environments within Gouldian finch habitat, which could be extremely challenging on this specialist species to cross over into unfamiliar and less preferred environments. An inability to adapt to changing habitat conditions and disperse into unfamiliar sites could ultimately determine whether the Gouldian finch can persist in the wild. This provides a unique opportunity to investigate how a habitat specialist responds to open and dense environmental conditions, that differ in density and complexity. Additionally, further investigation into the effects of personality (head colour; Williams et al 2012); age (Mettke-Hofmann 2012) and social conformity (partner head colour; King et al 2015) can be implemented within a spatial neophobia context. Finally, given species responses to types of novelty are not always correlated (Verbeek et al 1994; Boogert et al 2006; Ruuskanen & Laaksonen 2010; Greggor et al 2016a) we will determine the relationship between food neophobia and spatial neophobia within this species.

3.1.1 Aims and predictions

The aim of this research was to investigate the effect of habitat type, age, sex, head colour and partner head colour on spatial neophobia in Gouldian finches. In particular, we aim to determine how Gouldian finches respond to habitat types simulating preferred open savannah in-situ habitat conditions (Hutley et al 2000; Brazill-Boast et al 2011a) and those which represent less preferred, dense habitat conditions which they may encounter with changing habitat conditions. By doing so, assessing this specialists' responses to changed environmental conditions may provide greater insight into the conservation implications on this species to environmental change. The following predications were made:

1) Gouldian finches will approach and enter the open habitats sooner than dense habitats.
    - Gouldian finches are habitat specialists adapted to open savannah grasslands (Brazill Boast et al 2011a) and will be less hesitant to approach and enter open habitats than dense ones because they are more similar to in-situ habitat preferences.
2) Gouldian finch approach/avoidance conflict will be greater towards dense habitats than open ones.

  - Dense habitats present more novel stimuli within them than open habitats. Given open habitats represent in-situ habitat preferences (Tidemann et al 1992; Brazill Boast et al 2011a), Gouldian finches will demonstrate greater approach/avoidance conflict to dense habitats, which represent undesirable habitat density and complexity and greater uncertainty of potential danger within them.

3) Age.
  - Age has been included as a variable because previous research has shown age influences food neophobia (Chapter Two) and object neophobia (Mettke-Hofmann 2012), however these results are contradictory and on this basis a prediction on spatial neophobia cannot be made.

4) Male Gouldian finches will demonstrate less hesitancy to approach and enter novel habitats than females.
  - Male Gouldian finches have been shown to be more neophilic in novel object testing conditions (Williams et al 2012) and in-situ research has shown males take leadership to investigate prospective nest hollows whilst females elicit more caution (Goodwin 1982). Based on these findings it is expected males will demonstrate less hesitancy to approach and enter novel environments than females.

5a) Black-headed birds will demonstrate less hesitancy to approach novel habitats than red-headed birds.

5b) Black-headed birds will enter novel habitats sooner than red-headed birds.
  - Although head colour effects on neophobia have not been identified in this species (Chapter Two; Mettke-Hofmann 2012), previous research has shown black-headed birds are more explorative to investigate changes in their familiar environment and are more risk-taking than red-headed birds (Williams et al 2012). Therefore black-headed birds are expected to demonstrate less hesitancy to approach novel habitats than red-headed birds habitats.
  - Gouldian finches are nomadic and move frequently within their geographical range (Tidemann et al 1992; Dostine et al 2001) and as black-headed birds are more explorative and risk taking, are expected to be faster to enter novel habitats than red-headed birds.

6) Birds partnered with a black-headed finch will approach and enter habitats sooner than birds partnered with a red-headed finch.

- Changes in behaviour according to partner head colour (social conformity; King et al 2015) have not been identified in neophobia testing conditions (Chapter Two). However, as a consequence of reduced hesitancy demonstrated in black-headed birds (Prediction 5a & b), it is expected birds partnered with a black-headed finch will overcome their spatial neophobia sooner in comparison to birds partnered with a red-headed finch by approaching and entering habitats in accordance with black-headed partner responses.

3.2 Methods

3.2.1 Study group

Spatial neophobia testing took place the week after dietary wariness experimentation (Chapter Two). Bird pairings within the spatial neophobia testing conditions were the same as the dietary wariness testing conditions (See Table 2.1, Chapter Two). Furthermore, birds had already resided within the familiar cages for 10 days before spatial neophobia testing began and had habituated to these cages, partners and video cameras. Additional object neophobia and neophilia testing were conducted but has not been included within the analyses.

3.2.2 Experimental set up

The experimental set up of spatial neophobia replicated the design of the dietary wariness experimentation (Chapter Two) however tests were conducted within six experimental cages within these testing conditions. The middle cages (n=2) which were not utilised within dietary wariness testing conditions were allocated to creating novel rooms within spatial neophobia testing conditions (Fig 3.1). Novel room perch formation comprised of three perches, which were fixed to the front wire mesh wall and the back wooden wall of the cage and did not run parallel to the front and back walls (Fig 3.2). The left and right perches were positioned at equal heights and the middle perch was raised approximately 10cm higher than the other two perches (Fig 3.2). Data collection was recorded through the use of video cameras which were positioned one metre from the allocated testing cages.

Fig 3.1 Experimental cage set up of one outer (familiar) cage within a row of three cages. The middle cage was allocated to spatial neophobia testing (novel cage). This image also shows the position of the video cameras within spatial neophobia testing conditions positioned one metre from the testing cages.

Fig 3.2 Perch formation within cage F) one of four familiar cages and cage B) one of two novel cages

Adjacent compartments could be accessed via the window (15.5cm high x 19cm across) which were separated by a cardboard partition (Fig 3.3).

Fig 3.3 Window (Cardboard partition) separating the familiar cage (finches present) from the novel cage.

All birds were tested twice, once in either head colour combination (mixed or same head colour) therefore two open and two dense habitat types were implemented, one of each habitat type per trial condition. Within each trial condition, finches were exposed to one open habitat type and one dense habitat type. Open habitats were selected based on in-situ habitat preferences of Gouldian finches and dense habitats were selected based on features dissimilar to Gouldian finch habitat. Within trial one conditions the open habitat and dense habitat were also selected based on differences in leaf shape, colour and size. Additionally the dense habitat possessed flowers whilst the open habitat did not. Differences in plant properties were chosen to ensure both plant types were novel to the finches and prevent finches categorising open and dense habitats as similar (familiar) stimuli. The open and dense habitat types within trial one conditions were Eucalyptus (open) and Daises (dense; Fig 3.4). This selection of plant types based on plant properties were repeated for trial two conditions and the open and dense habitats implemented were Vines (open) and Roses (dense; Fig 3.4). Whilst open habitats (Eucalyptus and Vines) were implemented within different trial conditions, considerations were made to ensure open habitats differed in a few features such as leaf shape, size and shade to ensure these habitats were visually different and to prevent categorisation between trial conditions. These considerations were also implemented for dense habitat types. Six artificial plants were made for each of the four habitats. Each individual plant comprised of a 34cm cardboard tube and the plant type wrapped around the cardboard tube and fixed in position using cellotape or piercing holes in the tubes to thread the plant type within the tube (Fig 3.4).

Fig 3.4 Plant types implemented to create habitat types within spatial neophobia testing conditions. From left to right within the image the plants were 1) Eucalyptus (trial one simple habitat), 2) Daisies (trial one dense habitat), 3) Vines (trial two simple habitat), and 4) Roses (trial two dense habitat).

To create artificial habitats within the spatial neophobia testing conditions, metal keyrings were fixed to the wire mesh ceiling (top of the cage) in the same positions within both middle cages. Plants (dependent on trial condition and habitat type) were fixed within the same position for each testing condition by hooking these onto the metal keyrings (Figs 3.5 a-d). Although the same number of plants were used for both open and dense habitat types (n=6), the dense habitat types covered more space within the novel room than the open habitats, therefore reducing the availability of visible areas to the birds during experimentation (Figs 3.5 a-d).

Fig 3.5 Representation of space availability within cages from **a)** front wire mesh wall view of Eucalyptus habitat (trial one open habitat), **b)** front wire mesh wall view of Daisies habitat (trial one dense habitat), **c)** view from the window in a familiar cage to the Vine habitat (trial two open habitat) and **d)** view from the window in a familiar cage to the Roses habitat (Trial two dense habitat). Images 3.5c & d were taken after experimentation.

3.2.3 Data collection

As there were two novel cages and four familiar cages, two finch pairs were tested simultaneously each day. Habitat types were counterbalanced between cages. Within trial one conditions, the open (Eucalyptus) and dense (Daises) habitat types were alternated between the two novel cages each day. As only two novel cages were available, two finch pairs were tested in open and dense habitat conditions one day apart (Tuesday and Wednesday) and two finch pairs were tested three days apart (Monday and Thursday). Spatial neophobia testing took place between 12:00hrs and 15:00hrs and all birds were exposed to each habitat type once. All data collection was conducted using digital video cameras using GeoVision 1480 for later analyses. During the recording the experimenters (G.E and C.M.H) were not in the experimentation room. Spatial neophobia testing was conducted over a four week period for each trial to ensure all birds had been tested. Once the experiments were completed within trial one conditions, the experiments were repeated. Trial two conditions tested birds paired in a different head colour combination than in the previous trial and exposed them to Vines (open habitat) and Roses (dense habitat). The time between spatial neophobia repetitions (trial one and trial two) ranged between three to four weeks for each bird with the exception of one bird (Bird I.D. PB/16/9) which was tested in trial two conditions two weeks after trial one conditions. Birds were also tested in additional and counterbalanced object neophobia and neophilia testing conditions in the morning between 09:00hrs to 10:00hrs.

Ethical note

Holding and experimental aviaries conformed to Home Office codes of practice and were carried out in approved facilities within the University. All experiments are non-regulated by the Home Office and complied with the ethical and welfare guidelines for animals and the legal requirements of the University and the United Kingdom (Ethical approval ID number CMH_GE/2016-5).

3.2.4 Data manipulation and statistical analyses

All data were transcribed from the video recordings from GeoVision 1480 and all statistical analyses were performed within SPSS 23.

Following the removal of the cardboard partition, the following measures were recorded; (1) perch or window approach latencies were measured as the time elapsed from the beginning of the recording session to the first time (seconds) each bird landed on the perch closest to the window separating the familiar cage and middle cage (novel cage) or the window ledge separating the familiar and novel cages. Birds were always absent from the perch at the beginning of the recording as finches located on this perch flew away when the cardboard partition was in the process of being removed. (2) perch or window approach frequencies, measured as the number of times each bird landed on the perch closest to the novel cage or the window ledge before entering the novel cage. This was either by flight or by hopping onto the perch or window ledge from the adjacent perch which ran parallel to the front wire mesh wall. This measure was considered as a measure of the approach/avoidance conflict of entering the novel cage; increasing approach frequencies equates to greater approach/avoidance conflict to enter the novel cage (Fig 1.1, Chapter 1). (3) perch or window durations, measured as the lengths of time (s) each bird was in contact (perching/hopping) with the perch or window ledge before entering the novel cage. (4) Entry latencies, measured as the time elapsed from the beginning of the recording sessions to the first time (s) each bird entered the novel cage. This measure was considered as the ending point of spatial neophobia.

The perch approach frequencies and window frequencies were added together to generate one value. This was repreated for the perch and window duration measures. The latency and duration measures (s) were converted into minutes. Log transformations revealed the presence of negative integers in the data and rounding values to whole numbers and adding a constant to each data point prevented data points from being excluded from the GLMM as was experienced before data were manipulated in this way. To manipulate the frequency measures similarly to other measures, the same constant was added to these measures as was conducted in the latency and duration measures. None of the dependent variables within either trial were normally distributed. Spearman rank order correlations were performed on the dependent variables for each habitat type within each trial to assess relationships between dependent variables (perch approach latencies, perch approach frequencies, perch durations and entry latencies).

Bonferroni corrections were conducted to account for multiple testing. Positive and significant correlations were found to be persistent when perch approach frequencies and perch durations were correlated for both open and dense habitat types within both trial conditions (Tables 3.1 & 3.2). The relationships between the other dependent variables were significantly correlated in some contexts but not all (Tables 3.1 & 3.2).

Table 3.1 Spearman's Rank Order correlation outputs showing the relationship between the dependent variable measures recorded for all birds (n=32) to the open and dense habitat types within trial one conditions (Eucalyptus and Daisies). Bonferroni corrected significance value is *p*≤0.016 denoted as **. All values are to three decimal places.

Trial One Conditions	**Perch approach frequencies**	**Perch durations**	**Entry Latencies**
Perch approach latencies	Open, *rs*(32)=0.450, *p*=0.010** Dense, *rs*(32)=0.397, *p*=0.024	Open, *rs*(32)=0.196, *p*=0.281 Dense , *rs*(32)=-0.067, *p*=0.714	Open, *rs*(32)=0.264, *p*=0.145 Dense, *rs*(32)=0.404, *p*= 0.022
Perch approach frequencies	**X**	Open, *rs*(32)=0.519, *p*=0.002** Dense, *rs*(32)=0.505, p=0.003**	Open, *rs*(32)=0.191, *p*=0.296 Dense, *rs*(32)=0.570, *p*= 0.001**
Perch Durations	**X**	**X**	Open, *rs*(32)=0.107, p=0.559 Dense, *rs*(32)=0.543, p=0.001**

Table 3.2 Spearman's Rank Order correlation outputs showing the relationship between the dependent variable measures recorded for all birds (n=31) to the open and dense habitat types within trial two conditions (Vines and Roses). Bonferroni corrected significance value is *p*≤0.016 denoted as **. All values are to three decimal places.

Perch approach latencies	Open, *rs*(31)=0.148, *p*=0.427 Dense, *rs*(31)=-0.063, *p*=0.737	Open, *rs*(31)=-0.253, *p*=0.170 Dense, *rs*(31)=0.062, *p*=0.739	Open, *rs*(31)=0.548, *p*=0.001** Dense, *rs*(31)=0.533, *p*=0.002**
Perch approach frequencies	**X**	Open, *rs*(31)=0.625, *p*<0.001** Dense, *rs*(31)=0.554, *p*<0.001**	Open, *rs*(31)=0.410, *p*=0.022 Dense, *rs*(31)=0.243, *p*=0.189
Perch Durations	**X**	**X**	Open, *rs*(31)=0.366, *p*=0.043 Dense, *rs*(31)=0.221, *p*=0.233

The perch durations were excluded from the results because they represent the same outcomes as the perch approach frequencies (Tables 3.1 & 3.2). Perch approach frequencies were included within the results as oppose to perch durations because this frequency measure represents the approach/avoidance conflict of individual finches towards habitat types and is a more accurate measure to demonstrate the effects of spatial neophobia. The perch approach latencies were also removed from the analyses because of discrepancies of what this measure represented, given that birds only had three optional perches to land on in the familiar cages. Trial conditions were analysed separately because data structure became difficult to analyse when including both trials. The analyses of the perch approach frequencies and entry latencies within trial one conditions were conducted using GLMMs (Generalized Linear Mixed Models). The habitat types (open and dense) were compared as within factors along with the other independent variables as between factors (age, sex, head colour and partner head colour) for each dependent variable. The order in which the habitat types were presented was also included within the analyses to determine whether order effects were present within these spatial neophobia testing conditions. Bird I.D was included as a random effect. As response variables were not normally distributed, a Poisson distribution and a Log-link function were used for all analyses. As response variables were not normally distributed, a Poisson distribution and a Log-link function was used for all analyses. A step-wise removal of variables was conducted to determine only the significant effects on the dependent variables. This was performed by removal of the variable representing the highest *p*-value until only significant effects were present in the model. Interaction analyses were included within the model to determine potentially useful and significant interactions. . Interaction analyses were performed only when more than one fixed effect was significant to determine whether a significant interaction was present between these variables. The same analyses were performed within trial two conditions following repetition of experiments with the new pairings (head colour combination change). Spearman's Rank Order correlations were performed on the response variables (perch approach frequencies and entry latencies) to open and dense habitat types within each trial to determine whether responses to open and dense habitat types were correlated.

To test the relationship between food and spatial neophobia measures within trial one conditions the following data manipulations were conducted. The number of approach frequencies before initial feeding (Chapter Two) to the familiar food were subtracted from the approach frequencies before initial feeding to novel food to generate a difference score value for each bird (Perkovic & Mettke-Hofmann 2018). The difference score generated for each bird (n=32) was correlated with the perch approach frequencies to the open habitat (Eucalyptus) and the dense habitat (Daises) using Spearman rank order correlations. Bonferroni corrections were conducted to account for multiple testing. The same manipulation was performed on the initial feeding latencies data. The initial feeding latencies (minutes) on familiar food were subtracted from the initial feeding latencies on novel food to generate a difference score value for each bird. The difference score values were correlated with the entry latencies into the open habitat and the dense habitat using Spearman rank order correlations. The same data manipulation were repeated on data to trial two conditions (Red seed vs Vines and Roses).

3.3 Results

Trial one conditions

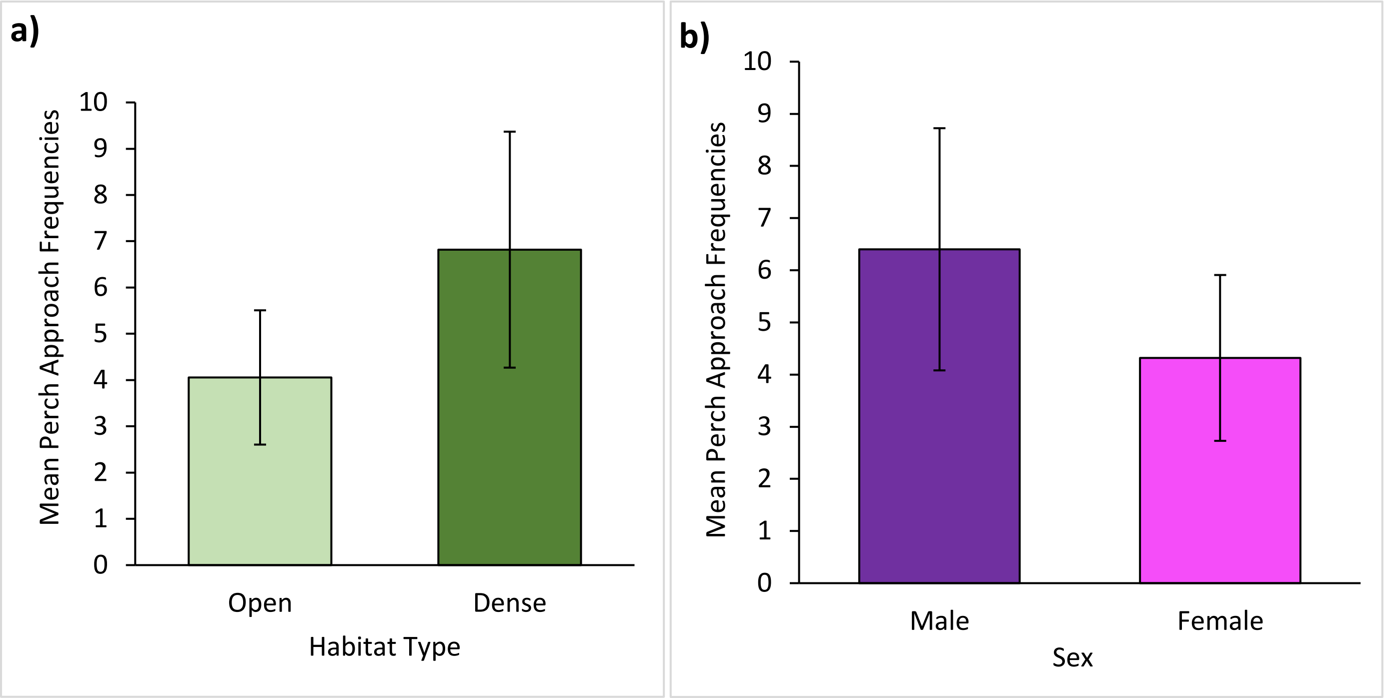
3.3.1 *Perch approach frequencies*

The final model showed habitat type and sex were the significant effects on the perch approach frequencies of Gouldian finches (n=32) within trial one conditions (Table 3.3).

Table 3.3 Final GLMM model results representing significant and non-significant fixed effects on the perch approach frequencies of Gouldian finches (n=32) to habitat types within trial one conditions. Significant effects are highlighted in bold. The interaction between habitat type and sex is donated as *.

Source	**F-Value**	**Significance value**
Corrected Model	**4.485**	***p*=0.002**
Habitat Type	**11.399**	***p*=0.001**
Head Colour	1.694	*p*=0.198
Age	0.023	*p*=0.880
Partner Head Colour	1.805	*p*=0.184
Sex	**6.929**	***p*=0.011**
Habitat Type*Sex	0.687	*p*=0.411

Gouldian finch perch approach frequencies were significantly greater when exposed to the dense habitat (Daises; 6.818±2.550) than the open habitat (Eucalyptus; 4.056±1.451; GLMM t-test; Habitat type, t=-0.519, *p*=0.001; Fig 3.6a). Males (6.402±2.322) approached significantly more often before entering than females (4.319±1.590), irrespective of habitat type (GLMM t-test; t=0.394, *p*=0.011; Fig 3.6b). No other variable or the random effect of Bird I.D. had a significant effect on the perch approach frequencies of Gouldian finches within trial one conditions.



Figs 3.6 Mean (SE) perch approach frequencies within trial one conditions of **a)** Gouldian finches (n=32) to open (Eucalyptus) and dense (Daises) habitat types and **b)** male (n=16) and female (n=16) Gouldian finches irrespective of habitat type.

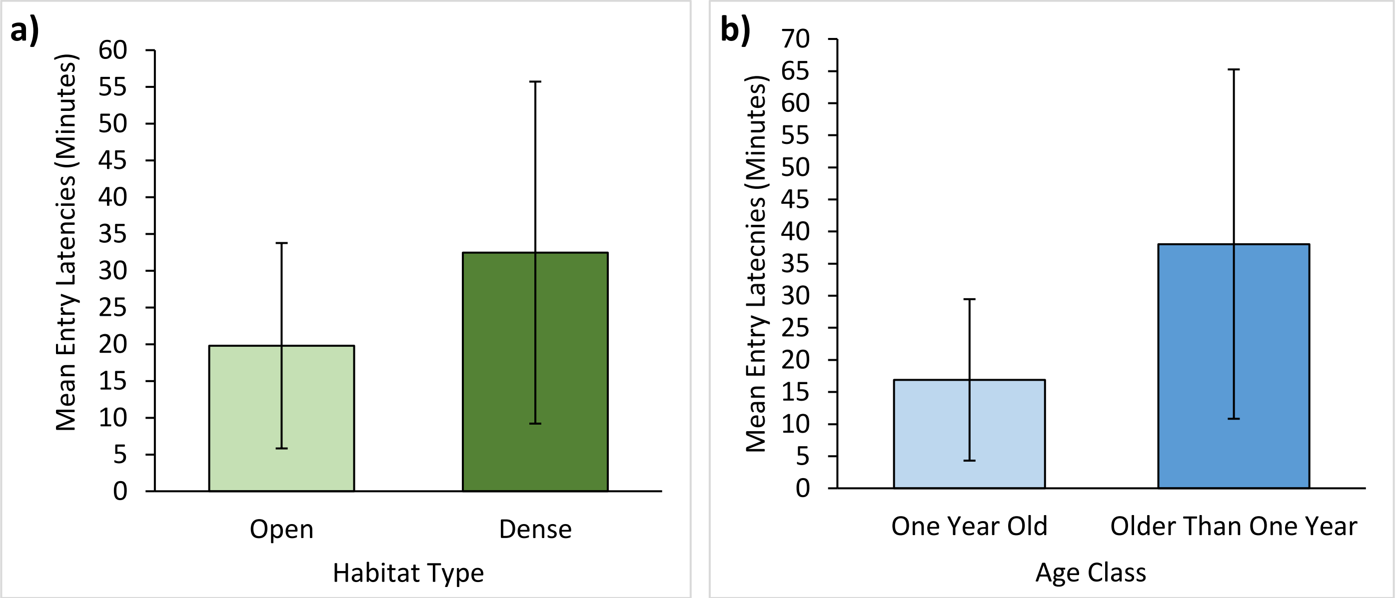
3.3.2 *Entry latencies*

The final model showed habitat type and age were significant the effects on the entry latencies of Gouldian finches (n=32) within trial one conditions (Table 3.4).

Table 3.4 Final GLMM model results representing significant and non-significant fixed effects on the entry latencies of Gouldian finches (n=32) to habitat types within trial one conditions. Significant effects are highlighted in bold. The interaction between habitat type and age is donated as *.

Source	F-Value	Significance value
Corrected Model	**3.139**	***p*=0.014**
Habitat Type	**8.089**	***p*=0.006**
Head Colour	1.504	*p*=0.225
Age	**4.736**	***p*=0.034**
Partner Head Colour	0.796	*p*=0.376
Sex	0.143	*p*=0.707
Habitat Type*Age	0.408	*p*=0.526

Entry latencies of Gouldian finches were significantly faster to the open habitat (Eucalyptus; 19.794±13.974 minutes) than the dense habitat (Daises; 32.459±23.261 minutes; GLMM t-test; t=-0.495, *p*=0.006 Fig 3.7a). One year old birds (16.888±12.578 minutes) entered novel cages significantly sooner than older birds (38.045±27.213 minutes), irrespective of habitat type (GLMM t-test; t=-0.812, *p*=0.034; Fig 3.7b).



Figs 3.7 Mean (SE) entry latencies (minutes) within trial one conditions of **a)** Gouldian finches (n=32) to open (Eucalyptus) and dense (Daises) habitat types and **b)** one year old (n=10) and older than one year old (n=22) Gouldian finches irrespective of habitat type.

No other variable had a significant effect on the entry latencies of Gouldian finches within trial one conditions. The random effect of Bird I.D was significant and showed the individual explained 53% of the variation in the entry latencies of Gouldian finches within trial one conditions, irrespective of habitat type (Random effect results; Estimate=0.533, SE=0.222, Z=2.400, *p*=0.016).

3.3.3 *Correlations of response variables within trial one conditions*

Perch approach frequencies to open (Eucalyptus) and dense (Daises) habitat types were not correlated within trial one conditions (Spearman correlation test: Perch approach frequencies, $r_s(32)=-0.088$, $p=0.633$). The entry latencies to open and dense habitat types were positively and significantly correlated within trial one conditions (Spearman correlation test; Entry latencies, $r_s(32)= 0.432$, $p=0.013$; Fig 3.8).

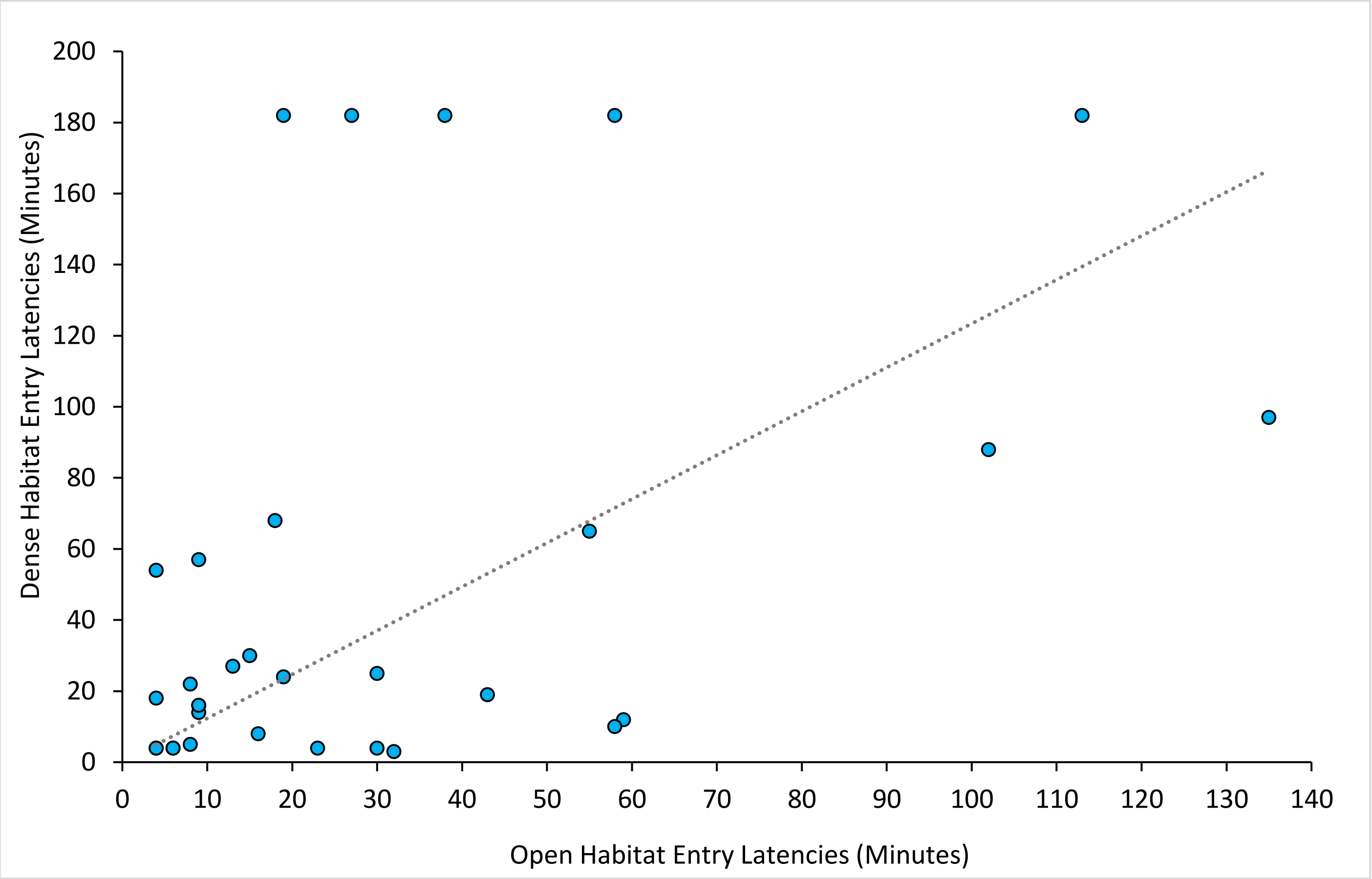


Fig 3.8 Positive and significant relationship of the entry latencies (minutes) of Gouldian finches to open (Eucalyptus) and dense (Daises) habitat types within trial one conditions.

Trial two

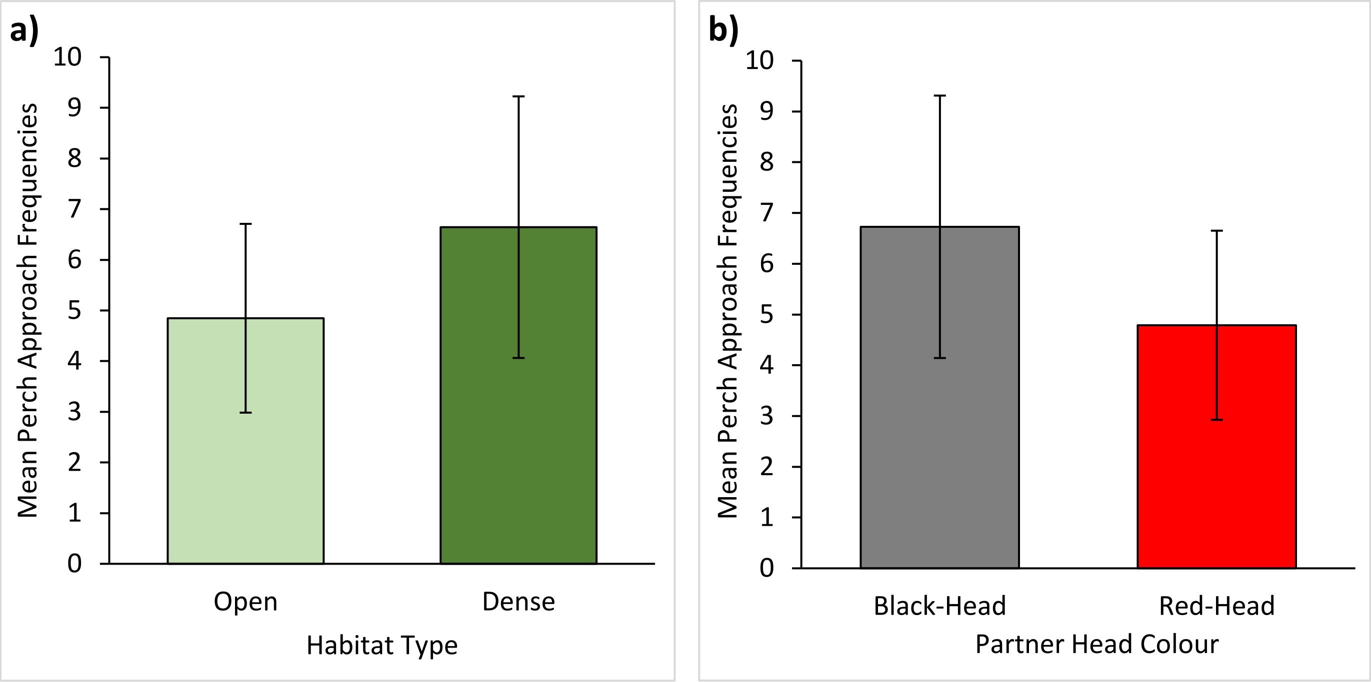
3.3.4 *Perch approach frequencies*

The final model showed habitat type and partner head colour were the significant effects on the perch approach frequencies of Gouldian finches (n=31) within trial two conditions (Table 3.5).

Table 3.5 Final GLMM model results representing significant and non-significant fixed effects on the perch approach frequencies of Gouldian finches (n=31) to habitat types within trial two conditions. Significant effects are highlighted in bold. The interaction between habitat type and partner head colour is donated as *.

Source	**F-Value**	**Significance value**
Corrected Model	**3.076**	***p*=0.016**
Habitat Type	**4.139**	***p*=0.047**
Head Colour	2.142	*p*=0.149
Age	0.036	*p*=0.850
Partner Head Colour	**4.712**	***p*=0.034**
Sex	2.218	*p*=0.150
Habitat Type*Partner Head Colour	1.775	*p*=0.188

Corresponding to trial one conditions, Gouldian finches approached the dense habitat (Roses; 6.645±2.582 times) significantly more often than the open habitat (Vines; 4.847±1.863 times) before entering (GLMM t-test; t=-0.316, *p*=0.047; Fig 3.9a). The effect of partner head colour showed birds partnered with a black-headed finch (6.727±2.585 times) approached significantly more often before entering than birds partnered with a red-headed finch (4.788±1.863 times), irrespective of habitat type (GLMM t-test; t=0.340, *p*=0.034; Fig 3.9b). No other variable or the random effect of Bird I.D. had a significant effect on the perch approach frequencies of Gouldian finches within trial two conditions.



Figs 3.9 Mean (SE) perch approach frequencies within trial two conditions of **a)** Gouldian finches (n=31) to open (Vines) and dense (Roses) habitat types and **b)** birds partnered with either a black-headed (n=17) or a red-headed bird (n=14).

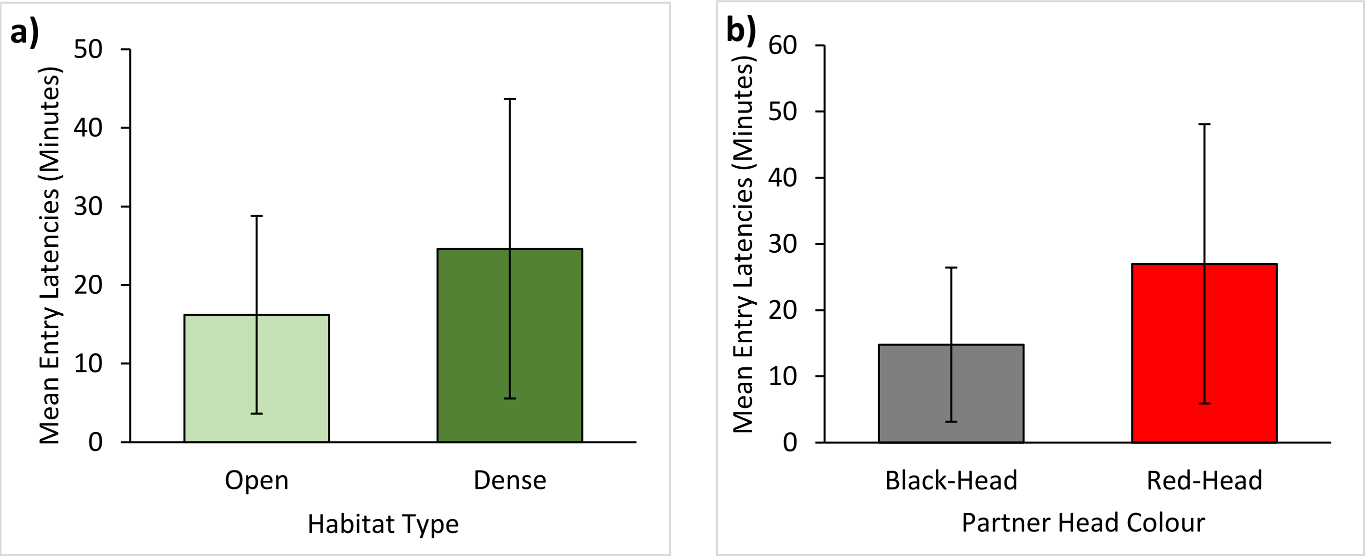
3.3.5 *Entry latencies*

As found within trial two perch approach frequencies, the final model showed habitat type and partner head colour were the significant effects on the entry latencies of Gouldian finches (n=31) within trial two conditions (Table 3.6).

Table 3.6 Final GLMM model results representing significant and non-significant fixed effects on the entry latencies of Gouldian finches (n=31) to habitat types within trial two conditions. Significant effects are highlighted in bold. The interaction between habitat type and partner head colour is donated as *.

Source	**F-Value**	**Significance value**
Corrected Model	**3.202**	***p*=0.013**
Habitat Type	**6.918**	***p*=0.011**
Head Colour	0.848	*p*=0.361
Age	1.441	*p*=0.235
Partner Head Colour	**4.359**	***p*=0.041**
Sex	0.599	*p*=0.442
Habitat Type*Partner Head Colour	2.169	*p*=0.147

Corresponding to trial one conditions, Gouldian finches entered the open habitat (Vines; 16.225±12.588) significantly sooner than the dense habitat (Roses; 24.618±19.057; GLMM t-test; t=-0.417, *p*=0.011; Fig 3.10a). The effect of partner head colour showed birds partnered with a black-headed finch (14.797±11.644 minutes) entered the novel cages significantly sooner than birds partnered with a red-headed finch (26.993±21.097 minutes), irrespective of habitat type (GLMM t-test; t=-0.601, *p*=0.041; Fig 3.10b).



Figs 3.10 Mean (SE) entry latencies (minutes) within trial two conditions of **a)** Gouldian finches (n=31) to open (Vines) and dense (Roses) habitat types and **b)** birds partnered with either a black-headed (n=17) or a red-headed bird (n=14) irrespective of habitat type.

No other variable significantly influenced the entry latencies of Gouldian finches within trial two conditions. The random effect of Bird I.D was significant, showing the individual explained 70% of the variation in the entry latencies of Gouldian finches within trial two conditions (Random effect results; Estimate=0.702, SE=0.287, Z=2443, *p*=0.015).

3.3.6 *Correlations of response variables within trial two conditions*

Perch approach frequencies to open (Vines) and dense (Roses) habitat types were not correlated within trial two conditions (Spearman correlation test: Perch approach frequencies, $r_s(31)= -0.052$, $p=0.782$). The entry latencies to open and dense habitat types were positively and significantly correlated within trial two conditions (Spearman correlation test: Entry latencies, $r_s(31)= 0.589$, $p<0.001$; Fig 3.11).

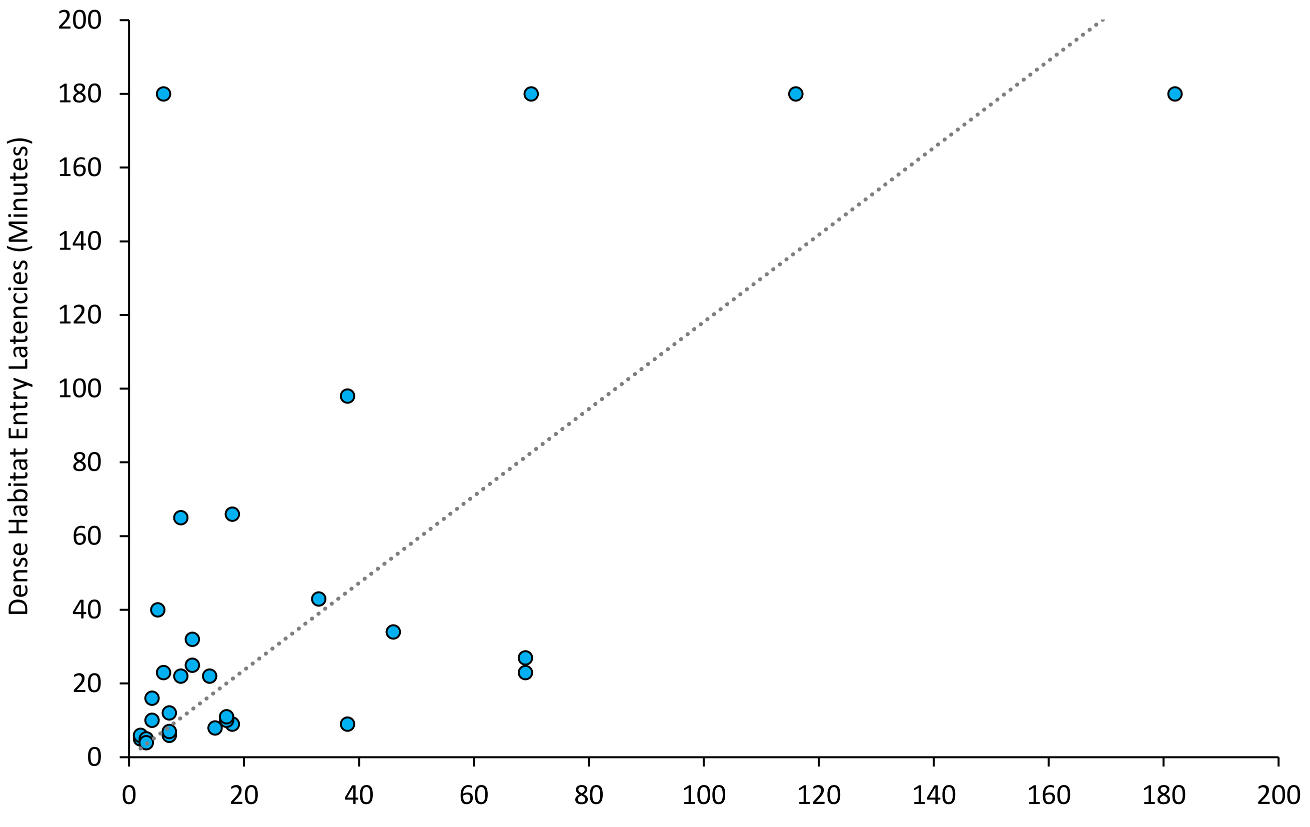


Fig 3.11 Positive and significant relationship of the entry latencies (minutes) of Gouldian finches to open (Vines) and dense (Roses) habitat types within trial two conditions.

3.3.7 *Correlations of food and spatial neophobia*

Significant correlations were found within trial one conditions only. The frequencies of approach (approach/avoidance conflict) to green seed within trial one conditions was positively correlated with the frequencies of approach to the dense habitat (Daises; Table 3.7). The initial feeding latencies to green seed was negatively correlated to the entry latencies into the open habitat (Eucalyptus; Table 3.7). No correlations between food neophobia and spatial neophobia were significant within trial two conditions, although the relationship between the initial feeding latencies to red seed and the entry latencies into the dense habitat (Roses) was marginally non-significant (Table 3.7).

Table 3.7 Spearman's Rank Order correlation outputs showing the relationship between the dependent variable measures recorded for all birds when exposed to novel food and novel habitats within trial one (n=31) and trial two conditions (n=31). Bonferroni corrected significance value is $p \leq 0.025$ denoted as **. All values are to three decimal places.

		Frequencies of approach **Food Neophobia** **Versus** **Spatial Neophobia**	**Food Neophobia** **Initial Feeding Latencies** **Versus** **Spatial Neophobia** **Entry Latencies**
Trial One	**Green Seed vs Open Habitat (Eucalyptus)**	*rs*(32)=-0.361, *p*=0.042	*rs*(32)=-0.454,*p*=0.009**
	Green Seed vs Dense Habitat (Daises)	*rs*(32)=0.905,*p*<0.001**	*rs*(32)=0.094, *p*=0.607
Trial Two	**Red Seed vs Open Habitat (Vines)**	*rs*(31)=0.130, *p*=0.487	*rs*(31)=0.027,*p*=0.883
	Red Seed vs Dense Habitat (Roses)	*rs*(31)=0.092, P=0.623	*rs*(31)=0.352,*p*=0.052

3.4 Discussion

This study investigated the responses of Gouldian finches to open and dense habitat types in mixed and same head colour pairs to determine whether spatial neophobia was affected by habitat type, age, sex, head colour and partner head colour. The exposure of Gouldian finches to habitat types clearly elicited spatial neophobia but strengths of neophobic responses varied dependent upon habitat type, as birds consistently approached open habitats less often and entered sooner compared to dense habitats. Within trial one conditions, male finches approached the novel environments more often than females before entering and younger birds entered novel habitats sooner than older birds, irrespective of habitat type. The effect of head colour of the focal bird did not influence spatial neophobia within any trial condition but there was an effect of partner head colour within trial two conditions. Birds partnered with black-headed finches approached novel environments significantly more often and entered sooner than birds partnered with a red-headed finches, irrespective of habitat type. Within both trial conditions, only the entry latencies to open and dense habitat types were significantly correlated. Finally, the relationships between food and spatial neophobia measures were correlated only within trial one conditions. These correlations showed inverse relationships between the initial feeding latencies on novel food (Green seed) and entry latencies into the open habitat type (Eucalyptus) and a positive relationship in the approach frequencies to novel food and the approach frequencies to the dense habitat type (Daises).

Gouldian finches are habitat specialists, adapted to open savannah grasslands (Brazill-Boast et al 2011a). In our study, we have shown that finches' behavioural responses to habitat types were repeatable, demonstrating less approach/avoidance conflict and entering open habitats sooner in both trial conditions, thus evidencing spatial neophobia is greater when exposed to dense habitats than open ones. These findings confirm our first two predictions (Predictions 1 and 2). Dense habitat types present greater novel stimuli, less available visible space and deviate greatly from Gouldian finch open savannah grassland preferences, eliciting greater avoidance responses. Spatial neophobia drives avoidance responses, which are governed by the perception of potential danger and assessment of whether compromising exposure to unfamiliar settings will be rewarding or costly (Mettke-Hofmann et al 2009; Wolf et al 2009). Greater uncertainty of the costs and benefits associated with dense habitats is demonstrated in the Gouldian finch because they showed greater hesitancy to enter undesirable, dense environments (Daises and Roses). Increased hesitancy to cross over into unsuitable environments could have considerable conservation implications on the Gouldian finch. Habitat fragmentation through anthropogenic practices are changing previously familiar open savannah landscapes (Maute et al 2015; Legge et al 2015; Weier et al 2016), posing strong selection pressures on Gouldian finch dispersal. Increasingly landscapes are becoming more unsuitable for this specialist species and greater deviation from familiar landscapes could influence greater hesitancy to cross over into unsuitable and unfamiliar landscapes to access suitable landscapes further away. These effects have been demonstrated in specialist butterfly species, the bog fritillary, *Proclossiana Eunomia* (Schtickzelle et al 2006) and the Lulworth Skipper, *Thymelicus acteon* (Louy et al 2007). These studies found that specialists were reluctant to enter unfamiliar habitats, which as a consequence reduced their ability to disperse and exploit habitats further away (Schtickzelle et al 2006). Later research found genetic diversity was reduced in specialist species compared to generalists because of the high degree of isolation among populations (Louy et al 2007) owing to habitat fragmentation. Although Gouldian finches are known to be nomadic and track superabundant resources (Davies 1982), increasing habitat modification could have significant fitness and dispersal costs. Longer hesitation to disperse into unfamiliar areas reduces dispersal success, increases time spent tracking resources, requires greater energy expenditure to track resources and quite possibly reduces survival rates (McKinney et al 1997; Schtickzelle et al 2006).

We could not make a prediction on the direction of hesitancy responses of age classes to habitat types. We found younger birds’ entry latencies were faster than older birds within trial one conditions, irrespective of habitat type. Previous research has shown younger individuals are generally less neophobic than older individuals (Tuorila et al 2001; Biondi et al 2010; Krueger et al 2014). Our spatial neophobia findings contradict those of object neophobia testing conditions (Mettke-Hofmann 2012) as older birds were less neophobic to feed by a novel object in comparison to younger birds. Object neophobia testing conditions forces finches to be in conflict with approaching the novel object and the motivation to feed (Mettke-Hofmann 2012) whilst spatial neophobia testing conditions within this study excluded this effect of food deprivation. It would appear that younger birds are less neophobic than older birds when exposed to spatial novelty, particularly as this was when birds were first exposed to novel environments. The effects of age were not repeatable within this study in responses to habitat types as younger birds were only faster to enter habitats within the first trial. Head colours and ages were not balanced within this research and younger birds were always partnered with an older bird. It is currently unknown whether younger birds respond similarly or differently to novel environments when partnered with another bird of the same age of the same and opposing head colours. Given the assemblage of head colours and ages within this study design were unbalanced, it would be beneficial to further investigate age biases within future research, particularly as age effects were identified within one trial condition for food neophobia (Chapter Two) and spatial neophobia. It is more likely that age is effecting novelty responses more strongly than another effect such as head colour because of the reduced number of black-headed birds within the younger age category (n=4). Therefore testing birds with same age partners would determine whether the age of the individual or partner bird significantly influences spatial neophobia or whether another variable, such as head colour of the focal bird and partner bird has a stronger influence on neophobic responses. This will be discussed later in this chapter.

We predicted male Gouldian finches would be less hesitant to approach and enter novel habitats sooner than females. We found an effect of sex within the first trial condition of spatial neophobia as males approached more often before entering than females, irrespective of habitat type. This evidences males demonstrate greater hesitancy because the approach/avoidance conflict to enter novel environments was greater in comparison to females, thus rejecting Prediction 4. Male Gouldian finches are more conspicuous than females (Brush & Seifried 1968; Pryke & Griffith 2007) and greater conflict to enter novel environments could be explained by male conspicuousness. Conspicuousness effects in relation to sex has been shown in several parrot species where the less conspicuous sex demonstrated less object neophobia than the more conspicuous sex (Mettke-Hofmann 2000). These findings were not consistent in regards to sex within the second trial and could be explored further although our data showed the frequencies in which males approached (approach/avoidance conflict) both habitat types in the second trial condition reduced overall. This suggests that familiarity with the testing situation may have suppressed this conflict between approach and avoidance in males. Within the second trial condition, female approach latencies and approach frequencies remained relatively unchanged, evidencing females are less spatially neophobic than males.

Corresponding to food neophobia (Chapter Two) and novel object tests (Mettke-Hofmann 2012; Williams et al 2012) we found no effect of focal bird head colour on spatial neophobia in Gouldian finches, therefore rejecting Prediction

5. We did find an effect of partner head colour within the second trial. Birds partnered with black-headed finches approached novel environments significantly more often before entering and entered sooner than birds partnered with a red-headed finches, irrespective of habitat type. This in part confirms Prediction 6. Changes in behaviour of Gouldian finches in accordance to partner head colour have been identified in a previous study (King et al 2015) where shyer partners influence the accompanying bird to be less shy itself and bolder partners influence greater boldness in the other bird. Further, black-headed finches have been shown to be more explorative and risk taking than red-headed finches (Williams et al 2012) and perhaps play the role of the producer (King et al 2015) by exploring novel resources first. Red-headed birds are less risking taking than black-headed finches because they are the most conspicuous morph and like other conspicuous individuals are more susceptible to predation than less conspicuous morphs (Huhta et al 2003). As a consequence, red-headed birds demonstrate greater hesitancy so not to compromise vigilance (Mettke-Hofmann 2012). This effect of conspicuousness would explain the greater entry latencies of birds partnered with a red-headed finch in spatial neophobia as partners have more time to overcome their neophobia to enter novel environments in comparison to when partnered with a black-headed finch. Furthermore, this longer latency to enter would explain why the approach/avoidance conflict was reduced in focal birds partnered with a red-headed finch. Black-headed finch partners demonstrated greater conflict before entering which suggests the presence of a black-headed finch influences partner birds to overcome their neophobia sooner by entering sooner and elicits greater hesitancy before entering. This effect of partner head colour could be crucial for Gouldian finch dispersal when considering the effects of habitat modification. Whilst Gouldian finches prefer open habitats, black-headed birds could play a vital role in locating and accessing resources and facilitate faster assessment of unfamiliar and less preferable habitat conditions and the subsequent cross over into these areas, thus facilitating greater dispersal. It would appear that black-headed birds are crucial within the social network to deal with novel and changing environmental conditions. What is interesting however is that the focal black-headed bird did not itself enter novel environments sooner only that the presence of this morph induces partner birds to explore novel environments sooner. This is intriguing as these effects were not repeatable because age effects were identified in trial one and partner head colour effects were identified in trial two. There does appear to be strong driving forces in responses to novel environments within this study, yet it would be beneficial to endeavour to disentangle effects of age and head colour in the future,

as our study design does present unequal age and head colour ratios. It is possible to further investigate whether head colour or age had a stronger effect on responses to novel environments in the future by implementation of a balanced design, which would require a larger sample size of birds.

Finally, we found consistency in the entry latencies to habitat types in both trial conditions as our investigation into the relationship between food and spatial neophobia showed significant relationships within trial one conditions only. The frequencies of approach (approach/avoidance conflict) to green seed within trial one conditions was positively correlated with the frequencies of approach to the dense habitat (Daises). The initial feeding latencies to green seed was negatively correlated to the entry latencies into the open habitat (Eucalyptus). Given finches were more neophobic to dense habitats and novel food (Chapter Two) it is not surprising the conflict demonstrated by finches to unfamiliar food and least preferred habitat types are correlated in this way. The negative relationship between the feeding latencies on green seed and the entry latencies into the open habitat (Eucalyptus) could be explained by the type of novelty itself. Our data showed the feeding latencies to green seed were generally much greater than the entry latencies into the Eucalyptus habitat. This suggests greater hesitancy is elicited to feed on novel food, whilst entry latencies into a new environment could be reduced because of the motivation to explore a new environment (spatial neophilia), which replicated in-situ habitat preferences. Correlations were only identified in the first trial condition, which is plausible because the second trial condition has been determined as being slightly familiar to the first trial condition but on this basis it does show these types of neophobia are somewhat correlated in the Gouldian finch. Furthering this research should consider exploration of Gouldian finches to novel habitats, demonstrating how birds are responding to novel habitats beyond the initial response to novelty. Additionally, further research into head colour within wild populations could be extremely insightful in conservation contexts to determine whether black-headed finches are facilitating greater dispersal in ever changing Gouldian finch habitat.

Chapter Four

Discussion

Supplementing conservation research through insights of a specialist birds' responses to novelty

4.1. Research advances and limitations

This study aimed to investigate different types of neophobia and the existence of dietary conservatism in relation to age, sex, head colour and partner head colour in Gouldian finches. We found Gouldian finches demonstrate food neophobia as approach frequencies and feeding latencies were greater to novel food in comparison to familiar food (Chapter Two). This is not a surprising result as Gouldian finches are a food specialist (Brazill-Boast et al 2011a) and the study group within this research had not previously been exposed to this form of food novelty, therefore I would expect greater hesitancy towards novel food than familiar food. The effects of sex, head colour and partner head colour did not influence neophobic responses of Gouldian finches to food types within either trial condition and younger birds ate novel food sooner than older birds within the second trial condition only. This is an interesting finding as younger individuals have been shown to be more hesitant than older individuals to feed on familiar food within object neophobia testing conditions (Mettke-Hofmann 2012), which demonstrates more experience in older individuals reduces the time in which the individual avoids the novelty. Research is often evidencing that responses to types of novelty are not correlated (Verbeek et al 1994; Boogert et al 2006; Ruuskanen & Laaksonen 2010; Greggor et al 2016a), which could explain the differences between object neophobia and food neophobia in this species. However, as this study design assembled younger birds with older birds consistently, the faster responses of younger birds to sample novel food could be due to dominance effects, whereby the presence of an older, more dominant partner forces younger individuals to act quickly and take greater risk to eat novel food. Age is often linked to dominance in birds (Holberton et al 1990; Smith et al 2001) and other animals living in groups (Mech 1999; de Villiers et al 2003; Fischer et al 2004; Robbins et al 2005) showing older individuals taking ownership of resources when in competition with younger, subordinate individuals. It would appear here that the presence of an older bird forces the younger individual to overcome food neophobia sooner in order to gain access to food. As discussed within Chapter

Two, age biases within this study cannot be overlooked and perhaps other driving factors are influencing responses to novel food that were not identified. For example, it is unknown whether younger birds would respond similarly or differently to novel food when partnered with a bird of a similar age of the same and opposing head colours or whether responses to novel food was an effect of an intrinsic colour preference for red seed, given younger birds were only faster within the second trial. Further investigation into age effects within a more balanced design would allow for equal ages and head colours to be compared and identify whether responses to novel food are clearly effects of age or whether a combination of other effects are influential, such as head colour and age for example. This does provide exciting opportunities to identify potential variation in novelty responses in regards to age and disentangle any other effects on responses to food types in the future.

In addition to the determination that Gouldian finches demonstrate food neophobia, this research has evidenced Gouldian finches are dietary conservative. The difference scores between feeding visits to familiar and novel food were greater on the first day of presentation (Monday). Repeated presentations of familiar and novel food throughout the remainder of the week shows some convergence between feeding visits on these food types but highlights Gouldian finches will not fully accept and incorporate novel food into the diet with repeated exposure and will not become adventurous consumers. Given these findings of food neophobia and dietary conservatism in the Gouldian finch, some insight of how wild populations of Gouldian finches will respond to novel foods have been provided and the conservation implications of these findings will be discussed later within this chapter.

Within Chapter Three, we found Gouldian finches elicited spatial neophobia and the strengths of neophobic responses were dependent on habitat type. Within both trial conditions, finches consistently approached open habitats less often and entered sooner compared to dense habitats, confirming our predictions that Gouldian finches would demonstrate less hesitancy towards open habitats and enter sooner as these represent in-situ habitat preferences (Chapter Three). In-situ research has shown Gouldian finches demonstrate strong preferences for open savannah grasslands and the food and nest resources within them (Tidemann et al 1992; Brazill-Boast et al 2011a), so it is not surprising Gouldian finches within this research responded to open and dense habitats differently and showed greater preferences for the open habitats in both trial conditions. As with food neophobia and dietary conservatism results (Chapter Two), our findings on spatial neophobia can provide insight into the conservation implications on this species and will be discussed later within this chapter.

Other than novelty type in the form of novel food and novel environments, the only reoccurring factor influencing neophobic responses was the effect of age. Younger birds fed on novel food sooner than older birds within the second trial condition (Chapter Two) and entered novel habitats sooner within the first trial, irrespective of habitat type (Chapter Three). Previous research has shown younger individuals are generally less neophobic than older individuals (Tuorila et al 2001; Biondi et al 2010; Krueger et al 2014). These findings of food and spatial neophobia contradict previous object neophobia testing conditions (Mettke-Hofmann 2012) which is likely due to the presence of an older bird forcing younger individuals to be more risk taking in accessing food resources (Chapter Two) and be more explorative in situations where food deprivation does not govern responses (Chapter Three). These findings do show for the most part that neophobia ceases first in younger birds and suggests that younger birds in wild populations may need to be more risk-taking in order to access resources when in competition with older, more dominant birds. These findings of age would need to be further tested both within ex-situ environments to disentangle other influential factors effecting neophobia. Moreover, further research within in-situ environments would be beneficial to validate what we have discovered in captive conditions because there are several factors which could have influenced these responses in younger birds which may not be replicated in wild populations. Firstly, our research was conducted on captive Gouldian finches and whilst our implementation of novelty does elicit fear responses in the form of hesitancy, captive birds are not exposed to predation risk (Brazill-Boast et al 2011a), competition with other species such as the long-tailed finch (Brazill-Boast et al 2011b) and are within safe environmental conditions compared to wild populations. Given wild populations are exposed to real threats on survival, neophobic responses in younger birds of wild populations could deviate greatly from what we have discovered in captive birds, owing to less experience of habitat, predators and novel stimuli in comparison to older, more experienced individuals (Nilsson et al 2016). This suggestion is viable because younger birds have been shown to be more neophobic in object neophobia testing conditions than older birds (Mettke-Hofmann 2012). Additionally, whilst birds in this study were categorised into age classes, these groups do not reflect juvenile versus adult groups as all birds are sexually mature, adult birds within the first twelve months of life (Pryke & Griffith 2009) and all birds within this study were at least twelve months of age.

Opportunities to test juvenile birds would be advantageous to investigate developmental stage on neophobic responses, furthering research in regards to experience and age in the Gouldian finch in both captive and wild settings.

An effect of sex was identified in spatial neophobia testing conditions, showing males demonstrating greater approach/avoidance conflict before entering novel habitats than females within trial one conditions. Given males are more conspicuous in natural backgrounds than females (Brush & Seifried 1968; Pryke & Griffith 2007), increased hesitancy to enter environments could be due to their conspicuousness. These findings are consistent with previous findings of several parrot species where the less conspicuous sex approached and investigated a novel object first (Mettke-Hofmann 2000). The relationship between conspicuousness and vigilance has been reported in other non-avian animals, for example, blue spotted slow worms (*Anguis fragilis;* Capula et al 1997), Lake Victoria cichlid fish (*Neochromis omnicaeruleus;* Maan et al 2008) and Eastern red-backed salamanders (*Plethodon cinereus*; Venesky & Anthony 2007), highlighting conspicuous morphs demonstrate greater vigilance than less conspicuous counterparts to reduce exposure to potential risk, such as predation.

The effect of head colour of the focal bird did not influence spatial neophobia within any trial condition but partner head colour did within trial two conditions. Birds partnered with black-headed finches approached novel environments significantly more often and entered sooner than birds partnered with red-headed finches, irrespective of habitat type. Changes in behaviour of Gouldian finches in accordance to partner head colour have been identified in a previous study (King et al 2015) where shyer partners influence the accompanying bird to be less shy itself and bolder partners influence greater boldness in the other bird. Whilst we could not show focal black-headed birds entered habitats sooner or showed less hesitancy than red-headed birds, the presence of a black-headed bird within spatial neophobia testing conditions suggests that partner birds overcome their neophobia sooner as approach/avoidance conflicts were greater but entry latencies were faster. This effect of head colour and links to social conformity could be crucial for Gouldian finch persistence within the wild as these results suggest black-headed finches are highly influential on the speed at which social partners assess and subsequently respond to novel conditions. These effects suggest black-headed birds facilitate movement in wild populations between habitats and are therefore crucial for dispersal.

Whilst this suggestion is viable, it is interesting that we did not identify head colour differences of the focal bird in spatial neophobia. Given black-headed birds influenced neohobic responses in their partners showing particularly that entry latencies were faster, it is surprising that the black-headed focal birds did not enter novel habitats sooner as well. As discussed in Chapter Three, this could be an effect of the assemblage of birds within this study design and is a likely cause because partner head colour and age effects were not repeatable within both trial conditions. Unequal age groups and pairing younger birds with older birds consistently limits our understanding of whether the age biases within this study are resulting in clear effects of age in response to novelty, or whether other effects are driving these responses, such as head colour or partner head colour for example. However, given there was a reduced number of one year old black-headed morphs in testing conditions; it is more likely age is driving these responses to environmental novelty than head colour particularly within the first trial condition. We have identified that there are strong driving forces influencing neophobic responses to environmental novelty and furthering this research would incorporate a more balanced design to allow for the disentanglement of age and head colour effects.

Time constraints did not allow me to transcribe the exploration data to supplement the spatial neophobia research. We conducted spatial neophobia experimentation over a three-hour period and most birds had entered these novel habitats before the three-hour experimentation period was completed. Although we do have the data, we are yet to provide evidence on Gouldian finch responses to novel environments once neophobia has ceased and therefore exploration beyond the initial responses to novelty should be investigated in the future. This would be particularly beneficial to determine the effects of head colour and age in a spatial exploration context as well as focussing on disentangling age and head colour effects within the analyses.

Whilst Gouldian finches have been shown to be neophobic to both novel food and environments in this thesis, it is clear that responses to novelty types are not consistent as we only found correlations within trial one conditions (Chapter Three). This is not especially surprising because previous research has shown responses to different forms of novelty are not correlated because neophobia is context specific (Verbeek et al 1994; Boogert et al 2006; Ruuskanen & Laaksonen 2010; Greggor et al 2016a). This would explain why we found effects of sex and head colour in the spatial neophobia testing conditions but not within food neophobia testing conditions before initial feeding. Additional object neophobia and neophilia testing conditions were implemented within this research, but time constraints did not allow me to transcribe this data. Previous research has investigated object neophobia and neophilia in this species (Mettke-Hofmann 2012; Williams et al 2012) but did not investigate other types of neophobia within the same group because the focus of research was not specifically on novelty responses. Here, Gouldian finches were exposed to the three most commonly tested forms of neophobia within both trial conditions, which allows for many relationships to be investigated between novelty types and finch responses. It would be interesting to further investigate object neophobia and neophilia in this group of captive finches to establish whether relationships between object neophobia and the other two forms of neophobia exist and also investigate how object neophilia relates to object neophobia and spatial exploration.

4.2 Ecological consequences of neophobia on Gouldian finch conservation and directions for future research

This research has shown Gouldian finches are food neophobia and will not incorporate novel food into the diet and become adventurous consumers once neophobia has ceased (Chapter Two). Furthermore, spatial neophobia is demonstrated in this species and is influenced by habitat type because deviation from in-situ habitat preferences elicits greater hesitancy in this specialist species (Chapter Three). To my knowledge, this research has provided the first evidence of food neophobia, dietary conservatism and spatial neophobia within the Gouldian finch. These findings are concerning when considering the conservation implications of Gouldian finch populations within the wild and how they will respond to changing environmental conditions, particularly as it has been shown here that they will not incorporate new food into the diet and will hesitate longer to cross over into less preferred environments.

Gouldian finches are nomadic and move frequently to track superabundant resources (Tidemann et al 1992; Dostine et al 2001). Habitat fragmentation will likely slow down Gouldian finch dispersal and restrict movement with changing environmental conditions because food and water patches will decrease with increasing habitat modification, compromising survival rates. However, we do not know how far wild populations of Gouldian finches travel within a day and previous capture-recapture studies have had limited success in estimating movement owing to Gouldian finch emigration, predation or both (Woinarski & Tidemann 1992; Tidemann & Woinarski 1994). Moreover, previous research has shown there is no great variation in the selective forces within the distributions of Gouldian finches across its geographical range (Franklin & Dostine 2000; Dostine et al 2001; Brazill-Boast et al 2011a) and that head colour morph frequencies are stable within different populations (Franklin & Dostine 2000; Gilby et al 2009; Bolton et al 2016). These findings suggest different populations will converge well (Bolton et al 2016). This is promising as it shows populations are not genetically isolated from one another and promotes genetic diversity between populations (Bolton et al 2016). To further research into population convergence and population movement, it would be extremely beneficial for future conservation research to implement tracking devices on populations to track movement of this highly mobile species and determine seasonal movements and distances travelled in order to assess how changing habitat conditions affect movement over its geographical range. Additionally, considerations into implementing habitat corridors within Gouldian finch habitat could provide crucial pathways between habitat patches. Gouldian finch movement is governed by the annual cycle of food abundance mostly (Dostine et al 2011). We have shown in this captive research that the majority of the population are not adventurous consumers and will avoid incorporating novel food into the diet once neophobia has waned (Chapter Two). It is expected similar responses to novel food will be demonstrated in wild populations, as changing habitat conditions could limit preferred food resources and elicit neophobic responses to novel but potentially optimal food resources. It is therefore anticipated that with changing conditions Gouldian finches will become vulnerable to environmental change because spatiotemporal changes to plant communities owing to habitat fragmentation and global warming are reducing suitable finch habitat (Maute et al 2015; Weier et al 2016). These driving forces could result in ever-increasing competition with the generalist long-tailed finch for nesting and food resources making competitive exclusion more likely (Brazill-Boast et al 2011b). Further effects of changing habitat conditions could isolate Gouldian finch populations as suitable dispersal sites become more limited, resulting in reduced food patch availability and a greater demand on energy reserves to track suitable resource sites. A consequence of this would be starvation and continual decline of this near-threatened species (Birdlife International 2018). Habitat familiarity and implementation of habitat corridors has been shown to be essential and extremely beneficial for many terrestrial specialist species, including butterflies (Krauss et al 2003; Brückmann et al 2010), birds (Gillies & St. Clair 2008), amphibians (Burbrink et al 1998), reptiles (Burbrink et al 1998) and mammals (Bright 1998; Acosta-Jamett & Simonetti 2004). Habitat corridors provide greater connectivity between preferred habitat types (Beier & Noss 1998), yielding greater dispersal and access to preferred resources (Hodgson et al 2011;

Noordijk et al 2011). It may be imperative to maintain connectivity between resource patches of Gouldian finch habitat by implementation, protection and management of habitat corridors linking crucial resources. We have shown Gouldian finches are more hesitant to explore less preferred habitats (Chapter Three). Longer hesitation to disperse into unfamiliar areas reduces dispersal success, increases time spent tracking resources, requires greater energy expenditure to track resources and quite possibly reduces survival rates (McKinney et al 1997; Schtickzelle et al 2006). Connectivity between preferred habitats could allow Gouldian finches to optimise these corridors and exploit the habitat patches and avoid fitness costs associated with crossing over into less preferred habitats. To do so would then require more control over the timing and management of fires and cattle implementation (Maute et al 2015; Weier et al 2016), so not to disturb and deteriorate habitat corridors.

There appears to be an exciting and promising discovery in regards to head colour. Spatial neophobia testing conditions (Chapter Three) suggest black-headed birds could have a vital role in facilitating the movement and subsequent dispersal of Gouldian finch flocks across new habitats. Whilst Gouldian finch conservation research is wealthy, there is a lack of focus on the effect of head colour to conservation issues (Brazill-Boast et al 2011a & b; 2013; Legge et al 2015; Maute et al 2015). Research on in-situ populations have overlooked head colour effects on responses to changing environmental conditions, yet here we have shown that head colour morph plays a particularly key role in responses to changed conditions. Previous research has shown colour-polymorphism can be advantageous with changing environmental conditions because different morphs implement different strategies according to the selection pressures they are faced with (Karrell et al 2011; Roulin 2014; Schilthuizen & Kellerman 2014). Black-headed finches explorative and risk-taking behaviour (Williams et al 2012) could be rewarding in regards to accessing resources sooner because they are less conspicuous than red-headed birds, who are more likely to suffer greater predation risk (Galeotii et al 2003; Huhta et al 2003; Mettke-Hofmann 2012). This is certainly worthy of further investigation in wild populations when considering responses to environmental change. If black-headed finches do play the role of the producer in wild populations as shown in captive social conformity research (King et al 2015), they would then be crucial for the persistence of this species in changing environmental conditions to facilitate movement across habitats. Although we could not show black-headed birds were themselves faster to enter habitats, investigation in of head colour morphs in wild populations could provide greater insight into head colour responses on novelty and augment our understanding on the roles head colour morphs play within the social network. Moreover, further investigation into the more cautious red-headed finch (Williams et al 2012) could provide insight into whether this head colour morph is particularly vulnerable to environmental change and relies on the black-headed finch to access resources.

4.3 Cognition for conservation

This research has delivered numerous and exciting discoveries and though our research was within captive conditions, our findings support previous research that neophobia as a cognitive mechanism can supplement conservation research for the purpose of working towards positive change in managing and preserving vulnerable species. Understanding animal cognition and harnessing animals' perceptual biases can produce successful outcomes in conservation management contexts (Greggor et al 2014; Marzluff & Swift 2017). For example, in-situ cognition research has been successful in conditioning varanid lizards, *Varanus panoptes,* through taste aversion to avoid toxic cane toads, *Rhinella marina,* in Australia, thereby restoring lizard populations (Ward-Fear et al 2016). Manipulating in-situ environments or features has been beneficial to tackle human-animal conflict, for example, applying chilli powder onto fencing enclosing farms to deter African elephant, *Loxodonta Africana*, herds from crop raiding (Hedges & Gunaryadi 2010; Karidozo & Osborn 2015). Moreover, predator recognition in naïve species using simulated predator threats have been beneficial to maintain and restore populations of previously highly predated species, by inducing predator neophobia and the desired anti-predator responses (McLean et al 1999; West et al 2018). This is particularly important as more evidence is becoming available showing marine and terrestrial species are moving further north with climate change (Perry et al 2005; Hitch & Leberg 2007; Chen et al 2011). Increases in global temperature alters the range of marine and terrestrial prey species and the predators that rely on them (Edwards & Richardson 2004; Hamilton et al 2017) and the seasonality in which plant species produce food resources, affecting species which rely on them (McCarty 2002). Changes in species distributions as a result of increasing temperature brings rise to novelty and increased threat to population persistence of vulnerable prey when unknown predators become resident in areas they previously did not inhabit (Reed et al 2011; Hazen et al 2013). Shifts in plant seasonality and geographical range (Dieleman et al 2015; Leishman & Gallagher 2015) could present novel food types, which could have significant detrimental effects on food acquisition in specialist species, particularly food neophobic and dietary conservative species like the Gouldian finch. Ultimately, it stands to reason that research from a cognition and behavioural approach is becoming increasingly necessary to inform conservation and aid in conservation management, particularly when cognition researchers, behavioural ecologists and conservationists share a common goal to aid species recovery and promote biodiversity.

4.4 Conclusions

Globally, the unmodified habitats for wildlife are ever decreasing at an accelerating rate. These changes to familiar habitats and resources within them are presenting more novel stimuli and creating great selection pressures on vulnerable species to adapt and respond effectively to these changes. Here, we have shown that neophobia is an effective cognitive mechanism to assess species responses to novelty and interpret these findings into ecologically relevant implications for wild population conservation. This research offers new opportunities both in captive and wild settings and I hope to inspire future research to further investigate these recommendations.

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