Personality, sociality and foraging

in the zebra finch (*Taeniopygia guttata*)

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GENERAL ABSTRACT

Personality, or individual differences in behaviour that are persistent over time and/or context, is a well-studied topic in the zebra finch. However, the majority of this work has failed to frame and emphasize the importance of the natural history of the species when considering personality. In particular, few personality studies have taken into account the importance of the social environment in this highly social species, which is important as it may influence how personality is formed and maintained. Moreover, no work has yet studied zebra finch personality in the wild, to examine the role of fitness. I addressed these questions by first examining the relationship between sociality and well-established personality traits in captivity, such as exploratory behaviour and activity, along with examining the effects of personality on fitness in a captive aviary population. I found that one personality trait, activity, seems to be established from a very young age, when individuals are only five days old. Furthermore, I found that an individual's level of sociability may constitute a personality trait that is linked to exploratory behaviour and activity in a social context. Secondly, I studied personality in the wild zebra finch for the first time. This work at Fowlers Gap Arid Research Station involved assessing typical group size at dams and on transects, measuring exploratory behaviour in individuals briefly brought into captivity, and the use of feeders in the wild using a PIT-tag monitoring system. This work confirmed the integral role of social relationships, and in particular that of the sexual partnership, plays in the wild zebra finch. Interestingly, I found that exploratory behaviour assayed in individuals brought briefly into captivity and exploratory behaviour and sociality in the wild were correlated in the opposite direction to that predicted from captive experiments. I did not find any significant relationship between the personality traits assayed and a measure of fitness, reproductive success at the breeding colonies. Hence, researchers should be aware that personality assayed in captivity may not be entirely predictive of personality in the wild.

DECLARATION

I certify that the work in this thesis entitled "**Personality, sociality and foraging in the zebra finch (*Taeniopygia guttata*)**" has not previously been submitted for a degree nor has it been submitted as part of the requirements for a degree to any university institution other than Macquarie University.

I certify that this thesis is an original piece of research and that it has been primarily written by me. Where co-authored chapters are included my contributions and those of all other authors have been clearly indicated (see Preface). Any help and assistance that I have received has been appropriately acknowledged. I certify that all information sources and literature used are indicated in this thesis.

The research presented in this thesis was approved by the Macquarie University Animal Ethics Committee (No. 2010/059 & 2011/041).

Luke S.C. McCowan

June, 2014

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I would also like to thank my two associate supervisors, Dr Martin Whiting and Dr Mylene Mariette. I must thank Mylene for her indispensable help in the field. Without her guidance, I would not even know how to begin in studying the zebra finch in its natural habitat. Without her often appearing like Danielle Rousseau from the thickets to give me a stern talking to, I would surely have been lost.

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PREFACE

Chapters Two to Six have been prepared for submission or already submitted to peer-reviewed scientific journals for publication and have therefore been formatted according to the corresponding journal's style. Title page photography credits for the main title page, Chapter Four and Five go to Luke McCowan, and for the title pages of Chapter One, Two, Three, Six and Seven go to Simon Griffith.

My academic supervisor, Simon Griffith, has assisted me broadly with the conception, writing and analysis of this thesis, and is co-author on every chapter. I have also had help with fieldwork and data analysis in Chapter Two from Mylene Mariette and fieldwork in Chapter Six from Mark Mainwaring, Fiona Finch, Jeff Yap and Nora Prior. Mark Mainwaring also offered advice or assisted with data analysis in Chapters Four to Six. My estimated contribution to each chapter is listed below:

Chapter One: Conception 100%, writing 100%.

Chapter Two: Conception 70%, data collection 40%, analysis 95%, writing 95%.

Chapter Three: Conception 80%, data collection 100%, analysis 90%, writing 95%.

Chapter Four: Conception 80%, data collection 60%, analysis 90%, writing 95%.

Chapter Five: Conception 80%, data collection 60%, analysis 90%, writing 95%.

Chapter Six: Conception 80%, data collection 70%, analysis 90%, writing 95%.

Chapter Seven: Conception 100%, writing 100%.

Chapter One

General Introduction

What is animal personality?

For the past two decades, 'personality' has been a buzzword in the field of animal behaviour. While the existence of personality differences between individuals has long been accepted in humans and our companion species, such as domestic dogs (*Canis lupus familiaris*) (Eysenck 1953; Svartberg & Forkman 2002), before this period ethologists considered differences in the way individuals of a species regularly behave to be nothing more than noise around an adaptive mean (Slater 1981). However, near the end of the 20th century, researchers began to accept that consistent individual behavioural differences (or 'personality') are highly prevalent across a wide variety of taxa, and therefore are likely adaptive (Slater 1981; Carere & Maestripieri 2013). From an ethological perspective, 'personality' may be defined as individual differences in behaviour that are persistent over time and/or context (Réale et al. 2007). More colloquially, it may be defined as the tendency of an individual to behave in a certain way in one or many different contexts over a significant period of their lifespan, which differs from the way some (or many) other individuals in that population or species tend to behave in those situations. Hence, personality consists of two attributes: individuals must differ from each other in their tendency to display certain behaviours (or mean levels of behaviour) in certain contexts, and they must also be consistent in behaving this way over time (Stamps & Groothuis 2010). The length of time that individuals must be consistent in their behaviour for it to be defined as 'personality' is debated (Groothuis & Trillmich 2011), and even in humans, personality attributes have been shown to change over the course of an individual's lifespan (Srivastava et al. 2003) However, it is generally expected that behavioural differences between individuals will be maintained even if the levels of these traits change with age or situation (Réale et al. 2007).

When correlations exist between different behavioural 'personality' traits across different situations or contexts, this is referred to by some authors as a 'behavioural syndrome', although the term is sometimes used interchangeably with personality or temperament (Garamszegi et al. 2009;

Sih et al. 2012; Carere & Maestripieri 2013). One oft-reported explanation for the existence of behavioural syndromes in various species is that they are reflective of individuals' different coping styles on the proactive-reactive axis (Coppens et al. 2010), with reactive individuals more attuned and responsive to cues and changes in their environment than proactive individuals (Minderman et al. 2009; Almberg 2013). Moreover, all three definitions (personality, behavioural syndromes and coping styles) may be linked to individuals exhibiting different stress-profiles or long-term stress reactivity, which suggests that these behavioural consistencies may be driven by underlying physiology (van Dongen et al. 2010; Aubin-Horth et al. 2012; Montiglio et al. 2012; Oswald et al. 2012; Bouwhuis et al. 2014; Shearer & Pruitt 2014)

Personality and fitness

An individual's personality may be formed by non-heritable environmental effects during ontogeny (Stamps & Groothuis 2010; Rödel & Meyer 2011; Guenther et al. 2014), by heritable genetic effects (van Oers et al. 2004; Sinn et al. 2006), or a combination of these factors (Carere et al. 2005). There have been a number of hypotheses put forward to explain the seemingly counter-intuitive evolution and maintenance of animal personality, which theoretically leads to individuals performing non-optimal behaviours in some situations (Avilés & Parejo 2011), such as pace-of-life or life-history trade-offs (Stamps 2007; Biro & Stamps 2008; Boon et al. 2008; Smith & Blumstein 2008; Réale et al. 2010), frequency-dependent selection (Wolf et al. 2008; Wolf & McNamara 2012), fluctuating selection (Dingemanse et al. 2004), differences in state and feedbacks between state and behaviour (Dingemanse & Wolf 2010). Studies in fish have also shown that behavioural syndromes (correlations between different personality traits) are more likely to form in the wild under harsh conditions or survival bottlenecks, such as when populations are exposed to predation (Bell & Sih 2007; Adriaenssens & Johnsson 2013). In all of these cases personality is expected to have an effect on the fitness of an individual. A number of studies have verified links between

personality and various fitness attributes, such as growth rate (Adriaenssens & Johnsson 2011; Heg et al. 2011), survival (Cavigelli & McClintock 2003; Réale & Festa-Bianchet 2003; Réale et al. 2009; Archard & Braithwaite 2011) and reproductive success (Boon et al. 2007; Wilson et al. 2010; Ariyomo & Watt 2012; Betini & Norris 2012; Keogh et al. 2012; Vrublevska et al. 2014), with some personality types faring better under certain conditions.

Why study the relationship between personality, social behaviour and fitness?

While personality is defined as consistent differences in behaviour between individuals, aspects of the social environment may influence how personality is formed and maintained. To illustrate this, it has been proposed that social niche specialisation might lead to the evolution of personality (Bergmüller & Taborsky 2010), with different personality types fulfilling different social roles, or as a result of social conflict. Moreover, there is some evidence that how social an individual is (which may be referred to as an individual's gregariousness or sociality) may constitute a personality trait (Cote et al. 2008; Cote et al. 2012). Regardless of this assertion, it is useful to study personality in a social context, as personality has been shown to be linked to aspects of social behaviour (Webster & Ward 2011) and social networks (Aplin et al. 2013). Despite this, the majority of personality research conducted thus far has focused on individuals in isolation, using assays such as the 'open-field' test (Dingemanse et al. 2002). These assays are useful for measuring certain personality attributes, especially those that influence behaviours most commonly performed alone, but they overlook behaviours that are generally performed in a social context, where conspecifics are likely to influence each individual's behavioural output. To elaborate, in social situations processes such as facilitation and conformity may result in both quantitative and qualitative changes in the expression of behaviour (Webster & Ward 2011). Moreover, in many species most natural behaviours are performed in a social context, which means that the effect of the social environment on behaviour (and the expression of personality) is highly ecologically

relevant, and strongly linked to an individual's fitness. For these reasons, it is important to take both the social environment and fitness into account when studying personality. This is particularly relevant in highly social species, such as my study species, the zebra finch (*Taeniopygia guttata*).

Personality in the zebra finch

The zebra finch is an estrildid finch, native to Australia, East Timor and Indonesia, which has been studied extensively, especially in the last half century (Zann 1996). Largely due to its capacity to thrive in captivity, the zebra finch has become the most important captive model passerine system in the world, and has been the subject of thousands of academic papers (Griffith & Buchanan 2010). For a passerine, the zebra finch is also extraordinarily easy to breed in captivity, as they breed opportunistically year-round and can reach sexual maturity in as little as 70 days of age (Griffith & Buchanan 2010). However, at least in recent years comparatively little work has been conducted on wild zebra finch populations. This is most likely due to the limited geographic range of the species and the greater ease with which complex experimental questions can be addressed under controlled captive conditions, although a great deal of information about the natural history of the zebra finch has already been collated by prominent researchers such as Richard Zann (Zann 1996; Griffith & Buchanan 2010). This is especially true for the topic of personality. Up until the end of 2013, there have been almost thirty articles published which address personality in the zebra finch as a major topic (outlined in Table 1.1), but as of yet, all of this focus has been on individuals bred in captivity with no work conducted under natural conditions. One of the aims of my thesis was to test the validity and implications of captive personality research (both my own and the work of others) in wild zebra finch populations for the first time. Moreover, the zebra finch is a highly social species, with individuals rarely found on their own under natural conditions, instead they usually live and move around either in pairs or small to large flocks (as described in Chapter 2). For this reason, I set out to address questions relevant to the natural behavioural ecology of this species, with particular

focus on the relationship between personality and social behaviour, and their links to fitness. In the next section I will address the way these questions were framed in my thesis.

Table 1.1. A table illustrating all of the work published thus far on individual differences in behaviour (personality) in the zebra finch.

Personality trait(s)	Summary of findings	Reference
Confidence, Excitability, Sociability	Subjective observer assessments showed that ZFs display consistent individual behavioural differences in personality traits described in primates by Stevenson-Hinde & Zunz (1978).	Figueredo, Cox & Rhine (1995)
Activity, Exploratory behaviour	More active and exploratory ZFs were more likely to play the leader roles to food searching within randomly allocated pairs. Activity and exploratory behaviour were measured concurrently by adding an opaque partition to a home cage to separate pairs.	Beauchamp (2000)
Producer-scrounger tactic use	ZFs showed behavioural consistency in their choice of foraging tactics in mixed-sex flocks, though this result may have been influenced by dominance or more widely-accepted personality traits.	Beauchamp (2001)
Mate choice	Female ZFs displayed individual consistency in their male mate choice preferences.	Forstmeier & Birkhead (2004)
Foraging tactic use	ZFs with low foraging efficiency were more likely to scrounge during foraging and more likely to be bolder in their arrival time to the foraging grid. Individual dominance status failed to predict the other behaviours.	Beauchamp (2006)
Exploratory behaviour, Neophobia, Risk-taking behaviour	This study used artificially selected lines of ZFs that differed in the levels of corticosterone produced in response to a manual restraint stressor, finding that exploratory behaviour and risk-taking behaviour were related to the levels of corticosterone produced, but neophobia (fear of a novel object) was not.	Martins, Roberts, Giblin, Huxham & Evans (2007)
Neophobia, Social dominance	ZF nestlings were exposed to exogenous corticosterone. Individuals that received the treatment displayed reduced social dominance and decreased neophobia in males compared with controls.	Spencer & Verhulst (2007)
Neophobia (Food and non-food objects)	ZFs were subjected to one of two treatments, either testosterone injected into their eggs before hatching, or they were sham controls. T-treated individuals were quicker to habituate to a novel food object, while control males showed reduced neophobia in the presence of a non-food novel object.	Tobler & Sandell (2007)
Boldness, Neophobia, Exploratory behaviour, Activity	Individuals that were raised under nutritional conditions that were consistently high or low were bolder (a combined measure of neophobia and exploratory behaviour) but not more active than those whose conditions switched between high and low during ontogeny. In a separate test, corticosterone supplementation of nestlings was not found to affect their adult personality traits.	Donaldson (2009)
Exploratory behaviour	ZFs were raised under high or low quality nutritional conditions, then exposed to a period of nutritional restriction as adults. Subjects who were raised in low quality nutritional conditions were quicker to engage in exploratory and foraging behaviour.	Krause, Honarmand, Wetzel & Naguib (2009)

Personality trait(s)	Summary of findings	Reference
Exploratory behaviour, Leadership	The exploratory tendencies of ZFs were measured in both social and asocial contexts, finding males to be more consistent than females across these contexts. The exploratory behaviour of companions were found to positively affect the exploratory behaviour of focal individuals. The exploratory behaviour levels of individuals also affected their leadership behaviour in foraging dyads.	Schuett & Dall (2009)
Social behaviour	A social relations model was developed of ZF social behaviour by measuring four ethological factors: social proximity, social contact, social submission and social aggression. Individuals displayed consistent behaviour in their social disposition over a five year period.	Figueredo, Olderbak & Moreno (2010)
Exploratory behaviour, activity, neophobia, risk-taking behaviour, obstinacy	Five behavioural traits were studied in female ZFs and were found to be significantly repeatable. All traits except for obstinacy were found to be correlated with each other, implying the existence of a behavioural syndrome in this species (proactive/reactive). Proactive individuals were more likely to be socially dominant.	David, Auclair & Cézilly (2011)
Exploratory behaviour, Mate choice	The results of female mate-choice tests were found to be significantly correlated with exploratory tendencies, suggesting either that the variables are related or that the mate-choice apparatuses often used may have a confounded design.	David & Cézilly (2011)
Exploratory behaviour	ZFs with high levels of exploratory behaviour were found to be less successful at playing the producer foraging tactic and hence had lower feeding success in a social foraging trial.	David, Cézilly & Giraldeau (2011)
Exploratory behaviour	ZFs were raised under high or low quality nutritional conditions, finding that individuals that displayed high compensatory growth tended to have low exploratory behaviour as adults.	Krause & Naguib (2011)
Exploratory behaviour, Boldness	ZFs were found to explore a novelty environment more when alone rather than with social companions. Females were found to be more exploratory than males on average in both contexts.	Mainwaring, Beal & Hartley (2011)
Neophilia	Approach to novel objects was measured in ZFs and found to be repeatable, but not correlated to reproductive success, promiscuity and extrapair paternity rates. However, sex ratio manipulations were found to influence the correlations between neophilia and extrapair paternity.	Schielzeth, Bolund, Kempenaers & Forstmeier (2011)
Exploratory behaviour, Aggression	ZF parents with similar personalities were found to have greater reproductive success (nestling fitness) in a cross-fostering experiment than individuals with dissimilar personalities, with those pairings where both partners were highly exploratory and aggressive found to have the greatest nestling fitness.	Schuett, Dall & Royle (2011)
Exploratory behaviour	Intermediate or highly exploratory female ZFs were found to prefer highly exploratory males in a mate choice test, while females with low exploratory behaviour did not show a preference.	Schuett, Godin & Dall (2011)
Exploratory behaviour, Struggling rate	The exploratory behaviour and struggling rate of ZFs were measured and found to be repeatable short term but only exploratory behaviour was repeatable long term. Inter-individual differences in the short term stability of exploratory behaviour were also found.	David, Auclair & Cézilly (2012)

Personality trait(s)	Summary of findings	Reference
Activity, Exploratory behaviour, Neophobia, Reaction to startle	The breathing rate during handling of ZFs, a measure of handling stress, was not found to be correlated with a number of personality traits, including activity, exploratory behaviour, neophobia and reaction to startle (often considered a measure of boldness).	David, Auclair, Dechaume-Moncharmont & Cézilly (2012)
Activity, Exploratory behaviour, Neophobia, Reaction to startle	ZFs with low body condition and those that are more proactive in their personality profile were shown to express a higher motivation to feed following food deprivation. However, personality was not found to be significantly correlated with body condition.	David, Auclair, Giraldeau & Cézilly (2012)
Social information use	Individual differences in the tendency of female ZFs to rely more heavily on personal information or social information was found, suggesting it may be associated with an individual's personality.	Rosa, Nguyen & Dubois (2012)
Activity, Fearfulness	The relationship between cognition and personality was studied with a reversal learning task. Personality did not affect the initial learning of the task but more active and fearful ZFs re-learned the association cue faster.	Brust, Wuerz & Krüger (2013)
Neophobia	Nutritional stress during ontogeny was not found to affect subsequent adult neophobia.	Kriengwatana (2013)
Exploratory behaviour, Neophobia	Late-hatched ZFs from asynchronous broods were found to have higher exploratory behaviour, but not neophobia, as adults than early-hatched ZFs or those than came from synchronous broods. Females had lower levels of neophobia, but not exploratory behaviour, than males.	Mainwaring & Hartley (2013)
Aggressive-ness	Characteristics on the social environment ZFs experience during adolescence were found to affect their adult levels of aggressiveness and courtship.	Ruploh, Bischof & von Engelhardt (2013)
Exploratory behaviour	The exploratory behaviour of genetic and foster parents was measured in a cross-fostering experiment and compared with the exploratory behaviour of their offspring at adulthood. Offspring exploratory behaviour was found to be predicted by the exploratory behaviour of the foster but not genetic parents.	Schuett, Dall, Wilson & Royle (2013)

THESIS OUTLINE

Social behaviour in the zebra finch: is it linked to personality?

Although considerable research has been conducted on the wild zebra finch, little is known about the typical size and compositions of groups that individuals generally feed, drink, travel and congregate in, and whether the pair bond plays a major role in determining group characteristics. Thus, I addressed this question at Fowlers Gap by observing groups performing these activities particularly around dams (**Chapter Two**). Next, in captivity at Macquarie University, I sought to experimentally address the relationship between well-established personality traits in the zebra finch, in particular exploratory behaviour and activity, and social behaviour (**Chapter Three**). This work led to the assertion that the gregariousness or 'sociality' of an individual is repeatable in this species and may be quantified as a personality trait in its own right.

**The role of personality in zebra finch reproduction and fitness**

After establishing that sociality plays an important role in zebra finch behaviour, and may constitute a personality trait, the next goal was to search for the causes and consequences of personality in the life of the zebra finch. First, I examined the stability of a personality trait that we had earlier shown to be linked to sociality, activity, over the majority of individuals' lifespans, by comparing the attribute in very young nestlings (five to seven days old) to adults near the end of their typical lifespans (**Chapter Four**). Once I had established that personality traits are relatively stable, I investigated how personality in captive birds can affect an individual's fitness, by influencing its reproductive success and the impacts this might have on captive breeding programs and research (**Chapter Five**). For this work I focussed on exploratory behaviour, but in particular exploratory behaviour in a social foraging context reflective of the environment typically experienced by the zebra finch in the wild. Finally, I sought to address these questions at Fowlers Gap and measure

personality in the wild zebra finch for the first time (**Chapter Six**). In this work, I measured

exploratory behaviour in individuals briefly brought into captivity, and their use of feeders in the

wild using a PIT-tag monitoring system. From this data, I was able to estimate personality traits

such as exploratory behaviour and sociality and compare them with reproductive success at the
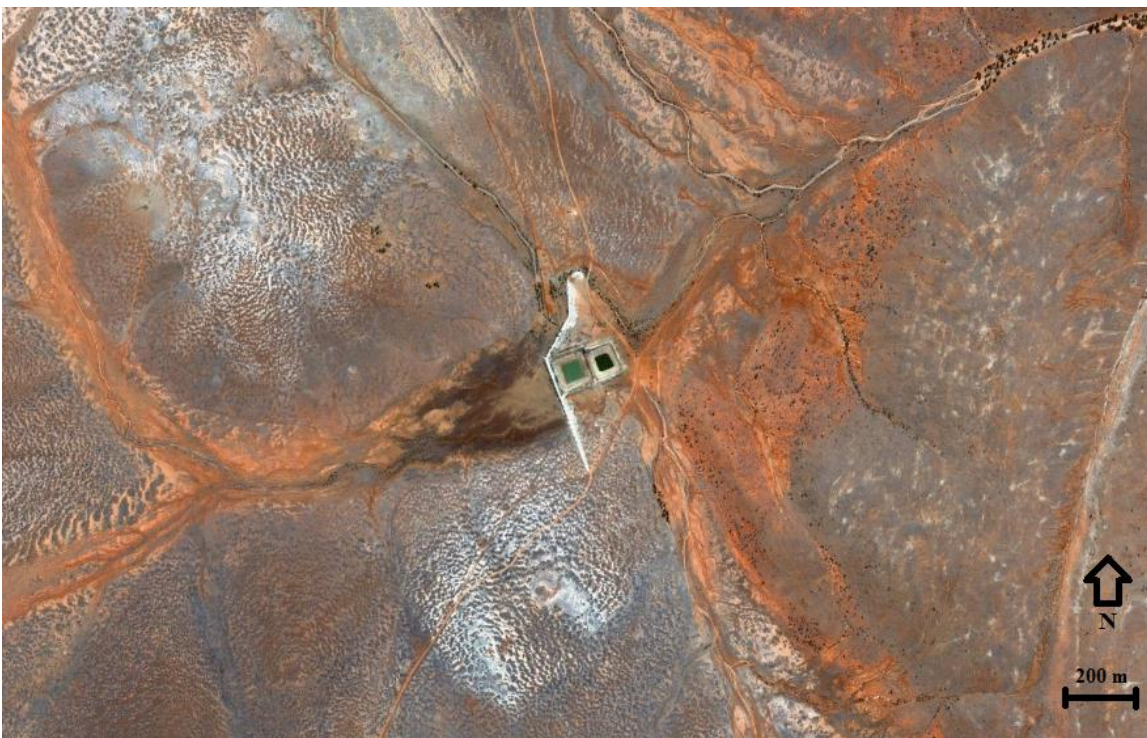
breeding colonies.

STUDY SITES

All fieldwork, as described in **Chapter Two** and **Chapter Six**, was conducted at Fowlers Gap Arid Research Station in western New South Wales, Australia in 2011 and 2012. Work was conducted at various locations at Fowlers Gap, with the two major study sites at Saloon (31º04'S, 141º50'E) and Sandstone (31º01'S, 141º41'E) illustrated in Figure 1.1 and Figure 1.2, respectively. Work has been conducted on the zebra finches at Fowlers Gap over the past ten years and this represents a typical wild population in ecology and behaviour (Griffith et al. 2008; Griffith et al. 2010).

Captive experiments were all conducted at the Department of Biological Sciences at Macquarie University, Marsfield, Sydney, NSW. The work focused on 50-100 zebra finches in indoor climate-controlled conditions or outdoors in sheltered aviaries. **Chapters Three to Five** focused on domesticated birds that were originally sourced from finch breeders in the Sydney area and had been maintained over several generations at Macquarie University.
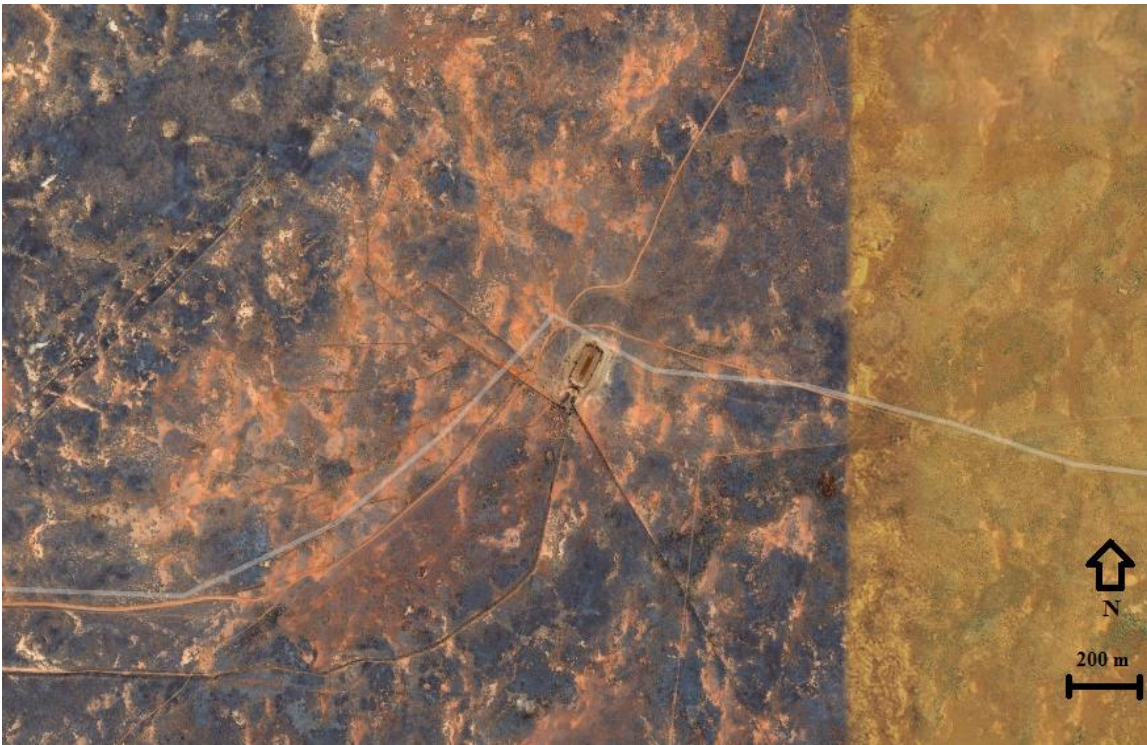
Figure 1.1: Aerial photograph of the study site at Saloon (Imagery © 2014 DigitalGlobe, Map data © 2014 Google), with the dam and adjacent southerly breeding colony shown near the centre.

Figure 1.2: The study site at Sandstone (Imagery © 2014 DigitalGlobe, Cnes/Spot Image Map data © 2014 Google) with the dam and adjacent northerly breeding colony shown near the centre.

Chapter Two

The social life of the zebra finch in the wild

Prepared as:

ABSTRACT

Despite the zebra finch being used as a model species in behavioural science, the size and composition of social groups that individuals typically live and move around in in the wild is not well described, which may affect the outcomes of experimental work in captivity. For this reason, we observed the group size and composition (sex) of free ranging zebra finches in areas adjacent to good breeding habitat and near semi-permanent water sources. We found that individuals most commonly foraged, watered and travelled around the colonies in groups of two, the overwhelming majority of which (94.2%) were mixed-sex, which most likely reflected sexual partnerships (pairs), or in larger groups of 3-10 individuals, with relatively few observations of groups larger than this observed. These observations indicate the central importance of the pair bond in the social life of the zebra finch, even during periods outside of active breeding. We also saw very few single sex groups and no large single sex groups in contrast to the way in which they are often housed in captivity. Our results suggest that researchers working on captive zebra finches should attempt to keep individuals in pairs or small social groups to best emulate the social environment they generally experience in the wild.

INTRODUCTION

The zebra finch is used as a model species to study a wide range of questions in behavioural science (Griffith & Buchanan 2010). However in laboratory populations, the social context in which individuals are kept and in which experimental work is conducted is determined largely by the set-up of the cages or aviaries, and the design of experimental protocols. As a result, it is relatively difficult to develop a good understanding of the social nature of this species by studies conducted in captivity. Yet, such understanding can be crucial, as ignoring the species' social requirements may in some cases lead to drastically different results (Vignal et al. 2004). Both scientific and welfare outcomes will be improved with a better understanding of the nature of sociality in this species. In particular, because of the unique ecological pressures of arid Australia (Zann 1996), some aspects of the zebra finch sociality are likely to differ from that of Northern hemisphere species, which the great majority of researchers working on captive zebra finches are most familiar with, and routinely observe in the wild.

Perhaps because the sight is so impressive, the most widely popularised images/ films of the zebra finch are of the congregations of thousands visiting waterholes to drink. However whilst such aggregations do occur, these are typically during drought conditions at the last remaining water sources (Zann 1996), and do not represent the typical social structure, particularly during reproductive activity. These extremely large aggregations of zebra finches are a product of the mobility of the species and the harsh conditions of the Australian arid zone. Zebra finches are very well adapted to the arid grasslands of Australia in which resources are extremely variable due to the unpredictability of rainfall both spatially and temporally (Morton et al. 2011). Breeding patterns are intricately linked to rainfall patterns due to the presence of green vegetation and grass seed in the environment (Zann et al. 1995; Zann 1996; Allen & Hume 1997). Group existence may be particularly relevant for the ecology of the species, and the scarcity of the resources zebra finches require, such as grass seeds and water, may select for group-living and the social coordination of

knowledge (Rubenstein & Lovette 2007; Silk 2007), with social information and networks utilised for the discovery of resources such as food (Beauchamp & Kacelnik 1991; Benskin et al. 2002; Aplin et al. 2012; Mariette & Griffith 2013).

Gregariousness, or sociality, has been shown to vary between species (Goodson & Kingsbury 2011). In some animal species, individuals live very much alone outside the breeding season, but in others they tend to live in mixed-sex groups or single-sex groups (Shannon et al. 2008). Departure from these species-specific social environments in captivity, especially when this occurs early in life, may influence individuals' behaviour, sometimes throughout their life. For example, the social environment individuals experience during adolescence has been found to influence several factors, such as song learning and sexual imprinting (Bischof 1997), pairing success (Mariette et al. 2013), the structure of the brain (Buwalda et al. 2011), responses to gonadal steroids (Sanz et al. 2008), the complexity of the prefrontal cortex (Radley et al. 2008), and levels of aggressiveness, anxiety and stress behaviour (Sachser et al. 2013). In captivity, the social environment individuals experience may influence welfare; male pigs *Sus scrofa* that were kept in mixed-sex groups were shown to exhibit greater welfare than those kept in single-sex groups, while in females the pattern was reversed (Boyle & Bjorklund 2007). In the zebra finch, males reared in mixed-sex pairs showed reduced aggression and courtship behaviour and higher initial attractiveness to females compared with males reared in mixed sex groups (Ruploh et al. 2013). In contrast, individuals that develop in mixed sex groups, rather than in pairs, tend to socially integrate more readily and easily (Ruploh et al. 2014).

There have been several studies of breeding colonies of zebra finches over either a single or multiple years. In seven separate past studies at ten different colonies around Australia, typical observed colony sizes ranged from 24-229 adults during breeding periods and 24-350 during non-breeding periods, with the size of the colonies fluctuating over time in response to resources and the movement of birds in and out (Frith & Tilt 1959; Immelmann 1962; Kikkawa 1980; Zann & Straw

1984; Zann 1994; Zann et al. 1995; Zann 1996). Moreover, in a recent study at Fowlers Gap, NSW, again the total size of the breeding colonies studied fluctuated across years (between 4 and 136 pairs) (Griffith et al. 2008; Mariette & Griffith 2012). In this latter study, the initiation dates of nests within the broader colony suggested that small groups of pairs were coordinating their activity with each other, and possibly even arrived in the breeding area together (Mariette & Griffith 2012). Zebra finch pairs have been described as 'inseparable', with males tending to lead females around breeding colonies during non-breeding periods and females leading males during breeding periods (Birkhead et al. 1988; Zann 1996). This data hints at how individuals operate at a social level within the colony, but this has not been the focus of specific study to date.

In our study we investigated variation in group size and composition both at semi-permanent dams in breeding areas and in the surrounding foraging habitat, using focal observations and transects (random walks) respectively. Our intent in this study was to characterise the social life of the zebra finch under normal conditions, in its sedentary phase.

METHODS

Dam observations

Observations were made at two semi-permanent artificial dams at Fowlers Gap Arid Research Station in September and October 2011, a period during which breeding normally occurs at these sites (Griffith et al. 2008), but did not occur at this time in 2011, possibly because of the absence of winter rain or an unusually high nest predator abundance (rodents and snakes). Artificially-created dams frequently feature in arid/semi-arid Australia to provide water for livestock, however, they may temporarily dry up during long periods of drought. These dams contain water for livestock and are relatively permanent. In total there were nine observation sessions at the 'Saloon' dam and six at

the 'Gap Hills' dam, c.a. 20 km away. All six of the observation sessions at Gap Hills were made by a single observer, while five were made by a single observer at Saloon, and four by two observers simultaneously at opposite corners of the dam (Gap Hills dimensions: 200 x 150 m). The position of the observers differed between trials, and there was not necessarily an observer sitting in the corner nearest the breeding colony. All but two of these observation sessions were made in the morning starting between 7 a.m. and 9:15 a.m. and running from one to three hours. In addition, one observation session occurred over the midday period, and one in the early afternoon. Both dams were large and it was unlikely that both observers would see the same movements of subjects from their different positions, especially since observers focused mostly on groups arriving to their side of the dam, near where they were sitting (this was also the case for observation sessions with only a single observer). To control for any overlap, in the six cases that both observers made a similar group sighting within the same 30-second period, one of these sightings was deleted from the final dataset at random, resulting in 414 total sightings from a total of 39.5 hours of observations. In total, between three and 56 sightings were made per session. During each observation session, observers sat on the rise above a corner of the dam and watched through either a telescope or binoculars all movements of zebra finches that they could see (or when there were two observers, those movements that occurred near their area of the dam preferentially). For each sighting we recorded the time, the number of individuals moving together (during both dam and transect observations individuals were defined as part of one group if they moved in the same direction when in flight, and had a maximum nearest neighbour distance of one metre), the sex of these individuals if it could be determined visually, whether they were 'arriving', 'leaving' or 'passing over' the dam, and which compass direction they were moving (e.g. from the north-west to the dam). In a number of cases, the direction of movement or sex of the focal individuals was not noted, and these sightings were retained in the overall dataset, but were not used in analyses referring to those parameters.

Transect observations

All five transect observation sessions were performed at different locations at Fowlers Gap Arid Research Station over a three-day period in April 2012. The location name, distance, number and mean group size of sightings recorded during each transect are noted in Table 2.1. The location and direction of each transect was chosen to cover a range of different habitats adjacent to areas in which zebra finches visit water and have bred previously (Griffith et al. 2008). Each transect followed a path that returned to the starting point for logistical reasons (to get back to a vehicle), with the minimum linear distance between any two transects of 4.2 km and the maximum 15.3 km. The widths of the transects varied from the narrowest transect at 300 m up to 1.7 km. Each transect session was performed in the morning except for the Home Paddock transect, which was performed in the afternoon, and took between one to three hours to complete (variation in duration occurred due to the differing distances of the transects, the difficulty of the terrain and the number of sightings recorded). During each transect, whenever an individual or group of zebra finches was seen, the time, number of individuals in the group, sex of these individuals, and their behaviour was noted. Three broad categories of behaviour were noted: 'flying', when individuals were first observed in flight, 'foraging' when individuals were initially disturbed or noticed foraging on the ground and 'perching' when individuals were observed perched in bushes or trees. Only three of the sightings included juveniles, which was consistent with the lack of breeding at this site across the spring and summer leading up to these observations. As a result, these sightings predominantly reflect social associations between independent adults rather than between adults and dependent offspring or juveniles.

Table 2.1: Details of the locations, distances and number of sightings made during each transect at Fowlers Gap Arid Research Station, along with the mean group size of those sightings. The mean group size of sightings where the three behaviours 'flying', 'foraging' or 'perching' are also listed, with the number of sightings these means were calculated from listed in brackets. Overall means are weighted by the respective sample size at each location.

Name	Total distance (km)	Number of sightings	Mean group size	Flying mean	Foraging mean	Perching mean
Connor's Creek	2.93	13	3.692	-	2.667(3)	3(3)
Saloon	5.01	21	4.429	4(11)	5.857(7)	2(1)
Gap Hills	5.14	32	4	3.25(8)	5(7)	4.462(13)
Home Paddock	2.78	8	5.875	2.667(3)	-	2.667(3)
Sandstone Tank	6.34	25	4.48	2(1)	4.636(11)	4.75(12)
Total/Mean	22.2	99	4.323	3.478(23)	4.821(28)	4.188(32)

Statistical analyses

All statistical analyses were performed in IBM SPSS v22.0 (IBM Corp 2012). For dam and transect sessions separately, we examined plots of the relationship between the time of the day sightings were made and group size per sighting and calculated Pearson correlation coefficients to examine whether group size varied in a linear manner with time of day. We also split all the sightings into hours (7-8 a.m., 8-9 a.m. etc) and conducted two independent-samples Kruskal-Wallis tests for the dam and transect observations separately to look for variation in mean group size depending on the time of day. Next, we calculated the mean and range of the number of individuals per sighting. To determine whether sightings with a group size of two were likely to consist of one male and one female, we conducted exact binomial tests on the dam observations and transect observations

separately for all observations where the sexes were identified. Similarly, to determine whether odd or even groups size were more likely to occur, we conducted exact binomial tests on the dam observations and transect observations separately, both with all possible group sizes, and with only group sizes of three or greater. For the dam observation dataset, we ran a generalised linear model with poisson error structure, with group size as the dependent variable, and the time of day as a fixed covariate term and location (i.e. Gap Hills or Saloon), date and direction of flight (arriving at, leaving or passing over the dam) as fixed factorial terms. Similarly, for the transect observation dataset, we ran a generalised linear model with poisson error structure, with group size as the dependent variable, and the time of day as a fixed covariate term and location, date and behaviour being performed ('flying', 'foraging' or 'perching') as fixed factorial terms. We did not include any interactions between terms in either model, due to insufficient statistical power. An independent-samples Kruskal-Wallis test was conducted to compare group size of the dam observations and transect observations. Finally, a further independent-samples Kruskal-Wallis test was conducted to compare three groups from all transect and dam sightings: where groups were flying, where groups were foraging and where groups were perching.

RESULTS

For both the dam and transect observations, the most common group size encountered (including a 'group size' of just a single individual) was two (as shown in Figure 2.1 and 2.2). For the dam observations, there was a mean group size from all observations of 2.9 (SD = 2.36, range = 1 – 21, $N = 413$), and a median and mode group size of 2, and for the transect observations, a mean group size of 4.3 (SD = 3.63, range = 1 – 23, $N = 99$), a median of 3 and a mode of 2. For both the dam and transect datasets, observations with a group size of two, and where the sex of the individuals were identified, were more likely to consist of one male and one female than would be expected by

chance (dam observations: exact binomial test, one male and one female = 59, other = 5, P < 0.0001; transect observations: exact binomial test, one male and one female = 39, other = 1, P < 0.0001). Moreover, all (100%) of the 10 dam and 21 transect observations of group sizes of three or larger, and where the sex of individuals was recorded, were mixed sex groups. Hence, there were no single sex groups of three or more individuals observed, and only 6 out of 104 (5.8%) of groups of two. For both the dam and transect observations, we found that even group sizes were significantly more likely to occur than odd group sizes (dam observations: exact binomial test, odd = 157, even = 256, P < 0.0001; transect observations: exact binomial test, odd = 26, even = 73, P < 0.0001), however this effect disappeared when group sizes of one or two were removed from the dataset (dam observations: exact binomial test, odd = 71, even = 70, P = 1.000; transect observations: exact binomial test, odd = 21, even = 31, P = 0.212). There was no apparent linear effect of the time of day sightings occurred on group size for either the dam observations (r = -0.40, N = 413, P = 0.415), or the transect observations (r = 0.105, N = 99, P = 0.300). We also did not find any significant variation in group size depending on the time of day (when comparing between one-hour periods) for either the dam (H_8 = 4.774, P = 0.781) or transect observations (H_7 = 5.686, P = 0.577). For the dam observations, there were no significant differences in group size found depending on the direction of travel (whether birds were 'arriving' at, 'leaving', or 'passing over' the dam) or the time of day (Table 2.2). However, there was a significant effect of both location and date on group size, with a higher mean group size recorded at Saloon dam (mean = 3.2, SD = 2.74, N = 243) than Gap Hills dam (mean = 2.4, SD = 1.56, N = 170) (Table 2.2). The different mean group sizes on different dates varied from 1.71 to 5.25 and are shown in Figure 2.3. For the transect observations, there were no significant differences in group size that were related to the behaviour recorded ('flying', 'foraging' or 'perching'), the time of day, the date or the location (Table 2.3). There was a significant difference between the transect group sizes and the dam group sizes (U = 14328, P < 0.0001), with a greater mean group size recorded during the transect observations than the dam observations. When all dam sightings were collated with the transect 'flying' group (as all of these

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sightings were of groups in flight), we found a signficant effect of group size on the type of behaviour being performed (H_2 = 18.799, P < 0.0001). From pairwise comparisons we found that the mean score for group size during the 'flying' condition (mean = 2.9, SD = 2.31, N = 431) was signficantly smaller than either the 'foraging' (mean = 4.8, SD = 3.81, N = 28; H_2 = -91.837, P = 0.002) or 'perching' conditions (mean = 4.2, SD = 3.17, N = 32; H_2 = -70.448, P = 0.014). However, the 'foraging' condition did not significantly differ from the 'perching' condition (H_2 = 21.388, P = 1.000).

Table 2.2: Summary of a Generalised Linear Model examining variation in the observed group size during dam sightings in relation to the direction of travel (arriving, leaving or passing over the dam), time of day, date and dam location. Date was nested within the dam location in our model, as the dam was never observed at both locations on the same day.

Explanatory term	Df	X^2	P value
Direction of travel	2	4.569	0.102
Time	1	3.523	0.061
Date	13	70.185	<0.0001
Dam location	1	12.415	<0.001
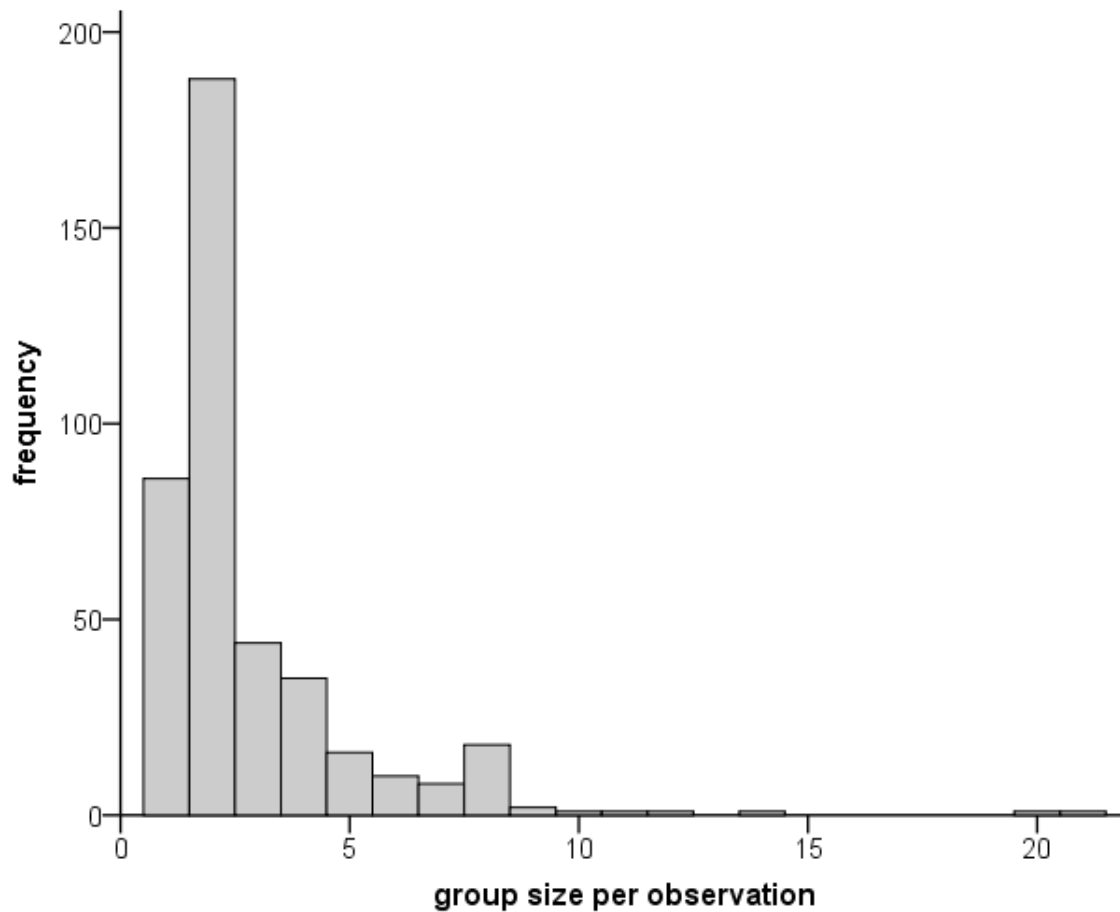
Figure 2.1: Histogram illustrating the frequency that different group sizes were observed for all dam observations.

Table 2.3: Summary of a Generalised Linear Model examining variation in the observed group size during transect sightings in relation to the behaviour being performed (flying, foraging or perching), time of day, date and location. Location was nested within date in our model, as some transects at different locations occurred on the same day.

Explanatory term	Df	X^2	P value
Behaviour	2	5.387	0.068
Time	1	1.767	0.184
Date	2	1.201	0.549
Location	4	7.812	0.099
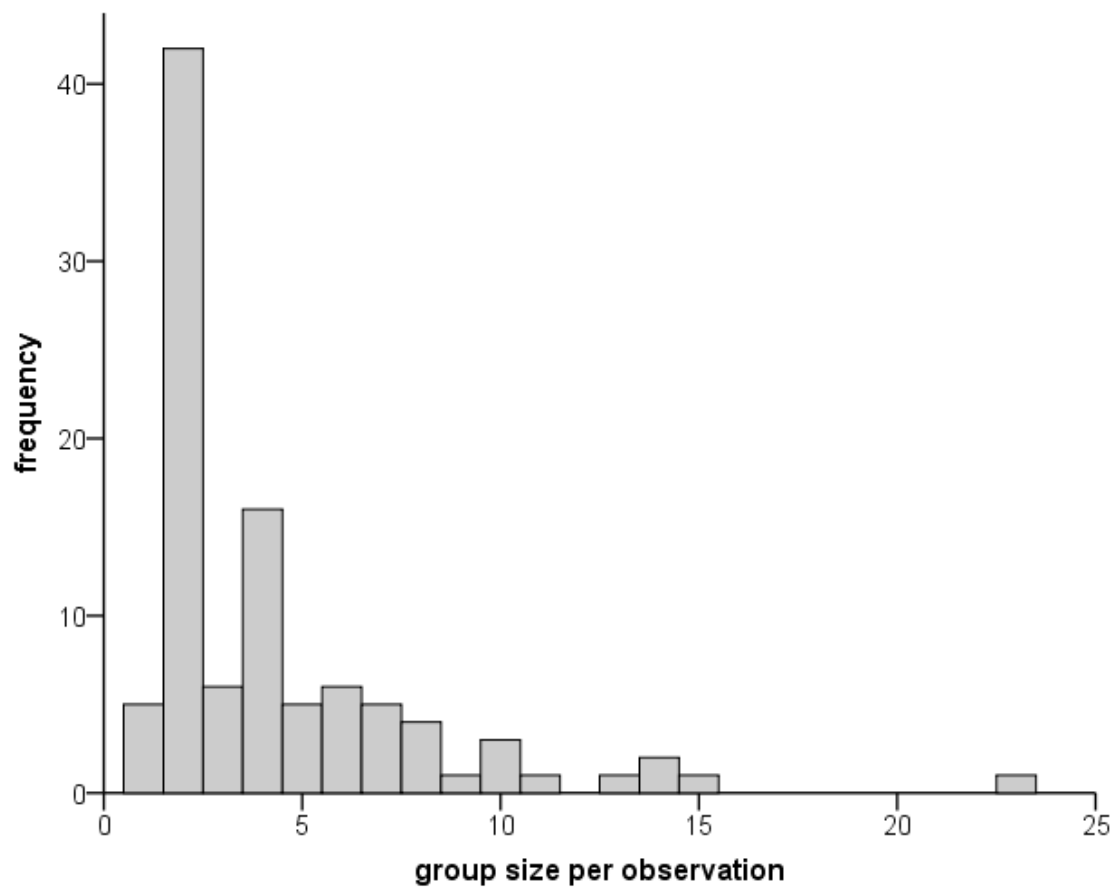
Figure 2.2: Histogram illustrating the frequency that different group sizes were observed for all transect observations.
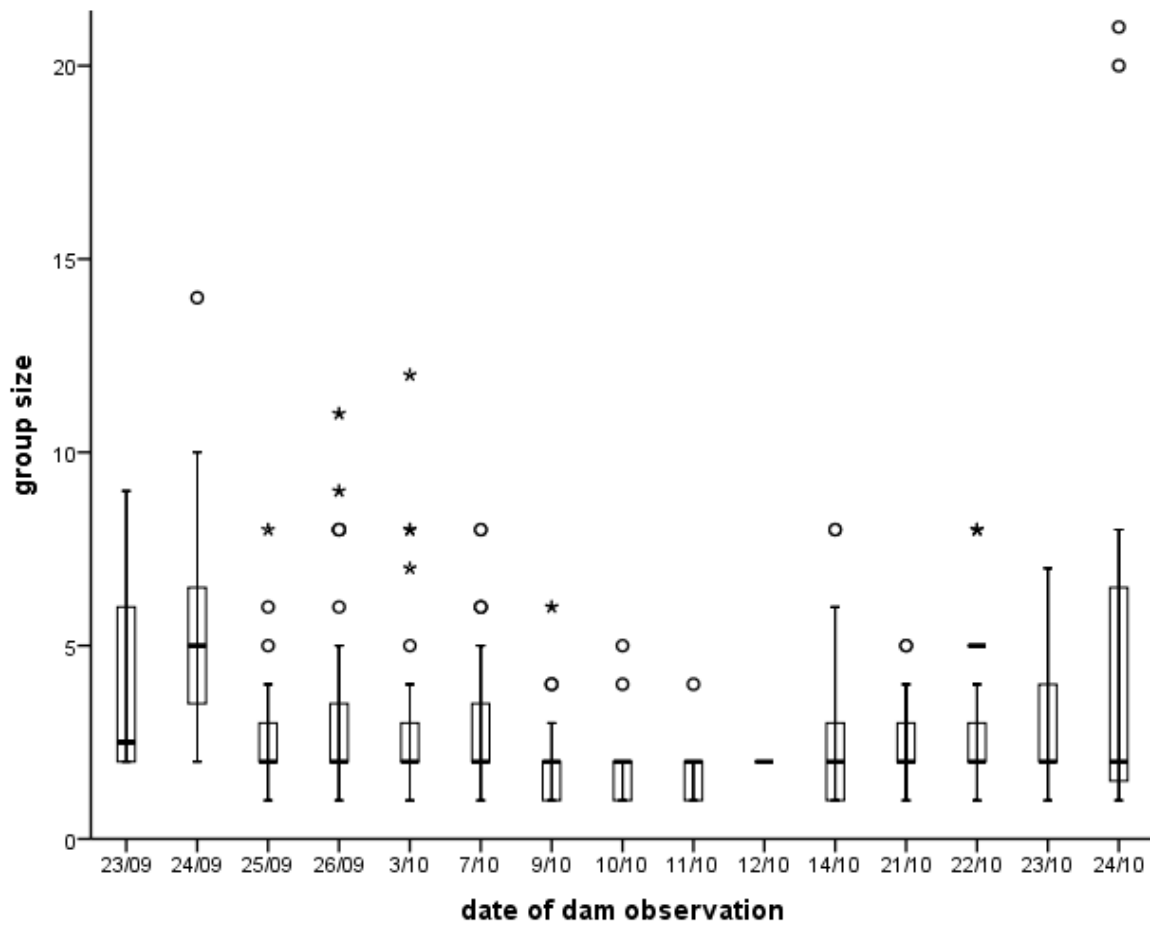
Figure 2.3: The relationship between the date that dam observations were made and group size per sighting. Outliers are denoted with circles if they are farther than 1.5 interquartile ranges yet closer than 3 interquartile ranges from the nearer edge of the box, and a star if they are farther than 3 interquartile ranges from the nearer edge of the box.

DISCUSSION

Whilst Immelmann (1965) characterised the zebra finch as highly nomadic and typically occurring in large aggregations, our findings support Zann's assertion that this is a mischaracterisation of the species (Zann 1996). Our data suggest that under normal sedentary conditions zebra finches are typically found in much smaller groups, with the pair (a male and female together) as the primary social unit. Slightly larger groups do occur as pairs or individuals cluster together in the environment when visiting water, foraging, or simply sitting in bushes or trees in slightly larger social groups (here these were limited to a few groups of around 20 individuals together). Individuals were rarely observed on their own, except when flying from the nearby colony to the dam, often to join a "social tree" near the water (Zann 1996). We did not record group size when drinking from the actual dam water itself, and groups rarely flew directly to the water's edge from the colony (which was at least a few metres from the nearest cover), but instead congregated in the vegetation around the dam before drinking. However, we observed that generally individuals did not drink alone, although one individual tended to lead the others to the water in many cases only to be joined soon after by others from the nearby social bush. Often groups spent long periods of time in these bushes around the dam, hence, the dam may function as a kind of 'social hotspot', where individuals come both to drink and socialise. The numbers seen here in this work at Fowlers Gap are fairly characteristic of the social group size that has been observed at this location over a longer period of study (Griffith et al. 2008; Mariette & Griffith 2012), through both breeding and non-breeding periods. Furthermore, consistent with earlier work, our study has again highlighted the degree to which the male and female are intimately associated with one another. Previous work at this same site using passive transponder tags to record individuals at both feeders and nest sites has found that the pair are together for most of the time whether actively breeding or not (Mariette et al. 2011; Mainwaring & Griffith 2013). Moreover, males have often been observed to lead their female

partners through their home colonies (Zann 1996). Whilst we were unable here to confirm that these pairs of males and females were sexual partners, the high incidence of mixed sex pairs relative to single sex pairs suggests that it is the sexual partnership rather than simply the group size of two that is the foundation of social behaviour in this species. Our observations here again indicate the strength of the pair bond between males and females, which are long-lasting (Adkins-Regan 2002; Adkins-Regan 2009) and faithful (Griffith et al. 2010). It is worth noting that these data were taken during an extended period of non-breeding and again this reflects the importance of the sexual partnership even outside of the reproductive season.

The mean and range of group sizes that are adopted for different tasks such as foraging or drinking in a species or population may be influenced by a variety of factors. Some work has been conducted on the physiological mechanisms producing and maintaining different group sizes in estrildid finches, with nonapeptide systems found to encode for social attractiveness or aversion and modulate anxiety-like behaviour (Goodson & Kingsbury 2011). However, the lower mean group size we observed for the dam observations in comparison to the transect observations is more likely to be related to environmental or behavioural factors, which is further emphasized by the significantly lower group sizes noted overall for groups in flight (which included all dam observations) compared with groups that were foraging or perching in a bush or tree. The level of risk of predation has been shown to influence not only choice of foraging site (Suhonen 1993), but also group size (Beauchamp 2004), with increasing group size generally decreasing predation risk due to the processes of earlier predator detection and/or risk dilution (Krause & Ruxton 2002). With increasing group size, individuals are also able to spend less time scanning their environment for predators (vigilance) and therefore can devote more of their time to foraging (Beauchamp 2013). This may have led individuals to prefer to perform certain behaviours (such as foraging or perching) in larger group sizes than other behaviours (such as flying or activity at the dam). As drinking is a relatively quick activity to perform compared to foraging, this may have reduced individuals' concern for performing the activity in a group any larger than just with their partner, as the risk of

predation is low. The two dams were also very close to the colony (<100m), so pairs and even single individuals could travel back and forth quite safely, which they may be more reluctant to do over the larger distances that the transects covered away from the colonies (up to 2km). In contrast, the difference between mean group sizes at dams and on transects may have occurred due to the relative lack of cover at the dam biasing the results by making smaller groups easier to observe, or similarly smaller groups in flight may have been easier to notice than those in amidst vegetation. Moreover, the transect observations and dam observations were performed six months apart, hence, there may simply have been more individuals in the area in April when the transect observations were performed, which may have affected mean group size. Another factor that may affect group size is the time of day. In many small passerines, body mass tends to increase over the course of the day in line with short-term fat reserves that will last through the night and be depleted by the morning, resulting in decreased flight performance and take-off speed (Metcalfe & Ure 1995; Gentle & Gosler 2001). This may result in changes in real or perceived predation risk, which may influence the preferred group size individuals congregate in, with larger group sizes often predicted to be favoured later in the day (Metcalfe & Ure 1995; Gentle & Gosler 2001). Variations in group size throughout the day could also occur due to larger groups of individuals heading to the water to drink during the hottest part of the day, or fewer birds may be active during the hottest part of the day, skewing the mean group size in one direction or another. Despite this we did not find any evidence that larger group sizes were more likely to occur later in the day for either the dam or transect observations, although our power to detect such a difference was weak given that most sampling was conducted in the morning.

In the zebra finch, the different group sizes may vary depending on attributes of each individual. Individual zebra finches have been shown to receive differing amounts of social attention, contact and aggression depending on a variety of attributes, such as their sex, dominance status and kinship (Figueredo et al. 2010). Different groups may be made up of individuals of different personality types and this may influence the dynamics and behaviour of the group

(Coleman & Mellgren 1994; Dyer et al. 2009; Mainwaring et al. 2011). Several studies have found that groups with individuals of similar personality types were more effective at coordinating behaviour resulting in increases in fitness (Both et al. 2005; Schuett & Dall 2009), and it is also conceivable the different group sizes tend to be preferred by different personality types, resulting in a range of different group sizes.

Despite a modal preference for a group size of two (which made up 45% of dam observations and 42% of transect observations), most likely reflecting sexual partnerships, observed group sizes around colonies ranged from a single individual up to 23 birds in one group. We found that mean group size at the Saloon dam were significantly larger than at the Gap Hills dam. This was likely driven by several large groups leaving or passing over Saloon dam. The reason that this occurred at Saloon but not Gap Hills might have been due to the presence of particularly popular social trees where individuals could congregate before leaving the dam at one end and the location of the dam on a flight path to a distant food resource. No single sex groups of more than two individuals were observed, and most of these groups consisted of roughly equal numbers of males and females, which suggests larger groups also tend to be composed of sexual partnerships congregating or travelling together. There was also a peak of four individuals per group in the transect data suggestive of groups of two pairs travelling together. Hence, it seems that in many cases there were alliances between a few sets of partners with them hanging around in small groups of between four and about ten. This suggests that individuals may form social bonds with just a small number of other individuals. This idea is consistent with the previous findings of reproductive coordination between just a few pairs (Mariette & Griffith 2012). This knowledge of zebra finch behaviour may prove useful in improving the amenability of this species in captive or domesticated populations. Our results show that zebra finches are highly social, rarely occurring in the wild on their own, and spend most their time moving around with their partner or in small mixed-sex groups which likely contain several pairs. This contrasts with the way zebra finches are often kept in captivity, where individuals are maintained on their own or in single-sex groups for long periods of

time to prevent unwanted breeding (Zann 1996). Moreover, for experimental reasons individuals are often allocated certain partners rather than being allowed to choose their own (Griffith & Buchanan 2010) and switched between many different partners over time. These fairly ubiquitous patterns of husbandry are somewhat at odds with the typical social context of the wild zebra finch. Interestingly, a few recent studies have investigated the extent to which the social rearing environment (mixed sex groups versus mixed or single sex pairs) affects the development of captive zebra finches. Males reared during adolescence in mixed sex groups appeared to be better at and showed less stress when socially integrating with conspecifics (Ruploh et al. 2014). However, they showed less courtship and aggressive behaviour and lower attractiveness to females than either males that grew up with another single male, which showed a medium level of these attributes, or males that grew up with a single female, which displayed the highest levels of these traits (Ruploh et al. 2013). Mariette et al. (2013) found that males reared in mixed rather than single sex dyads as juveniles had more complete courtships, though adult pairing success was reduced in individuals that failed to pair with juvenile females, due to a winner and loser effect. Rearing individuals from a young age without the presence of an adult male causes auditory perceptual deficits (Sturdy et al. 2001), which is likely to result in difficulties in social integration and reproduction for these individuals when they reach adulthood. Therefore, both the size and sex composition of groups experienced during early life appear to be able to influence an individual's subsequent adult reproductive and social behaviour. For this reason, it must be considered whether altering the usual natural patterns of behaviour may influence the results of experimental studies. Social isolation in social species has been shown to increase baseline stress levels which may influence experimental results, and in their recent work Perez et al. (2012) found that social isolation caused elevated levels of corticosterone in captive zebra finches. We believe that a greater understanding of the typical social life of the wild zebra finch will improve the design of future work on areas of personality, physiology, communication and even neurobiology of this important model species. In addition it may help us to better understand and interpret work that has been conducted to date. To date, it is

difficult to evaluate the effect of maintaining zebra finches in quite unnatural social contexts (such as large single sex groups) for long periods, but we believe that such work should be done, and recent work on the development of social skills in juveniles provides some important guidance (Mariette et al. 2013; Ruploh et al. 2013; Ruploh et al. 2014).

Chapter Three

Active but antisocial: exploration and activity is linked to social behaviour in a colonially breeding finch

ABSTRACT

The existence and fitness advantages of animal personality are currently a focus of major interest in behavioural ecology, with particular attention focused on the proactive-reactive axis, which can be assayed in individually-held captive animals, and is expected to relate to the food-finding skills of different individuals. However, another largely neglected component of foraging behaviour will be an individual's propensity to move and feed alongside others. We monitored the foraging behaviour of male and female captive zebra finches in large social groups in large enclosures using a PIT-tag system, and also separately assayed activity levels in a home cage with a social partner. We found that more active individuals found novel feeders more quickly in a large environment and more active males fed less socially than inactive birds. Furthermore, more active females made more leader visits to feeders in the large social environment. Our findings suggest that variation in foraging behaviour in the zebra finch is driven by social factors as well as individual variation in exploration. Some individuals are very active but asocial, whilst others are less active but more social. This work suggests that degrees of sociality – the intrinsic propensity with which individuals interact with and coordinate their activity with other conspecifics – is an important component of personality that contributes to consistent differences in behaviour among individuals, and needs to be accounted for in future work in social animals.

INTRODUCTION

Early work on foraging behaviour mostly focused on the perspective of the independent individual (Giraldeau & Caraco 2000), and most recent studies of personality have continued this theme through the use of the 'open-field' test and a number of other assays to measure the personality of individually held animals (David et al. 2012a; Dingemanse et al. 2002; Webster & Ward 2011). These tests have uncovered the existence of two different coping styles or behavioural types across a broad range of species (Koolhaas et al. 1999). Proactive individuals are more active, exploratory, risk-taking and less neophobic than reactive individuals (Coppens et al. 2010; David et al. 2011a). These behavioural syndromes have been linked to productivity, reproductive success and fitness (Biro and Stamps 2008; Smith & Blumstein 2008). Furthermore, they are heritable and may be maintained by fluctuating or frequency-dependent selection in the wild (Dingemanse & Wolf 2010; Dingemanse et al. 2004; Höjesjö et al. 2004). One species which has been studied extensively both in captivity and the wild, is the great tit. Not only has a behavioural syndrome among personality traits such as activity, exploration and boldness been uncovered (Verbeek et al. 1994), but these traits have also been linked to survival and breeding success in the wild (Dingemanse et al. 2004). However, although assays that focus on individually held-animals are useful for investigating an individual's personality attributes such as general activity levels and their ability to find food but they ignore the social interactions that occur under more natural conditions. This oversight is particularly relevant in a highly gregarious colonial species like the zebra finch (*Taeniopygia guttata*), as in this species foraging and other behaviours are usually performed in a social context (Zann 1996). Moreover, it has been postulated that consistent behavioural differences may evolve as a result of individuals attempting to fill different social niches (Bergmüller & Taborsky 2010), which further emphasizes the importance of investigating the role of sociality in personality.

The zebra finch is a nomadic estrildine that feeds almost exclusively on the seeds of grasses that are patchily distributed in the environment (Zann 1996). Individuals travel in feeding flocks that vary in size from a few individuals up to hundreds of birds depending on the time of year and region that they inhabit. In a captive setting, new residents in an aviary tended to follow prior residents to a previously established food patch (Beauchamp 2000a), and this pattern is likely to be similar in the wild, with new residents in an area often relying on the environmental knowledge of previous residents. Breeding density is variable, with most individuals attracted to the presence of conspecifics when choosing a breeding site (Mariette & Griffith 2012). However, inter-individual variation is high, with some individuals consistently choosing to breed away from conspecifics, indicating the presence of different breeding strategies with respect to sociality (Mariette & Griffith 2012). This variation may reflect an underlying difference between individuals in their levels of social attraction, potentially mediated by differences in neural or endocrinal characteristics (Goodson et al. 2009). Furthermore, solitary breeding individuals have been found to be quicker at discovering experimental food patches than colonial individuals (Mariette & Griffith 2013). This is the opposite outcome to that predicted under the 'information center hypothesis' (Brown 1988), which suggests that coloniality decreases food-searching time due to individuals obtaining information about the location of food patches from successful foragers in the colony. A possible explanation for this incongruity is that solitary and colonial breeders, or individuals that are generally more or less social, differ in their foraging abilities or strategies, perhaps driven by a difference in their personality. Therefore, rather than coloniality resulting in a decrease in food-searching time for all individuals, solitary breeders may be intrinsically better foragers than colonial breeders, or more suited to solitary food-searching, or prefer to feed on different types of food patches than colonial individuals, and hence employ a different breeding and foraging strategy (Barta & Giraldeau 1998). This 'difference in individual quality' viewpoint is supported by individual breeding success, with some experimental evidence suggesting that solitary breeders in a wild context are more effective at optimally adjusting the food provisioning rate to their offspring in

response to differences in brood size (Mariette & Griffith 2013). Sociality in a breeding context has previously been linked to personality in the barn swallow (*Hirundo rustica*), with more socially tolerant and less neophobic individuals preferring to breed in the largest colonies (Dardenne et al. 2013).

A few studies have attempted to address the influence of social behaviour by measuring the personality of individuals in a social group. There is some limited evidence that in social species more active, risk-averse or exploratory individuals tend to spend more time alone (Beauchamp 2000b; Budaev 1997), and tend to take on the leadership role when approaching new food patches (Kurvers et al. 2011; Schuett & Dall 2009). In the zebra finch, proactive females are more likely to be socially dominant in within-group competition (David et al. 2011a). On the other hand, social dominance apparently fails to predict leadership in food-searching behaviour (Beauchamp 2000b). Less exploratory zebra finches have been found to spend more time with a social partner at a risky feeder than highly exploratory individuals, suggesting that these individuals are more social in a risky foraging context (Schuett & Dall 2009). Moreover, in small captive social groups more exploratory zebra finches were found to be less effective at finding food (playing the producer tactic) within a food patch (David et al. 2011b). Personality has also shown to influence social learning and cognition, with more active and fearful zebra finches relearning a cue-reward association faster than less active and fearful individuals (Brust et al. 2013). Moreover, individuals with different behavioural types may rely on social information to a differing extent depending on their sensitivities to environmental and social cues (Benskin et al. 2002; Katz & Lachlan 2003; Rosa et al. 2012).

In this study we sought to determine whether the link between sociality and foraging behaviour in the wild zebra finch (Mariette & Griffith 2013) is being driven by personality variation amongst individuals. We hypothesized that those individuals that tend to avoid the company of conspecifics, or are less social, would be quicker at discovering new food patches in a captive

context. Moreover, we proposed that both their sociality levels and their foraging behaviour are linked to an individual's personality. In order to achieve this we assayed several measures of personality in several different social contexts, in particular focusing on personality traits which may be indicative of behavioural type, such as activity levels (measured in a familiar environment), exploratory behaviour (measured in an unfamiliar environment), along with social foraging behaviour in a large space.

MATERIALS AND METHODS

General Methods

Data were collected from February 2011 to June 2012 from domestic 'wild-type' zebra finches originally obtained from aviculturists in the Sydney region in 2005 and bred at Macquarie University for either three or four generations (Tschirren et al. 2009). All subjects were between two and three years old at the time of the experiments, and had spent the majority of their lives in single or mixed-sex outdoor aviaries (8 x 10 x 2 m), with brief periods spent indoors in home cages (77 x 48 x 40 cm), holding one to four individuals while these experiments were conducted. Individuals were provided with ad libitum commercial finch seed along with water, grit, cuttlefish and a daily provision of chopped spinach and peas. During experimental trials, aviaries and cages were supplied with water ad libitum, and featured a number of perches so individuals could find a perch away from or as near to conspecifics as they wanted. Aviaries were also supplied with nest boxes during trials. Individuals were kept on an 11:13 h light:dark regime when housed indoors at a constant temperature of 24 ºC. At the end of the experiments the birds were returned to a large holding aviary where they have since been maintained for further behavioural work.

Part 1: Aviary Foraging Test

Prior to the start of the aviary foraging test, individuals were kept indoors and housed singly in the home cages for two months in a large room where they had acoustic access to other individuals. The aviary foraging tests were conducted between July-August 2011 with the remaining 34 males and 25 females, due to the death of one female between tests. The aviary was situated outdoors and was subject to ambient conditions in Sydney at the time (July: maximum: 17.4ºC; minimum: 8.6 ºC; August: maximum: 19.8 ºC; minimum 10.7 ºC; Australian Bureau of Meteorology, www.bom.gov.au), but featured a roof that covered 60% of the aviary and all of the feeders to prevent rainfall from influencing the use of the feeders. In the first round of trials the individuals were split into five small single-sex groups of roughly the same size: two groups of 11 males and one group of 12 males, one group of 12 females and one group of 13 females. In the second round of trials all of the available males and females were grouped together into two single-sex groups (34 males in one and 25 females in the other). Each trial ran for six consecutive days, beginning between 2-3 pm on the first day and ending at 12 pm on the final day, meaning each individual was in the aviary for almost five full days. Between 1:30 - 2:30 p.m. on the first day, individuals were captured from their home cages and fitted with a passive integrated transponder (PIT) ID100 tag (11 x 2 mm; Trovan; Hessle, UK) glued onto a plastic colour ring, before being transferred to a carry box. This process took no longer than an hour and ad libitum seed and water was provided within the carry box, with individuals in the carry-box for an average of half an hour. They were then transported to the large outdoor flight aviary (8 x 10 x 2 m) and the group was released simultaneously. At the end of the trial all individuals were captured with mist nets and returned to their home cages to await the next trial.

The aviary contained three feeding cages (70 x 40 x 50 cm), henceforth referred to as feeders, the location of which was changed between the first and second round of trials. Together with many perches on which individuals could land and socialize, the aviaries contained several

large wooden baffles near feeders and sheets of shade cloth hanging from the roof to make the environment more complex and difficult to navigate, and the feeders more difficult to find and visually independent from one another. The locations of the feeders, crates and mesh were changed between the first and second sets of trials (Figure 3.1). Each of the feeders were essentially finch cages containing a 50 x 30 cm seed tray with plentiful commercial finch mix (there was always enough food remaining in the seed trays to allow individuals to continue feeding from this source at a fast rate during the trials) that could only be entered through a 11 x 11 cm circular opening around which was attached to a powered antenna (11 cm diameter) connected to a PIT-tag detection system (LID-665 decoder; Trovan, UK) that automatically recorded the unique identification of any tagged bird going through the entrance along with date and time information (following Mariette et al. 2011). To determine the error rate of the reader, the entrance of one of the most popular feeders was videoed for 1 hour before the completion of each trial to compare the rate of visits recorded on the film with visits logged by the decoder. From this video data the success rate of the PIT-tag detection system at detecting an individual during a visit to the feeder was estimated at 94% for even the busiest feeders in the trials (data omissions generally occurred when two individuals passed through the antenna at roughly the same time). This may have led to a slightly deflated number of total visits recorded for those individuals that frequent the most popular feeder, or tend to pass through the entrance at roughly the same time as other individuals. From this data we calculated that the average visit length to the feeders was roughly two minutes in length, but they ranged from 10 seconds up to 12 minutes. During each trial the batteries on the decoders were replaced between 2 - 3 p.m. every day, and the data from the decoders downloaded. This involved entering the aviary for no more than 30 minutes each day, but otherwise the birds were undisturbed. No birds were noted to feed while observers were present in the aviary but they quickly resumed foraging once observers exited the aviary (observed from the recorded data). When each individual was recaptured at the end of the trial, the presence or absence of the PIT-tag was noted (in several cases the tag broke off the band due to the glue failing). Overall, five males lost their PIT-tags in the first trial, while one

female and two males lost them in the second trial. Data from the days during which these individuals lost their PIT-tag and all following days within the trial were discarded from data analysis.
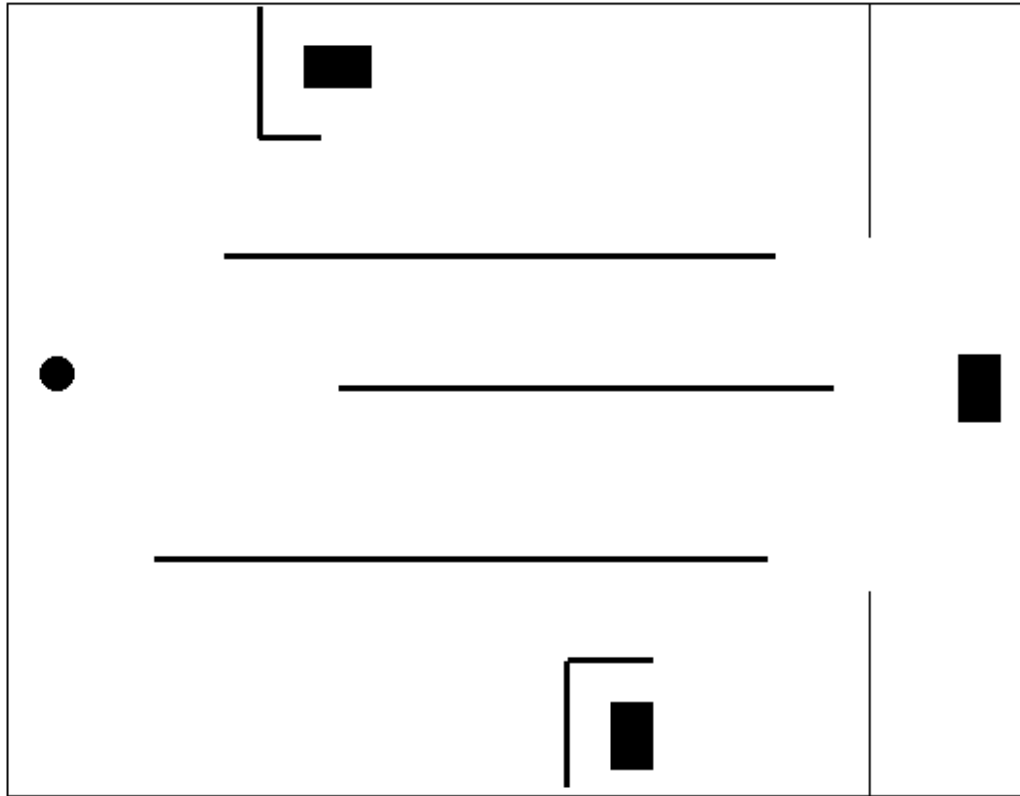
Fig. 3.1: Plan view of the outdoor aviary foraging experiment (trial 1). The three solid rectangles represent the feeders and the solid circle represents the water bowl. Thin lines indicate the walls of the aviary, while thick lines represent obstructions added to the aviary, such as wooden crates or shade cloth to make the discovery of new feeders more difficult. All individuals in a trial were released simultaneously into the aviary from next to the water bowl. The aviary measured 8 x 10 x 2 m, and the feeders measured 70 x 40 x 50 cm.

Data Analysis

Three distinct foraging measures were calculated from the PIT-tag data from the aviary experiment: Exploration Score, Sociality Score and Active Feeding Score. To calculate the Exploration Score several steps were taken. In all of the trials, one of the feeders was used much less than the other two overall. When we looked at the data from all of the trials, only a minority of individuals (37%) were found to have visited all three of the feeders during the trial, but almost all (95%) visited two out of the three. For this reason, the amount of time required for each individual to visit two

different feeders was recorded (rather than all three), and used to calculate the rank order out of all individuals in the trial for an individual to enter its second feeder. This rank order was further divided by the number of birds in the trial to give an order score between 0 and 1. The six individuals in the trials that did not visit two out of the three feeders were given an equal last order. Each individual's rank order number was subtracted from 1 so that fast explorers had a more positive exploration score. The mean scores from the two trials, excluding those individuals that lost their PIT-tags during one of the trials, was calculated and recorded as a measure of exploratory behaviour (Exploration Score). The time taken in hours for each individual to find two different feeders (excluding all overnight non-feeding periods) was also calculated (Exploration Time), to allow for the direct comparison of the mean exploration speed of males and females. In justification of our method for calculating the Exploration Score, the order to find two feeders was determined to be the only measure with enough variability between individuals to be used as a measure of exploratory behaviour, as most individuals only found two out of three feeders, so the order to find three could not be used, and the total number of feeders found could not have been used as most individuals found a total of two feeders in each trial. The only other measure with enough variation to be used is the order to find a single feeder, however, this measure was likely influenced by how long it had been since and individual had last fed (which may have varied by a magnitude of hours) which would have affected motivation to visit a new feeder to a greater degree than visiting two feeders (as finding another feeder was probably not motivated by hunger but the desire to explore). For this reason, we felt that the order to visit two out of three feeders was the variable most likely to be reflective of exploratory behaviour in a social group.

For the two other variables measured, we focused only on day three to five to give individuals time to habituate to their new environment. We focused on the second trial only (when all the birds of a sex were in the aviary together) to calculate sociality and leadership behaviour in feeder use. We used only this trial for this component of the work for a number of reasons. In the first trial up to two individuals within a trial (which only contained 11 individuals in total) lost their

PIT-tags which may have influenced the social foraging scores recorded for other individuals that may have been foraging with them, undetected. The influence of the PIT-tag losses during the second trial would have been minimal given the much larger number of individuals in the aviary. Second, potential group effects of the different trials were eliminated by only including a single trial for males and a single trial for females to be analysed separately. Finally, the first trial did not feature enough individuals in the aviary to properly demonstrate asociality in behaviour, as socially inhibited individuals may not have had to actively avoid conspecifics in their feeding behaviour at this small group size, and low density in the aviary.

To calculate a score for sociality, days three to five were broken into five-minute segments, a period chosen that was large enough that most feeder visits made by an individual would occupy only a single segment, but small enough that it was unlikely it would reflect entirely different social groups visiting the feeder at separate times. When an individual visited a feeder during a five-minute segment, the total number of other individuals that visited the same feeder during this five-minute segment was recorded. The Sociality Score of each individual was the average number of other birds that visited a feeder during the same five minute segments that the focal bird visited. The Active Feeding Score was calculated as the number of visits made to any feeder over the course of a day where no other individual was recorded as visiting that feeder in the preceding two minutes. This length of time was chosen as it was slightly longer than the mean feeder visit length of 90 seconds, so individuals were unlikely to actually be following others through the feeder entrance after two minutes had passed. For this score we did not distinguish between visits where an individual was playing a leader role and followed by other birds into the feeder and visits where the individual visited a feeder alone. However, unlike these 'active' feeder visits, this score was intended to rule out any feeder visits where individuals were playing a 'passive' role by following others to and from feeders. Moreover, as we could not determine for certain whether an individual was arriving at or leaving a feeder during a visit, this likely would have included some visits where an individual was the first to leave a feeder in a two-minute period rather than the first to arrive at a

feeder. However, being to the first to leave a feeder was still considered an 'active' behaviour in a foraging context, so the distinction was unimportant.

We assumed that data omissions during PIT-tag detection, caused by failure of the PIT-tag reader, along with the small number of individuals in a trial that had lost their PIT-tag (at most two birds per trial) and therefore could not be tracked, would likely only reduce the Sociality Score of the most social individuals while having little effect on the scores of less social individuals, weakening the potential differences between social and asocial birds. Furthermore, it is unlikely to have significantly affected the Exploration Score, as although 6% of first visits to a feeder may have been missed, individuals were likely to return again to the feeder within a short time frame and Exploration Score was mostly dependent on the use of less popular feeders at which the success rate was likely higher. The Active Feeding Score was also unlikely to have been significantly affected by data omissions as first visits to a feeder were unlikely to be missed and were likely to occur at roughly the same level for all individuals. However, it is possible though unlikely that some individuals may have been regularly following an individual in the trial that had lost its PIT-tag to feeders, which would have inflated their active feeding scores.

Home Cage Activity Test

The home cage activity test was conducted in June 2012 on 21 pairs consisting of a single socially bonded male and female in each. The sample size for this test was lower than previous tests as several individuals had deceased by this time. Most pairs (17 out of 21) were established naturally in August- December 2011 in an aviary in which birds were placed and allowed to choose partners and breed, with those individuals that bred together constituting a pair. The remainder of pairs (4 out of 21), were randomly made by placing a male and female together in a holding cage for at least 30 days before the trial. In May 2012, the pairs were moved from the outdoor aviary into home cages (77 x 48 x 40 cm) inside and allowed to acclimate for a month. These cages consisted of 4

perches, a feeder, a grit container, a water container and cuttlefish. At 12 pm on the day before the home cage test commenced, a sheet was placed over the home cage and it was transported to an isolated room (acoustically and visually from all other birds and stimuli) where the data would be collected. The pair were given the afternoon to adjust to their new surroundings (although they remained in the same cage they had been held in for the previous month). Just after dark, the room was discretely entered and filming was commenced with a video camera positioned two metres from the home cage (HDD/SD Card Hybrid Camcorder, SDR-H101, Panasonic, www.panansonic.com.au). The camera was left recording for the entire next day, and was not collected again till after dark. The lighting in the room was under a similar light:dark regime to that which the pairs were accustomed to in the room they were moved from. The lights came on at 6:59 am and gradually increased to full brightness over 20 minutes. They began to dim again at 5:37 pm and went off at 5:57 pm.

Video Analysis

Total movements were recorded from the video data during the first 30 seconds of every 10 minute period commencing when the lights came on at 6:59 am. A movement was defined as any movement greater than two body lengths, which consisted of either flights, or hops across the floor of the cage. Activity Score was calculated by dividing the total movements recorded overall by the number of 30 s periods analysed ($N = 66$), to note a single measure for each individual of the mean movements per each 30 s period. In total we directly quantified the amount of movements that individuals made in a period that was equal to $1/20^{th}$ of the day, but in time periods that were very evenly distributed across the whole day.

Statistical Analyses

Repeatability (*R*) values were calculated in R (R Development Core Team 2013) using the add-on package rptR, following the methods described in Nakagawa & Schielzeth (2010). Due to sex differences in the consistencies of behaviour noted from previous studies, repeatability scores for males and females were calculated separately (Mainwaring et al. 2011; Schuett & Dall 2009). Repeatability was calculated for the Exploration Scores and the Sociality Scores using Gaussian methods as this data was approximately normally-distributed, although this method was not designed to be used with ordered data (Exploration Score). These LMM-based methods utilised parametric bootstrapping and Bayesian methods for interval estimation and randomization for interval estimation (Nakagawa & Schielzeth 2010). Repeatability of the Active Feeding Score from the aviary foraging test and the Activity Score from the home cage activity test were calculated using the methods described for count data. These methods utilised multiplicative dispersion GLMMs with a log link for estimating repeatability on the original scale. Scores from the first and second trials were compared to calculate repeatability of the Exploration Scores, while the repeatabilities of the Sociality Scores and Active Feeding Scores were calculated by comparing the 3rd, 4th and 5th days in the second trial (see details in the Data Analysis section). In the home cage activity test, the repeatability of activity levels were calculated from all 30-second intervals across the entire day excluding the first three and last three measurements taken, during which time individuals were waking up or preparing for sleep. Due to discrepancies between LRT *P* values and 95% confidence intervals, *P* values were not reported, and instead instances where the lower confidence interval was below 0 were considered non-significant (Nakagawa & Cuthill 2007). Spearman correlations were conducted to examine the relationships between the different variables from the aviary foraging test and the home cage activity test using the statistical software programme IBM SPSS v21.0 (IBM Corp 2012). Each of these four variables (Exploration Score, Active Feeding Score, Sociality Score and Activity Score) consisted of repeated measures clumped

into a single measurement to avoid pseudoreplication. Data from the males and females were again analysed separately to compare sex differences in personality and foraging behaviour.

Part 2: Novel Environment Test

Although it was not included in the final submitted manuscript to *Behavioral Ecology and Sociobiology* to reduce the overall length of the manuscript, we also conducted a novel environment test, which is a classic measure of 'exploratory behaviour', between February and April 2011 on the same group of individuals (34 males and 26 females). The novel environment test was similar to an open-field test, except it was conducted in a large cage rather than a room with opaque walls (50 x 80 x 130 cm). The large cage contained 8 perches of various length and spacing. These perches were similar to the ones present in the individuals' home cages. The locations of the perches were changed between the first and second trials to enhance the novelty of the environment. The large cage was filmed with a video camera (High Definition Video Camera HDC-HS20, Panasonic, http://panasonic.net) through a hole in a curtain that separated the large cage from all other visual stimuli. During the test, each individual was visually but not acoustically isolated from conspecifics. Between 2 and 4 pm each day, three individuals were run through the test. The test was repeated four to six weeks later and with individual order randomised between the trials. At the start of each trial, an individual was captured from its home cage and placed in a small wooden box (16 x 17 x 11 cm). The box contained a small gap at the bottom through which light could enter. The box was then immediately placed within the large cage with a piece of fishing wire attached to the door of the box. Individuals were able to see only the wire mesh of the back wall of the large cage through the gap in the box. The experimenter then exited the room. After five minutes elapsed, the experimenter entered the room, began filming, and pulled open the door of the box with the fishing wire from behind the curtain, causing the door to open and land on the floor of the large cage providing a large gap (95 x 145 mm) through which individuals could exit. The experimenter then

quietly exited the room again out of sight of the focal bird. After 10 minutes, the trial stopped and the test subjects were captured and returned to their home cage. The experimenter then exited the room for 30 minutes to give all individuals in the holding room time to settle down before the next individual was captured and placed into the large experimental cage.

Video Analysis

Video analysis was conducted on the five minutes after each individual exited the confines of the box and entered the large cage. Most individuals fled the box into the large cage soon after the door was opened, but some individuals were slower to exit. In three out of 120 cases the camera did not record properly and in two cases an individual took longer than five minutes to exit the box preventing a full five minutes of video being recorded, therefore these results were not included in the dataset. The novel environment was split into 13 different areas: the floor of the large cage, the four wire mesh sides and the eight perches. The number of flights was calculated as our measure of exploratory behaviour, 'novel environment exploration'. A flight was defined as a flight between two 'areas', or a flight within the same area. Hops within the same area were infrequent and difficult to quantify, so were not measured. This measure is frequently used in personality assays of exploratory behaviour (Montiglio et al. 2010).

Statistical Analyses

Data were analysed using the statistical software programme IBM SPSS v21.0 (SPSS Inc., Chicago, IL, U.S.A.). Repeatability (R) values within each trial were calculated using the popular ANOVA-based method (Lessells & Boag 1987). This is the most commonly used method to calculate repeatabilities and uses the F table of an ANOVA with the individual identities treated as factorial predictors. Due to sex differences in the consistencies of behaviour noted from previous studies,

repeatability scores for males and females were calculated separately (Mainwaring, Beal & Hartley 2011; Schuett & Dall 2009). Scores from the first and second trials were compared to calculate repeatability. We conducted Spearman correlations to compare Novel Environment Exploration from the novel environment test with Exploration Score from the aviary foraging test and Activity Score from the home cage activity test.

RESULTS

Repeatability of Behavioural Tests

All behavioural variables measured were significantly repeatable in males (Table 3.1), including Novel Environment Exploration (Mean $\pm$ SE = 28.643 $\pm$ 7.514, $R \pm$ SE = 0.338 $\pm$ 0.165, $F_{29,30}$ = 2.020, P = 0.030). In females, Activity Score was significantly repeatable, but Sociality Score and Exploration Score were not (Table 3.1). Novel Environment Exploration in females was not significantly repeatable (Mean $\pm$ SE = 23.882 $\pm$ 4.079, $R \pm$ SE = -0.007 $\pm$ 0.209, $F_{23,24}$ = 0.986, P = 0.512). The overall mean values for the behavioural scores were similar for males and females for Exploration Score and Activity Score (Table 3.1). The mean Sociality Score of females was higher than for males and the Active Feeding Score higher in males, despite the lower number of individuals present in the female trial, suggesting that females tended to visit feeders with a larger number of conspecifics on average than males and that males tend to make more leader visits to and from feeders (Table 3.1), however we did not statistically test for a difference between the sexes in this traits. The average Activity Scores were similar for males and females (Table 3.1), but the range was wider in males (males: range = 0.64 – 15.21; females: range = 0.21 – 10.5). These estimates suggest that on average individuals are making about 7336 movements per day with the

range across the population going from just 280 to the most active individual making 20080 movements in the eleven hours of daylight (see distribution in Figure 3.2).

Table 3.1: Mean values and repeatability (R) of individuals' behaviour in the (a) aviary foraging test and (b) home cage activity test. Repeatability was calculated by comparing the scores from the two separate trials for Exploration Score, or comparing days three, four and five of the second trial, for Sociality Score and Active Feeding Score. The mean Exploration Score value was calculated from the exploration time in hours but repeatability was calculated from exploration order. Repeatability was calculated by comparing the middle 60 30-second movement scores over the course of the day for Activity Score.

Component	Mean ± SE	R ± SE	N	Lower CI	Upper CI
(a) Aviary Foraging Test					
Exploration Score					
Male	18.346 ± 2.140	0.462 ± 0.155	26	0.117	0.726
Female	21.816 ± 2.492	0.291 ± 0.171	25	0	0.607
Sociality Score (trial 2)					
Male	9.196 ± 0.634	0.748 ± 0.066	31	0.587	0.849
Female	11.869 ± 0.251	0.217 ± 0.117	24	0	0.436
Active Feeding Score					
(trial 2)					
Male	17.273 ± 2.591	0.524 ± 0.101	32	0.308	0.702
Female	10.273 ± 1.756	0.551 ± 0.119	24	0.286	0.752
(b) Home cage activity test					
Activity Score (per 30s)					
Male	5.506 ± 0.940	0.282 ± 0.07	21	0.14	0.416
Female	5.633 ± 0.721	0.411 ± 0.088	21	0.233	0.577

Correlations between Foraging and Personality Variables

In males, the Sociality Score was significantly negatively correlated with Exploration Score and Active Feeding Score (Table 3.2). By contrast, in females the three aviary foraging test variables were not significantly correlated with one another (Table 3.3). Activity Score in the home cage activity test was significantly positively correlated with Exploration Score in both males and females, indicating more active individuals were quicker on average at finding two different feeders in the aviary (Table 3.2, Table 3.3 and Fig. 3.3a). Moreover, Activity Score was significantly negatively correlated with Sociality Score in males (Table 3.2 and Fig. 3.3b) and significantly positively correlated with Active Feeding Score in females (Table 3.3). Finally, Novel Environment Exploration was weakly but significantly positively correlated ($rs = 0.322$, $N = 46$, $P = 0.029$) with Exploration Score from the aviary foraging test, but not with Activity Score from the home cage foraging test ($rs = 0.089$, $N = 37$, $P = 0.600$).
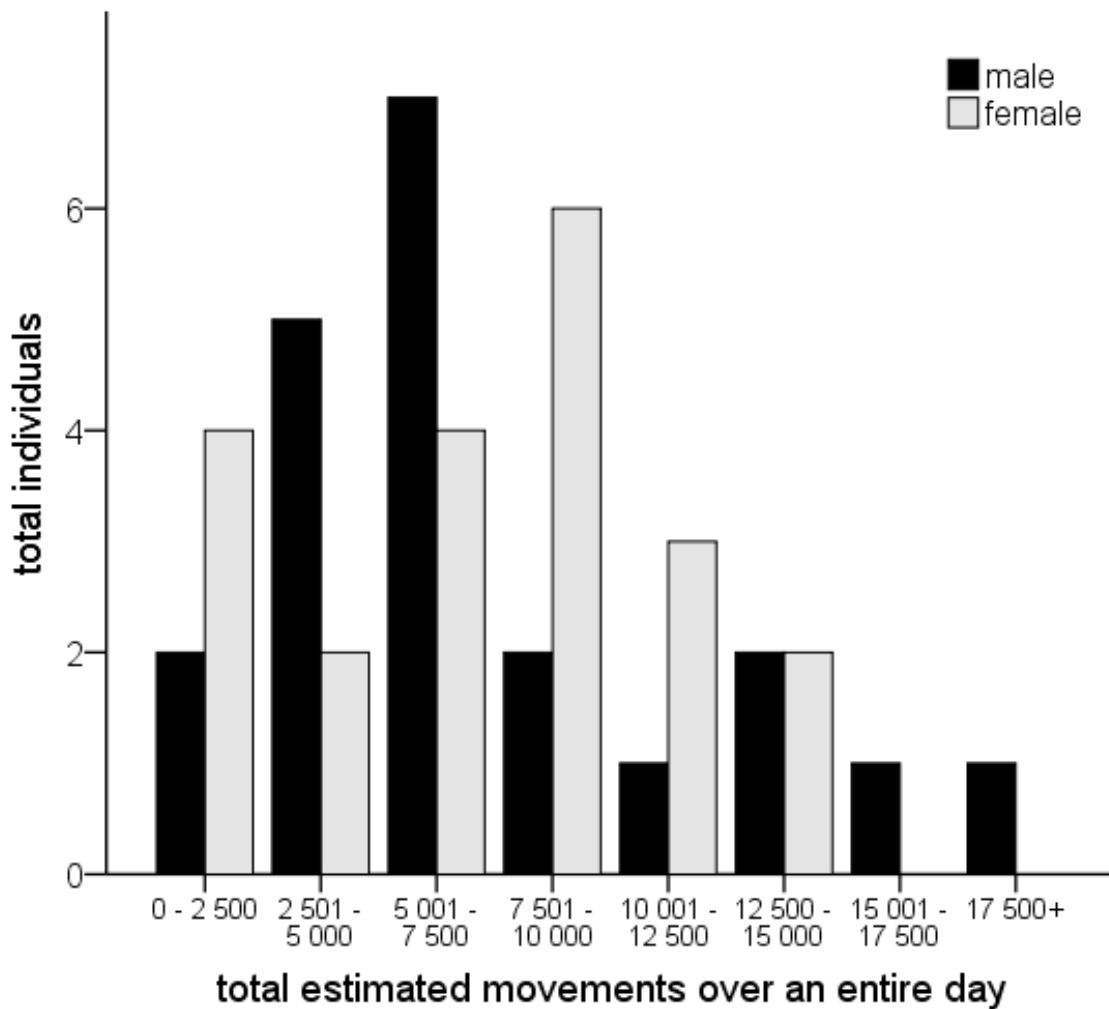
Fig. 3.2: Estimated total movements per individual over the course of the entire day. Estimates were calculated by analysing total movements during $1/20^{th}$ of the total day and multiplying the total by 20.

Table 3.2: Spearman correlations for males between the three variables measured in the aviary foraging test, Exploration Score, Sociality Score and Active Feeding Score and the Activity Score from the home cage activity test, listed as *rs*, *N*, *P* value.

Variable	Sociality Score	Active Feeding Score	Activity Score
Exploration Score	-0.429, 26, 0.029*	0.368, 26, 0.064	0.615, 17, 0.009**
Sociality Score	-	-0.587, 31, 0.001**	-0.588, 20, 0.006**
Active Feeding Score	-	-	0.247, 20, 0.294

Table 3.3: Spearman correlations for females between the three variables measured in the aviary foraging test, Exploration Score, Sociality Score and Active Feeding Score and the Activity Score from the home cage activity test, listed as *rs*, *N*, *P* value.

Variable	Sociality Score	Active Feeding Score	Activity Score
Exploration Score	-0.078, 24, 0.716	0.370, 24, 0.075	0.492, 21, 0.023*
Sociality Score	-	-0.270, 24, 0.202	-0.243, 20, 0.302
Active Feeding Score	-	-	0.680, 20, 0.001**
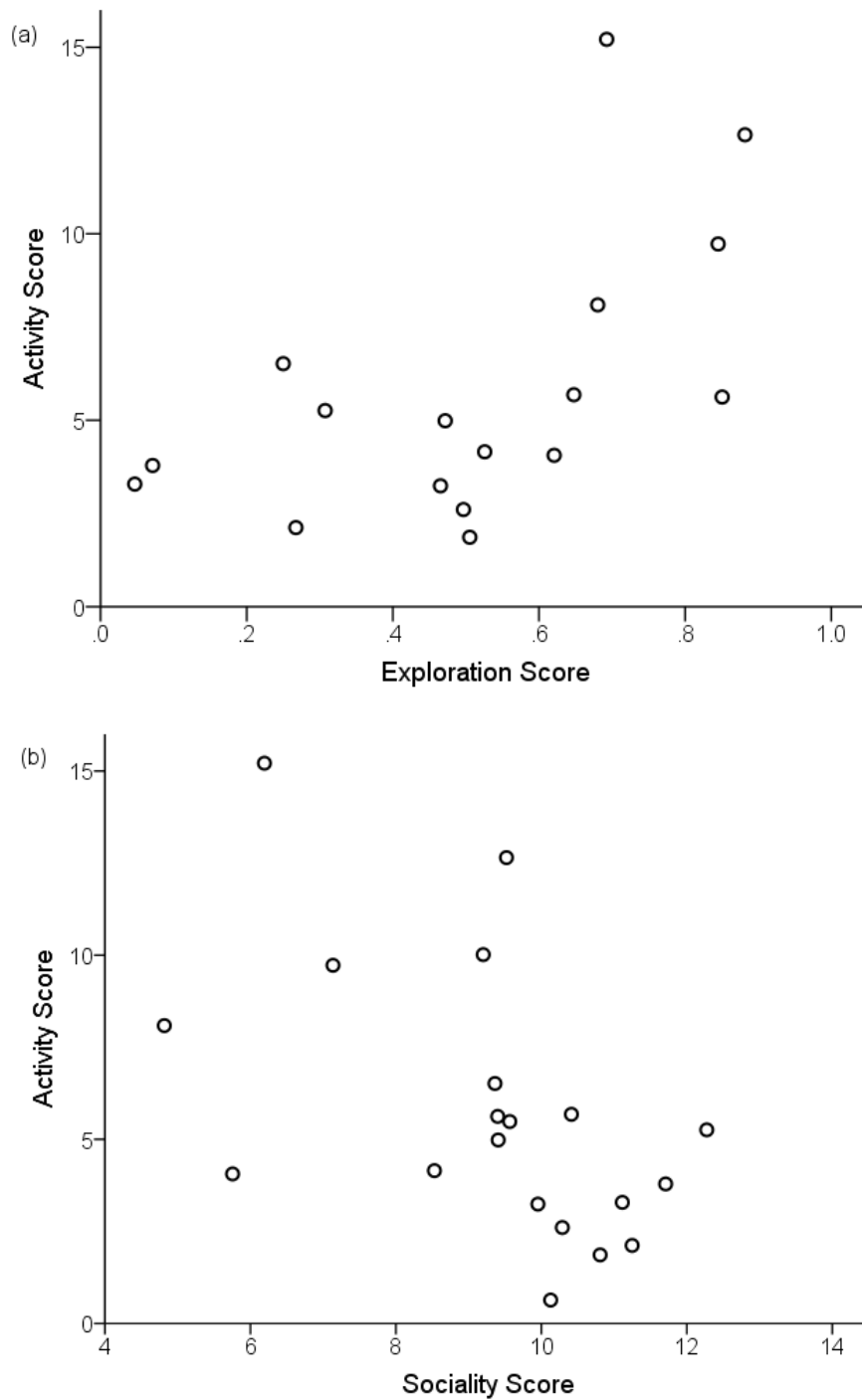
Fig. 3.3: Scatterplot showing the correlation between male activity levels in the home cage test (Activity Score) and (a) Exploration Scores and (b) Sociality Scores in the aviary foraging test. A higher Activity Score indicates a greater number of mean movements per 30-second interval made over the course of the day. A higher Exploration Score indicates a faster mean comparative order to find 2 out of the 3 feeders in the aviary over the two trials. A higher Sociality Score indicates a higher mean number of conspecifics feeding concurrently during feeder visits of the focal individual.

DISCUSSION

During our study we investigated correlations between three separate measures of behavioural type, a classic exploratory behaviour measure in a novel environment, exploration in a social foraging context and general activity levels over the course of a day. As expected, our measures of behavioural type were positively correlated, despite the tests measuring different personality attributes in different social contexts. This confirms the results of previous studies, showing that a behavioural syndrome is present in this species, with high activity levels predicting faster exploratory behaviour (David et al. 2011a; Martins et al. 2007). Furthermore, we found that individual zebra finches employ different social foraging strategies and that these are correlated with other elements of personality, particularly activity. In single-sex social groups, more active individuals (potentially displaying a proactive behavioural type) were quicker to discover new food patches, and hence, appear to explore the environment faster. Moreover, more active females made more leader visits to and from the feeders on average than less active females. In *Drosophila* fruit flies, research showed that a single gene, *for*, influences the foraging behaviour strategies employed by producing a small difference in cGMP-dependent protein kinase activity and hence general activity levels, which suggests minor genetically-determined differences in activity levels between individuals can result in considerable changes in foraging strategy (Sokolowski 2001). However, in a separate study social environment was also shown to account for a large portion of the variation in activity levels (Higgins et al. 2005). In our study, male activity levels were not strongly linked to leader behaviour, but they were linked to sociality. Less active (reactive) males generally seem to visit feeders in the presence of more conspecifics than more active individuals; hence they are more social in their foraging behaviour. This result is consistent with previous work, which found that proactive individuals spend more time alone (Beauchamp 2000b; Budaev 1997). Furthermore, our results support a recent study of the wild zebra finch, in which greater sociality in a breeding context was linked to a reduced rate of detection of experimental novel feeders (Mariette & Griffith

2013). This implies that males that can locate feeders faster are less social not only in a foraging context, but also a breeding context. However, further studies are required to test whether these asocial breeders are in fact exhibiting a proactive behavioural type. In support of this idea, in the barn swallow more social breeders tend to be more neophobic, which suggests they may be displaying a reactive behavioural type (Dardenne et al. 2013).

There are a number of potential explanations as to why sociality is negatively correlated with activity levels and exploration speed in males. Firstly, proactive individuals may be attempting to avoid interference or scramble competition from conspecifics by feeding at novel or less-frequented sites. This may be driven by an inferior competitive ability. However, highly exploratory individuals have been shown to be more aggressive in mirror tests and proactive females (this test was not conducted in males) more likely to be socially dominant in within-group foraging competition, and so proactive individuals are unlikely to be inferior competitors (Schuett et al. 2011a). Furthermore, one study found that proactive individuals were more likely to play the scrounger role than reactives, which contradicts the notion that they are actively avoiding scramble competition (David et al. 2011b). Instead, the difference may be underlined by a superior speed or ability of proactive males in exploring the environment and discovering new food patches. In support of this idea, in our study the speed with which males entered new feeders was negatively correlated with sociality and positively correlated with activity levels. Moreover, proactive individuals have been shown to be more likely to lead others to food patches (Beauchamp 2000b), just as more active females were more likely to lead feeder visits in our study. However, David et al.'s (2011b) study, which showed that proactive individuals were more likely to play the scrounger foraging role (exploiting the food discoveries of others) than reactive individuals, appears to contradict this prediction, as it implies that proactive individuals are less successful at discovering food (playing the producer role in social foraging). However, in their study, the experiment was conducted in a single small foraging patch and individuals were not given the option to search for novel foraging patches farther afield. Reactive individuals may be more successful at discovering

food at a fine scale due to their tendency to search more slowly and thoroughly, their greater sensitivity to external cues and greater flexibility in their behaviour (Coppens et al. 2010; Guillette et al. 2011; Verbeek et al. 1994). By contrast, proactive individuals are likely more effective at discovering novel food patches on a larger scale by employing faster, wider-ranging and potentially superficial search methods (Verbeek et al. 1994).

Another explanation for the links between sociality in a foraging context and behavioural type is that proactive and reactive individuals display different levels of risk-taking behaviour. Reactive individuals may be taking advantage of the presence of conspecifics to reduce the risk of predation or the total time they spend foraging. Flock size has been linked to both reduced predation risk and decreased foraging time due to a reduced amount of time spent in predator surveillance (Beauchamp 2002; Elgar & Catterall 1981; Lindström 1989). In support of this idea, Schuett & Dall (2009) found that less exploratory individuals, particularly males, spent more time with a social partner at a risky feeder than more exploratory individuals. Moreover, the presence of conspecifics has been found to lead to individuals becoming less bold and exploratory in their behaviour (Mainwaring et al. 2011; van Oers et al. 2005b). Hence, through social facilitation, reactive individuals may be able to avoid the feeders in the aviary that are perceived to be risky or preferentially remain in a group and exploit the food discoveries of others rather than search for food on their own (Webster & Ward 2011). This behaviour could potentially result in an overall increased feeding rate for the group as a whole (Dyer et al. 2009). Moreover, different behavioural types may differ in their levels of social conformity (Webster & Ward 2011). In particular, less active individuals may be driven to a greater extent by the desire to conform to the behaviour of their flockmates and hence are more likely to feed in large social groups with their conspecifics.

One of the most obvious differences between the sexes uncovered in this study is that while activity levels were positively correlated in both males and females, the negative relationship with sociality was only present in males. Furthermore, the mean Sociality Score was significantly higher

in females than males, which implies that females tend to feed in larger groups on average, suggesting they are less motivated to visit unpopular food patches. This relationship could potentially be explained by lower conspecific aggression at feeders amongst females. In mirror tests, females have been shown to be less aggressive towards their reflection than males (Schuett et al. 2011a). This may explain the lack of a relationship between sociality and behavioural type in females, by indicating that females tend to be highly social in general, regardless of their activity levels or behavioural type. However, to confirm this, higher sample sizes may be required to adequately rule out a relationship between the two variables. Conversely, it has been suggested that males tend to lead females to food patches in the wild (Zann 1996). This might explain why females are more reluctant to visit less well-established feeders when feeding in a single-sex flock, as without an established group leader, individuals may simply end up feeding from the closest feeder to a popular perching or water site. In contrast, Active Feeding Scores for females were significantly positively correlated with activity levels in females but not males, which suggests that proactive females are more likely to take on a leadership role in a single-sex foraging groups. Finally, the repeatability of the Sociality Score was lower in females than males. This result is consistent with previous work which shows that males are more consistent than females in various measures of their personality (Mainwaring et al. 2011; Schuett & Dall 2009), or it may instead be reflective of less variation in sociality in females in general.

In summary, this work provided an in-depth look at the influence of behavioural type on social foraging behaviour at both a small and large scale and raises a number of possibilities for future work. Although our work provided insight into the feeding behaviour of single-sex aviary groups, these groups do not normally occur in the wild, which may have resulted in unusual agonistic interactions and leadership/following behaviours among individuals within the trials. Therefore, similar experiments performed in a large mixed-sex aviary would likely provide a clearer picture of how these foraging tactics are employed in more natural social groups in the wild. This study did not examine the social foraging behaviour of pairs within a social group, and it is possible

that the foraging behaviour of pairs might complement each other in a natural context. It would also be fruitful to investigate whether the use of social information depends on behavioural type in this species. It may well be that reactive individuals rely on social information to a much large degree than proactive individuals in the discovery of new food patches. One of the main implications of our study is that individual foraging patterns in social species are clearly determined by an individuals' propensity to interact with other conspecifics as well as their own ability to explore the environment and find food, which itself may be influenced by an individual's personality. In this particular well studied social species, we have shown that these two important behavioural repertoires are related but that may not always be the case. It is important for our understanding of foraging ability and behaviour that future studies should consider the social element of foraging.

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ETHICAL NOTE

Animal welfare and methodological design were approved by the Animal Ethics Committee at Macquarie University (AEC reference number: 2010/059), and comply with the current laws of Australia, the country where they were performed. The health and condition of all birds were monitored on a daily basis and no individuals were noted to be unduly distressed by the experimental procedures or housing conditions.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

Chapter Four

Nestling activity levels during begging behaviour predict activity levels in adulthood

ABSTRACT

Across a range of species including humans, personality traits, or differences in behaviour between individuals that are consistent over time, have been demonstrated. However, few studies have measured whether these consistent differences are evident in very young animals, and whether they persist over an individual's entire lifespan. Here we investigated the begging behaviour of very young zebra finch nestlings and the relationship between that and adult activity levels. We found a link between the nestling activity behaviour head movements during begging, measured at just five and seven days after hatching, and adult activity levels, measured when individuals were between three and three and a half years old. Moreover, body mass was found to be negatively correlated with both nestling and adult activity levels, suggesting that individuals which carry less body fat as adults are less active both as adults and during begging as nestlings. The nestlings in our study were cross-fostered, with hatching order and brood size experimentally manipulated, factors previously shown to affect the nestling begging behaviour. Consequently, this suggests that the personality traits identified here in both very young nestlings and adults may be largely determined by environmental sources of variation and may also be linked to physiological factors such as metabolism. Moreover, our work suggests it may be possible to predict an individual's future adult personality at a very young age, opening up new avenues for future work to explore the relationship between personality and a number of aspects of individual life history and survival.

INTRODUCTION

Animals can produce complex adaptive behaviours early in ontogeny, which may be similar to or greatly differ from subsequent adult behaviour (Groothuis & Trillmich 2011). Food begging is a behaviour performed by young animals of various species that tends to diminish or disappear by adulthood, though it may be maintained in some species in certain situations (Ellis et al. 2009). However, it is conceivable that differences in the characteristics or intensity of begging behaviour between individuals, or at least the underlying physiological differences that produce them, may be maintained and visible in the subsequent behaviour of adults (Roulin et al. 2010). When the behaviour displayed by individuals in a population or species is characterised by both inter-individual variation and intra-individual consistency over time and/or context, this infers the existence of personality differences between individuals (Carere & Maestripieri 2013; Réale et al. 2007). As young animals often express different behaviours from adults it is useful to examine whether these differences result from changes in the expression of personality over life stages or whether personality itself changes as an individual grows (Groothuis & Trillmich 2011).

One example of a commonly measured personality trait, which has been established and measured in a range of species, is activity (Beauchamp 2000). 'Activity' can be defined as the general activity level of an individual, usually measured in an environment that is not novel or risky to reduce interference with other personality traits such as exploration or boldness (Réale et al. 2007). Activity has often been shown to be repeatable when measured across lengths of time that make up a considerable portion of an individual's lifespan (Herde & Eccard 2013; Martin & Réale 2008). Moreover, several studies have shown that activity is repeatable over different life stages from ontogeny to adulthood (Kanda et al. 2012), and even across metamorphosis in species that undergo it (Wilson & Krause 2012). In young nestling birds, individuals may vary in their levels of activity, and this may influence their interactions with both their parents and siblings in the nest, thereby influencing the amount of food they receive and their growth patterns, although high

activity levels may have an energetic cost (Roulin 2001; Roulin et al. 2010). These differences may be evident in the begging behaviour of nestlings (Roulin et al. 2010).

Begging in young birds is made up of a number of separate behaviours which are often performed at the same time during a begging bout, such as auditory calling, raising of the head, body posture, bill gaping, pecking and approaching the parent, and movements of the head and tongue (Eising & Groothuis 2003; Gilby et al. 2012; Kacelnik et al. 1995; Ruuskanen & Laaksonen 2013). In the zebra finch, *Taeniopygia guttata*, the mean intensity with which nestlings produce several of these different begging behaviours has been shown to be positively correlated, e.g. greater mean head movements is positively correlated with greater mean tongue movements (Gilby et al. 2012). Differences in begging behaviour between individuals may result from nestlings adapting to the personality of their parents, but they may also provide indications of underlying individual differences in their own personality, which may have been shaped by genetic differences or maternal effects such as the allocation of hormones during ontogeny (Roulin et al. 2010; von Engelhardt et al. 2006). In the zebra finch, nestlings shake their heads from side to side and produce lateral movements of their tongues in their gaping mouths during begging (Boyd & Alle 1948; Zann 1996). The mean rate of lateral tongue movements when they are being performed increases with age (Muller & Smith 1978). Moreover, nestlings younger than five days of age make continuous stereotyped movements of their tongue, while individuals older than about seven days of age tend to only move their tongue when parents are at the nest feeding their young (Muller & Smith 1978).

In a similar manner to auditory begging calls (Muller & Smith 1978), head and tongue movements are believed to attract the attention of the parents, soliciting provisioning and enable effective sibling competition for food (Kilner & Johnstone 1997). The level of begging behaviour displayed by nestlings is linked to offspring need and usually related to the amount of food an individual receives from its parents (Gilby et al. 2011a; Kilner & Johnstone 1997). However, in zebra finches there is no significant correlation between the mean rate of tongue movements made

by a nestling and the frequency that this nestling is fed by the parents (Muller & Smith 1978), negating the idea that nestlings increase their tongue movement speed in order to receive more food. Hence, the speed of these movements during begging bouts (shown by their mean rate during a bout) may be more reflective of an individual's general activity levels, which is widely considered a personality trait, both in the zebra finch and across a range of species (Réale et al. 2007). Conversely, other begging variables, such as the duration of begging, gape width and the latency to start begging, while correlated with tongue and head movements, may be more closely linked to nutritional need, and predictive of food received than a nestling's general activity level. Moreover, typical begging traits such as gape width and latency to start begging do not measure repetitive movement behaviours, such as those typically measured in traits which are the target of personality studies of activity in adults (David et al. 2011a).

Previous evidence that begging intensity may be reflective of personality was shown in a study conducted on great tits (*Parus major*), which found that individuals from a line selected to be more 'proactive' (highly exploratory and aggressive) tended to beg more intensely than a line selected to be more 'reactive' (Carere 2003). In addition, the speed and activity levels of very young turkeys in 'T-maze' and 'open field' tests differed between selection lines (Huff et al. 2007). Two studies have found that certain behaviours produced by young birds display differences between individuals and consistency over time, namely activity in novel environments in pied flycatchers (Ruuskanen & Laaksonen 2010) and a variety of behaviours in a novel environment, neophobia and tonic immobility in chickens (Vennerholm 2012). Moreover, several non-begging nestling behaviours in blue tits (*Cyanistes caeruleus*) produced under mildly stressful conditions, namely handling aggression, docility and breathing rate, constitute personality traits and show heritable variation between individuals (Brommer & Kluen 2012). Another study in great tits found that handling stress as measured by breathing rate at just 14 days of age is both repeatable and correlated with adult exploration levels (Fucikova et al. 2009). Several other studies have found that certain personality traits are repeatable across life stages when measured in juveniles and again as adults,

such as exploratory behaviour in zebra finches (first measured at two months of age) (David et al. 2012a), and activity, docility and exploratory behaviour in mammals (Herde & Eccard 2013; Kanda et al. 2012; Petelle et al. 2013) and amphibians (Wilson & Krause 2012). However, this is not the case for all personality traits that have been measured between juvenile and adult life stages (Herde & Eccard 2013; Kanda et al. 2012; Wilson & Krause 2012); therefore it cannot be assumed that all behavioural traits that are repeatable within a life stage are repeatable across different life stages.

In this study, we investigated whether very early nestling mechanical behaviours produced during begging are related to adult personality in the zebra finch, a well-used model system for the study of parental care and personality. This study is the first to compare behavioural traits exhibited during food begging with personality much later in life. Specifically, we focused on those begging behaviours commonly performed by young nestlings most likely to be indicative of general activity levels, namely tongue movements and head movements, and contrasted these with general activity levels measured in adults in a relatively low-stress environment, with a social partner in a familiar home cage. We predicted that nestling activity levels during begging would be positively correlated with their subsequent activity levels as adults.

METHODS

General Methods

Data were collected from January 2009 to July 2012 from domestic 'wild-type' zebra finches originally obtained from aviculturists in the Sydney region in 2005 and bred at Macquarie University for either three or four generations (Tschirren et al. 2009). All subjects spent the majority of their lives under the same conditions in single or mixed-sex outdoor aviaries (8 x 10 x 2 m), with brief periods spent indoors in home wire cages (77 x 48 x 40 cm), holding one to four

individuals while experiments were conducted (usually individuals were held in pairs or small social groups for social enrichment). In both environments, individuals were provided with ad libitum commercial finch seed and drinking water, along with grit, cuttlefish bone and a daily provision of chopped spinach and peas. Both environments featured a number of perches so individuals could find a perch away from or as near to conspecifics as they wanted and did not require bedding as individuals roost on open perches, and aviaries featured ad libitum dust for bathing. Individuals were kept on a 11:13 h light:dark regime when housed indoors at a constant temperature of 24 ºC and relative humidity maintained at around 40- 50%. Individuals were subjected to the ambient conditions in Sydney, Australia when housed in outdoor aviaries, which are generally less extreme than those experienced by zebra finches in the wild. The aviaries featured a roof that covered most of the aviary, so individuals could seek shelter from the rain. At the end of the experiments the birds were returned to a large holding aviary where they were maintained for further behavioural work.

Nestling begging behaviour

All individuals were reared by domestic 'wild-type' foster parents between January and December 2009 in experimentally manipulated asynchronous broods (Gilby et al. 2012), produced by parents in an aviary (8 x 10 x 2 m) containing 20 males and 20 females. On the morning an egg was laid, it was replaced with an imitation egg, marked and placed in an artificial incubator until hatching. On the day of hatching, nestlings were individually-marked (by clipping a claw) and randomly cross-fostered to either a 'control' or 'reverse' experimental brood in the aviary (but never returned to the nest of their genetic parents) (Gilby et al. 2012). Each brood consisted of either five or six nestlings, placed into the nest in two groups of two to three nestlings 48 hours apart. In 'control' broods, the first 2-3 nestlings placed into a nest were from position 1-3 of the laying sequence, and the latter 2-3 nestlings from position 4-6. In 'reverse' broods this pattern was reversed. In total there were 28 successful experimental broods containing 98 nestlings, 15 'control' and 13 'reverse', which came from 43 different genetic nests. When each nestling was five days old, and again at seven days old,

it was removed from its nest and individually placed in an artificial nest on a heat pad to assay begging behaviour. Only a single nestling was taken from a nest at a time in random order, hence the time that each nestling was removed varied (range 11 a.m. – 4 p.m.). Begging was measured in two rounds of three trials each day, the first round began 15 minutes after the nestling was placed on top of a heat pad in the laboratory, and this did not control for the level of provisioning the nestling was subject to when removed from its nest. To control for this, the nestling was fed with liquefied egg and biscuit rearing and conditioning food mix until satiation and then left for one hour, before begging behaviour was again assayed. Here we focused on the begging behaviour recorded during the subsequent three trials, which provided the best measure of intrinsic differences in activity and begging behaviour by controlling for initial state. During each begging measure, begging was initiated using a standardised procedure with a red pen to tap the nesting material around the nestling, the nestling's beak and their left and right wing. This routine was conducted three times, with three minutes between each repeat. From video recordings, six different begging variables were quantified: Latency, Duration, Raised head, Head movements, Open mouth and Tongue movements. In total, all of the 98 nestlings (47 males and 51 females) completed the begging assays, producing a total of 568 observations. Further details of the procedures performed on the birds during this relatively early stage of development are described in (Gilby et al. 2012). Unfortunately, as three and a half years is roughly the average lifespan of the zebra finch in captivity (Heidinger et al. 2012), a large number of individuals had succumbed to old age by the start of the adult component of the work in 2012. Due to this natural attrition and the complex design of the cross-fostering experiment we did not have a sufficient sample size to explore the relationship between characteristics of their upbringing in direct comparison to adult activity levels (e.g. whether individuals were early or late laid or hatched). Nevertheless, the determinants of the experiment treatments and brood size on the level of activity during begging in the larger sample of nestlings that were investigated are detailed in the earlier study (Gilby et al. 2012). Here, we focused on the previously measured variables that were likely to be most reflective of mechanical

speed and activity levels within a begging bout, namely Head movements and Tongue movements. 'Head movements' was defined as the average number of half turns of the nestling's head made per second while the nestling was begging. 'Tongue movements' was defined as the average number of times the tongue moved from one side of the mouth to the other per second while the nestling was begging.

Adult activity levels

All further data was collected from the surviving adults in 2012 when the remaining 19 males and 16 females from the cross-fostering experiment were between 36 and 42 months old. The 35 surviving adults had been produced by 22 pairs and were reared in 20 foster nests (none were raised by their genetic parents). In April 2012, the tarsus length of all individuals were measured, and in late May, the body mass of all individuals were measured (at roughly the same time of day, in the early afternoon). The home cage activity test was conducted in June 2012. Pairs for the test were established in August- December 2011 in an aviary in which birds were placed and allowed to choose partners and breed, with those individuals that bred together constituting a pair. These 19 males and 16 females all featured in that trial, along with a further 15 males and 9 females of the same age and from a similar upbringing. Most of the individuals (15 of 19 males and 12 of 16 females) from the cross-fostering experiment paired up with a partner during this test, and the rest were randomly paired with an opposite sex partner in a holding cage for at least 30 days before the trial to allow them to bond with one another. This resulted in a total of 21 pairs consisting of a single socially bonded male and female in each trial, 17 of which were established naturally and four which were randomly comprised. Of the 21 pairs, there were seven where the data from only one of the individuals was included in this study, as that individual's chosen or allocated partner was not assayed as a nestling in the begging experiment. In May 2012, the pairs were moved (or established, for the randomly allocated pairs) from the outdoor aviary into home cages (77 x 48 x 40 cm) inside and allowed to acclimate for a month (both members of the pair lived together in a single

cage). These cages were provided with four perches (which were aligned in the same configuration for each cage at different angles and heights from 5-30 cm above the floor of the cage), a feeder, a grit container, a water container and cuttlefish. At 12 pm on the day before the home cage test commenced, a sheet was placed over the home cage and it was transported to an isolated room (acoustically and visually from all other birds and stimuli) where the data would be collected. The pair were given the afternoon to adjust to their new surroundings (although they remained in the same cage in which they had been held in for the previous month). Just after dark, the room was discretely entered and filming was commenced with a video camera positioned two metres from the home cage (HDD/SD Card Hybrid Camcorder, SDR-H101, Panasonic, www.panasonic.com.au). The camera recorded video continuously for the entire next day, and was not collected again till after dark. The lighting in the room was under a similar light:dark regime to that which the pairs were accustomed to in the room they were moved from. The lights came on at 6:59 am and gradually increased to full brightness over 20 minutes, and began to dim again at 5:37 pm and went off at 5:57 pm. Total movements were recorded from the video data during the first 30 seconds of every 10 minute period commencing when the lights came on at 6:59 am. A movement was defined as any movement greater than two body lengths, and consisted of either flights, or hops across the floor of the cage. This resulted in a total of 2310 observations recorded for the 35 individuals that completed the test.

Ethical note

Animal welfare and methodological design were approved by the Animal Ethics Committee at Macquarie University (AEC reference number 2010/059). The health and condition of all birds were monitored on a daily basis and no individuals were noted to be unduly distressed by the experimental procedures or housing conditions.

Statistical Analyses

Due to sex differences in the consistencies in behaviours noted from previous studies (Mainwaring et al. 2011; Schuett & Dall 2009), the repeatability scores for males and females were analysed separately. Repeatability (*R*) values were calculated in R (R Development Core Team 2013) using the add-on package rptR, following the methods described by Nakagawa & Schielzeth (2010). Repeatability was calculated for the Head movements and Tongue movements begging variables over all six trials per individual. The repeatability of these variables was calculated for all of the nestlings that were raised in the original begging experiment (47 males and 51 females) and separately for just the 19 males and 16 females that survived to be later assayed in the home cage activity test. The repeatability of the Activity scores from the home cage activity test was calculated from all sixty 30-second intervals across the entire day excluding the first three and last three measurements taken, during which time individuals were in low level lighting and either waking up or preparing for sleep, and so generally more or less active than usual. This method of measuring repeatability differs from some other studies which measured behaviour only two or three times with days or weeks between measures and hence over a longer overall timeframe. However, we feel that the very high number of repeat measures (60 within the day) make up for our shorter overall timeframe. The data recorded for the Tongue movements, Head movements and Activity score variables were typical of count data following a Poisson distribution and so repeatability was calculated using the methods described for count data for these variables. These methods utilised multiplicative dispersion GLMMs (in which the overdispersion is modelled as a further parameter to the distribution from which the original responses are assumed to be derived) with a log link for estimating repeatability on the original scale (Nakagawa & Schielzeth 2010). Due to discrepancies between LRT *P* values and 95% confidence intervals (as is often the case when following these methods, the LRT *P* values were too small, (Shinichi Nakagawa, pers. comm.), *P* values were not reported, and instead instances where the lower confidence interval was above 0 were considered significant (Nakagawa & Cuthill 2007). For further analyses were conducted with the statistical

software programme IBM SPSS v21.0 (IBM Corp 2012), the mean scores from the three later begging trials conducted on day five and day seven were averaged to produce a single Head movements and Tongue movements score for each individual. An Activity score was calculated for each individual which completed the home cage activity test by dividing the total movements recorded overall by the number of 30 s periods analysed ($N = 66$), to note the mean movements per each 30 s period. A generalised linear model utilising a binomial distribution with logit link was conducted to analyse the variation in survival of individuals that completed the begging assays to completion of the adult activity test. Head movements and Tongue movements were included as fixed covariates, and Sex as a fixed factorial terms. The maximal model had all of the fixed effects and their two-way interaction terms and the model was rotated in a stepwise manner so each term was tested for significance when they were the last term in the model. Non-significant effects were dropped if their inclusion did not increase the explanatory power of the model until the minimal model was produced. A GLMM utilising a normal distribution with an identity link was performed to analyse the variation in adult activity levels, with covariates of Tongue movements, Head movements, Sex and the interactions of the former two variables with Sex. Foster nest identity, Genetic nest identity and Pair identity (in the adult activity test) were included as random effects. However, as this model did not converge properly, we conducted two separate GLMMs (using normal distribution with identity link) for Tongue movements and Head movements with the above-mentioned random effects included and Sex and the interaction with Sex included as fixed effects. Finally, we ran three separate multiple regressions to predict body mass from tarsus length and either adult activity levels, nestling head movements or nestling tongue movements.

RESULTS

Both nestling begging activity behaviours measured (Head movements and Tongue movements) were significantly repeatable in males and females, both in the larger sample (all nestlings in the

original experiment) and for the smaller set of individuals that completed the home cage activity test, as shown in Table 4.1. Head movements and tongue movements were significantly positively correlated with each other at both the observation ($r = 0.633$, $N = 568$, $P < 0.0001$) and individual level ($r = 0.750$, $N = 98$, $P < 0.0001$). In the home cage activity test, activity levels of adults were significantly repeatable in males and females for the measurements made over the course of the day, also shown in Table 4.1. As shown in Table 4.2, Sex was determined to be the most likely factor predicting whether an individual died during the period between the day 7 begging assay and the adult activity test when individuals were 36-42 months old, with females more likely to die during this period than males. In contrast, neither Tongue movements nor Head movements were found to significantly influence survival (Table 4.2). The mean number of head movements during begging was found to be significantly positively correlated with adult activity levels measured 36-42 months later (Table 4.3). However, the mean number of tongue movements was not significantly correlated with adult activity levels (Table 4.3). Moreover, as shown above, neither the sex of the focal individual nor the interactions between sex and either head or tongue movements were significantly correlated with adult activity levels in either model (Table 4.3). From a multiple regression with adult activity levels ($F_{2,38} = 4.717$, $P = 0.015$, $R^2 = 0.199$), we found that adult activity levels predicted body mass ($P = 0.007$) but tarsus length did not ($P = 0.134$) (Figure 4.1). Similarly, from a multiple regression ($F_{2,39} = 4.405$, $P = 0.019$, $R^2 = 0.184$), we found that head movements predicted body mass ($P = 0.006$) but tarsus length did not ($P = 0.833$) (Figure 4.2). However, from a further multiple regression ($F_{2,39} = 1.731$, $P = 0.190$, $R^2 = 0.082$), we found that neither tongue movements ($P = 0.077$) nor tarsus length ($P = 0.876$) predicted body mass.

Table 4.1: The repeatability (*R*) of individuals' behaviour in the (a) nestling begging experiment and (b) home cage activity test. Repeatability in (a) was calculated from all of the six individual begging trials available for each individual. Repeatability of Activity score was calculated by comparing the middle 60 30-second movement scores over the course of the day.

Component	*R* ± SE	N	Lower CI	Upper CI
(a) Nestling begging activity				
All nestlings				
Head movements				
Male	0.601 ± 0.081	47	0.310	0.625
Female	0.572 ± 0.078	51	0.364	0.659
Tongue movements				
Male	0.606 ± 0.077	47	0.246	0.545
Female	0.571 ± 0.073	51	0.267	0.551
Nestlings that matured only				
Head movements				
Male	0.562 ± 0.120	19	0.213	0.678
Female	0.675 ± 0.149	16	0.191	0.787
Tongue movements				
Male	0.395 ± 0.116	19	0.040	0.499
Female	0.596 ± 0.135	16	0.106	0.637
(b) Home cage activity test				
Activity score				
Male	0.319 ± 0.083	19	0.149	0.469
Female	0.439 ± 0.104	16	0.21	0.615

Table 4.2: Summary of Generalised Linear Model (GLM) examining how the sex of the focal bird and the mean number of head movements and tongue movements produced by nestlings during begging influenced survival to the home cage activity test.

Term	B	SE	DF	Wald Chi-Square	*P* value	Upper CI	Lower CI
Sex of focal bird	1.064 (female)	0.422	1	6.371	0.012	0.238	1.890
Tongue movements	0.101	0.263	1	0.147	0.702	-0.415	0.617
Head movements	0.027	0.456	1	0.004	0.953	-0.866	0.921
Tongue movements x sex of focal bird	-0.304 (female)	0.536	1	0.322	0.570	-1.355	0.746
Head movements x sex of focal bird	0.367 (female)	0.928	1	0.156	0.693	-1.451	2.184

Table 4.3: Summary of Generalised Linear Mixed Models (GLMMs) examining: (a) how the mean number of head movements and the sex of the focal bird influence adult activity levels during the home cage activity test and (b) how the mean number of tongue movements and the sex of the focal bird influence adult activity levels during the home cage activity test.

Term	Coefficient	SE/SD	DF	F-Value	P value	Upper CI	Lower CI
(a) Head movements							
GLMM							
Head movements	2.114	0.633	33	11.144	0.002	0.826	3.402
Sex of focal bird	1.025 (male)	0.829	32	1.528	0.225	-0.664	2.714
Head movements x sex of focal bird	1.157 (male)	1.418	31	0.666	0.421	1.735	4.049
Foster nest identity	6.238	SD: 2.498					
Genetic nest identity	1.756	SD: 1.325					
Pair identity	2.083	SD: 1.443					
(b) Tongue movements							
GLMM							
Tongue movements	1.335	0.810	33	2.717	0.109	-0.313	2.983
Sex of focal bird	1.140 (male)	0.992	32	2.020	0.165	-0.611	3.430
Tongue movements x sex of focal bird	1.905 (male)	1.390	31	1.878	0.180	-0.930	4.739
Foster nest identity	1.990	SD: 1.411					
Genetic nest identity	3.692	SD: 1.921					
Pair identity	1.722	SD: 1.312					
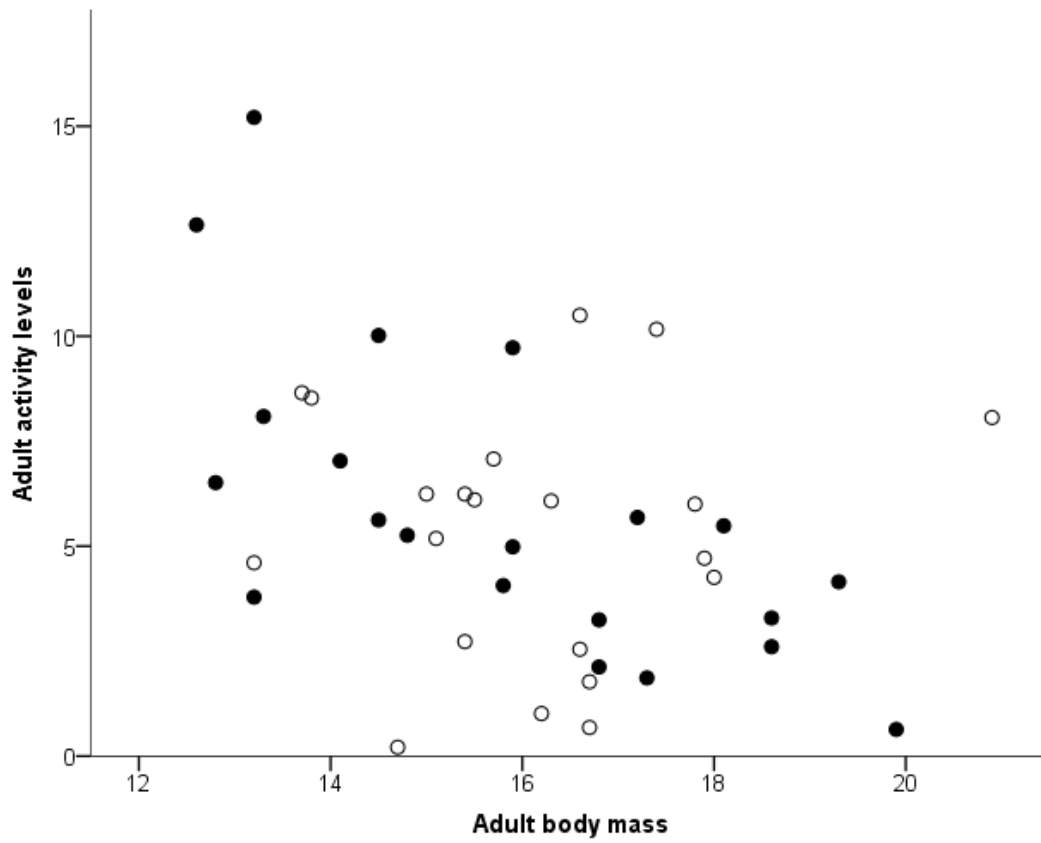
Figure 4.1: Correlation between adult body mass and adult activity levels. Males are represented with filled circles and females with open circles.
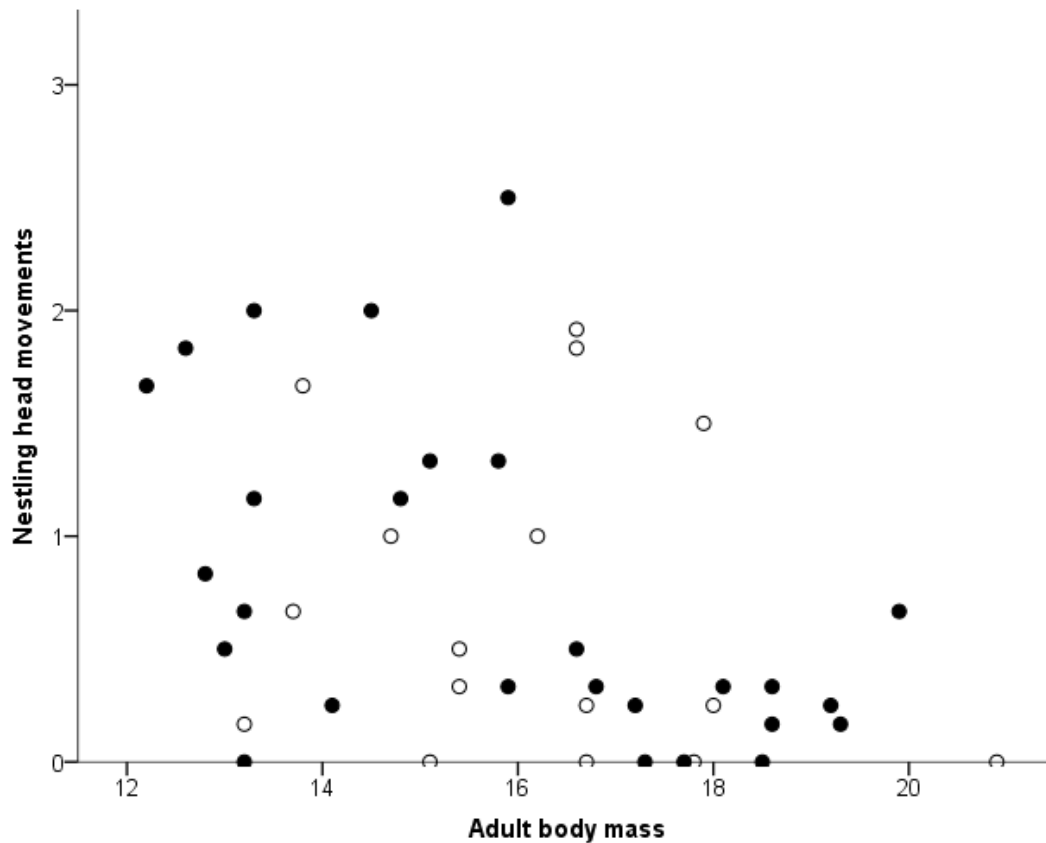
Figure 4.2: Correlation between adult body mass and nestling head movements. Males are represented with filled circles and females with open circles.

DISCUSSION

Our study confirms that the number of head and tongue movements made during nestling begging bouts were repeatable over time (in this study, roughly a 48-hour period) in zebra finch nestlings, providing evidence that 'begging activity' may constitute a personality variable that is measurable at a very young age. Moreover, the mean number of head movements, but not the mean number of tongue movements made during the nestling begging assays, was significantly positively correlated with adult activity levels measured much later in their life, several years later. This suggests that the tendency for individuals to be more active in different contexts persists over the majority of their lifespan, and is established very early in life. This is the first study in a bird to uncover evidence that nestling behaviour is predictive of long-term adult phenotype (but see Fucikova et al., 2009),

and the first to compare a personality trait measured in very young birds with a similar trait much later in life. Previous work on the same species has demonstrated links between activity and other personality traits such as boldness, aggression, neophobia, dominance, leadership and the use of producer/scrounger foraging tactics (Beauchamp 2000; David et al. 2011a; David et al. 2011b; David et al. 2012; Martins et al. 2007; Schuett & Dall 2009; Schuett et al. 2011a). These correlations between personality traits imply the existence of what is often referred to as a behavioural syndrome in this species, whereby individuals tend to occupy one of two behavioural types: 'fast/proactive' or 'slow/reactive' (David et al. 2011a). This raises the possibility that nestling begging activity is correlated with these other adult personality traits, and may potentially be used to predict not only adult phenotypes but also an individual's behavioural type ('fast/proactive' versus 'slow/reactive' at a very young age). However, further work is needed to directly verify these potential links.

It is unclear why we found a significant positive relationship between the mean number of nestling head movements during begging movements and adult activity levels, but failed to find a significant relationship between adult activity levels and the mean number of tongue movements. While both behaviours are thought to be produced to attract the attention of parents and provoke feeding (Kilner & Johnstone 1997), it may be that the speed of movement of a large part of the body (the entire head and neck region) is more reflective of the general activity levels of an individual than the comparatively smaller tongue region. As a possible explanation for this, head movements are more likely to require a larger amount of energy to perform, while, in contrast, tongue movements may be more reflective of begging effort. However, it has been shown that there is no significant correlation between the mean rate of tongue movements made by a nestling and the frequency that this nestling is fed by the parents (Muller & Smith 1978), negating the idea that tongue movement speed could be considered as a direct measure of begging intensity. Sex was found to be a significant factor explaining whether or not an individual survived the 36-42 month period until the home cage activity test was conducted, with males more likely to survive than

females, a result that is consistent with previous captive studies (Burley 1985). However, sex did not significantly explain the significant relationship between nestling head movements and adult activity levels, which suggests that the positive relationship between the two variables is not sex-specific. In contrast, one factor that was significantly correlated with nestling and adult behaviour was adult body mass. Individuals with a comparatively higher body mass tended to make less head movements during begging as nestlings and tended to have lower activity levels as adults in the home cage activity test. Hence, more active individuals during begging as nestlings are lighter adults on average. Unfortunately, it is difficult to disentangle the cause and effect of this relationship, as individuals may differ in nestling head movements either due to intrinsic differences in activity or because they are trying to acquire more food via begging. A previous study found that food-rationed great tit nestlings tended to display higher exploratory behaviour as adults than control nestlings (Carere et al. 2005), which suggests that receiving less food during ontogeny might produce differences in adult personality. Lighter adults were also more active. There are a number of reasons why individuals who are carrying excess weight would exhibit lower activity levels. Individuals might be following different energy storage tactics, with some individuals storing large amounts of energy as fat to preserve against starvation, and others maintaining little fat to remain light and agile (thereby making it easier to escape from predators). In this manner, general activity levels may been linked to the relationship between energetic gains and mortality, with different individuals employing different life-history tactics with regards to factors such as growth and fecundity (Stamps 2007, Biro & Stamps 2008). Moreover, the long-lasting link we found between general activity levels and body mass suggests that activity might be tied to individual differences in metabolic rate, especially as high levels of movements are energetically costly (Careau et al. 2008). A number of different factors have been shown to influence resting metabolic rate in the zebra finch, such as individual genetics, early environment and maternal effects (Nilsson et al. 2011), and these factors are purported to be linked to metabolic rate while an individual is

active (Houston 2010). We suggest that this inference should be addressed by future work that directly measures metabolic rate.

Due to the relatively low sample size of individuals that survived to the onset of our adult activity test, this study did not attempt to directly address whether ontogenetic factors, such as hatch order, yolk hormonal distribution, nutrition and the specifics of the social environment influenced adult personality and behaviour. However, our earlier work, on the much larger sample size of nestlings available, established experimentally that both hatch order and brood size influence begging intensity (both begging activity measures, head movements and tongue movements, were included as attributes of begging intensity), and later-hatched males from natural broods beg with a greater intensity than early-hatched males, particularly when brood size was large (Gilby et al. 2012). These results are supported by other work showing that hatch order and brood size are positively correlated with begging activity (Kacelnik et al. 1995; Saino et al. 2001). Moreover, in a separate study of the zebra finch, hatch order (early or late) affected subsequent adult exploratory behaviour, with late-hatched individuals exploring a novel environment faster than early-hatched individuals (Mainwaring & Hartley 2013). Hence, it is quite feasible that later-hatched individuals may be more likely to display higher activity levels as adults. This idea is consistent with the finding of a positive correlation between adult and offspring exploration behaviour (Schuett et al. 2013), although this study did not find any effect of hatch order, rearing regime and clutch size. A number of other factors have also been shown to influence juvenile and adult personality, such as the sex-ratio of an individual's brood (Mendl & Paul 1991; Naguib et al. 2011), their endocrine profile (Ruuskanen & Laaksonen 2010; Tobler & Sandell 2007; van Oers et al. 2011; Zimmer et al. 2013), nutrition and food availability (de Rooij et al. 2012; Krause & Naguib 2011; Mendl & Paul 1991; Zimmer et al. 2013), adult body condition (David et al. 2012c) and aspects of the immune system (Butler et al. 2012; Moreno-Rueda 2010; Moreno-Rueda et al. 2012; Saino et al. 2001; van Oers et al. 2011). Together with the results reported here, this suggests that adaptations to environmental variation in early life (greater begging intensity and activity to compete with older

nest mates) may persist into adulthood (Roulin et al. 2010). These adaptations may affect fitness, as activity has been shown to influence fitness attributes such as predator-prey interactions, resource acquisition and the risk of mortality (Sweeney et al. 2013; Werner & Anholt 1993). Our findings suggest that the zebra finch may make a good candidate system for the study of the influences of ontogeny on adult personality. Moreover, the fact that our results suggest we can predict adult phenotype on the basis of a trait expressed very early in life (just 18 days after the formation of the zygote), will enable the examination of selection on these aspects of personality (as many individuals die in the first months of life).

Chapter Five

Personality in captivity: more exploratory males reproduce better

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ABSTRACT

The existence of animal personality is well-established across a wide range of species, with the majority of evidence for this being obtained from individuals held in captivity. However, individuals tend to be exposed to different selective pressures in captivity from those generally experienced in the wild, which may result in phenotypic changes in their behaviour, and different patterns of selection. Whilst this does not alter their utility as model systems, we do have to be cautious about the potential biases that may result. For example, if some personality types are better suited to the captive environment but not in the wild (where processes such as fluctuating selection may offset the fitness advantages of these personality traits over time), those individuals may be overrepresented in experimental samples and through the production of offspring. We measured whether the reproductive behaviour and success of zebra finches in a captive mixed-sex aviary environment was influenced by an aspect of their personality, their exploratory behaviour in a single-sex social aviary. We found that more exploratory males made a greater number of breeding attempts and raised more nestlings than less exploratory males. These results were not confounded by extra-pair paternity, which was not related to personality, or by the individuals that did not initiate any reproductive attempts at all. Our work provides evidence that attributes of personality may influence the degree to which individuals cope with, and thrive in a captive environment and this should be accounted for in both experimental design and the interpretation of results. Furthermore, this suggests that there may be selection on these traits as part of the domestication process.

INTRODUCTION

In the wild, evolution has shaped individuals' behaviour to optimize reproductive success. However, in captivity individuals are often freed from certain selective pressures experienced in the wild such as resource acquisition and predator avoidance (McPhee 2003). This dramatic alteration in selection pressures may result in phenotypic changes in physiology and behaviour, which may also be produced by genetic mechanisms such as genetic drift, inbreeding and artificial selection, or be brought on by processes that occur during development (Price 1970; Lickliter & Ness 1990; McPhee 2003; Moorhouse et al. 2007; Jones et al. 2011). The captive populations used in scientific work have often been subjected to many generations of breeding under artificial conditions (McPhee 2003), providing ample opportunity for the relaxed or different selective pressures associated with captivity to affect their subsequent behaviour. When subjected to the different stressors experienced in captivity compared with the wild, certain individuals may be better able to cope with captive life and hence are more likely to reproduce (Carlstead et al. 1999; Wielebnowski 1999; Carere & Maestripieri 2013), resulting in individuals better adapted to captivity in subsequent generations. Personality traits, or behaviour that shows both differential and context generality and behavioural consistency, are one factor that may be influenced by or determining an individual's tolerance to captivity (Koolhaas et al. 1999; Carere et al. 2003; Groothuis & Trillmich 2011; Carere & Maestripieri 2013).

Much work has been conducted on measuring animal personality in captivity (Carere & Maestripieri 2013), but there has been little focus on relating these individual differences in behaviour to fitness attributes. In the wild, even though personality has only a limited genetic basis (van Oers et al. 2005a), personality differences have been hypothesized to be maintained when they contribute to consistent individual differences in life history traits such as productivity, reproductive success, growth and survival but trade-offs occur between these traits; for example, one personality

type might generally lead to higher reproductive success but also lower survival (Biro & Stamps 2008). Moreover, the pace-of-life syndrome hypothesis (Réale et al. 2010), predicts that more proactive individuals (which tend to display personality traits such as high exploratory and risk-taking behaviour) are more likely to maximise current over future reproduction than reactive individuals (Wolf et al. 2007). Individuals from populations with reduced predation risk have also been shown to have increased reproductive investment (Reznick et al. 1996), and higher boldness (Fraser & Gilliam 1987), which suggests that relaxed predation risk can influence not only reproductive behaviour but also personality (Réale et al. 2010). In captivity, the potential decoupling of life-history trade-offs may lead to biased results, produce personality types that are not well-suited for life in the wild, and lead to reduced genetic diversity and behavioural variation (Carere & Maestripieri 2013). Even relatively short periods in captivity (within 20 generations) may influence the behaviour or personality attributes of captive populations (Lacy et al. 2013). Individuals bred in captivity have been shown to display increased boldness or risk-taking behaviour than their wild equivalents (Yoerg & Shier 1997; Roberts et al. 2011), possibly resulting from greater reproductive success of bold individuals in captivity relative to their shy counterparts (Smith & Blumstein 2008). In the wild, predation and resource acquisition appear to reduce the survival of bold individuals compared with shy individuals (Smith & Blumstein 2008), while in great tits *Parus major*, fitness has been shown to be linked to exploratory behaviour, though the relationship varies with sex and environmental conditions (Dingemanse et al. 2004). However, in captivity, individuals are usually not subject to predation risk and often receive resources such as food *ad libitum* (McPhee 2003), which may allow, all else being equal, the bold individuals to prosper and pass on this trait to their offspring (Roberts et al. 2011). In other species, captivity has also been shown to influence selection on these personality traits. For example, in some of the earliest work in this field, Price (1970) demonstrated that in deer mice, *Peromyscus maniculatus bairdii*, 20-25 generations in captivity increased the latency and likelihood of individuals to explore an open-field chamber. Conversely, in oldfield mice, *Peromyscus polionotus subgriseus*, 35

generations in captivity resulted in reduced exploration of an open-field chamber (McPhee 2003). Levels of dominance, aggression and anti-predator behaviour have also been shown to be influenced by artificial conditions; however the direction of this change differs between species (Mathews et al. 2005; Kelley et al. 2006; Blanchet et al. 2008; Håkansson & Jensen 2008).

The loss of intrinsic personality variation caused by captivity may be affecting experimental outcomes, by biasing studied samples towards individuals that have become dissimilar behaviourally to their wild ancestors, and only represent a small subset of the personality traits of the general population (i.e. the most bold or tame individuals), due to selection. This bias may start with the influence of personality on the susceptibility of individuals to be trapped in the wild, with more exploratory and risk-taking individuals generally more likely to be captured from the wild (Garamszegi et al. 2009; Carter et al. 2012; Biro 2013). In addition to the initial cohort of captive animals being a biased subset of the population (Biro & Dingemanse 2009) (a founder effect), it is also possible that personality variation will determine which individuals prosper and breed under captive conditions (selection). In the zebra finch, breeding behaviour is a major area of focus, with breeding experiments conducted in small breeding cages or aviaries (Griffith & Buchanan 2010). Typically, studies utilize sub-sampling by focusing only on those individuals that manage to breed, with unsuccessful breeders not contributing to experimental datasets (especially for the research focused on reproductive behaviour or physiology) and not contributing to the next generation of laboratory stock. However, in any one experiment, the propensity of individuals to breed, which partner they select to breed with or the comparative number of offspring produced may be linked to their personality, leading to bias in the experimental design, and potentially in the interpretation of results, particularly with respect to attempting to relate experimental results back to adaptive outcomes in wild populations. Schielzeth et al. (2011) found that in the zebra finch, the repeatable personality trait neophilia, or speed of approach to a novel object, was not significantly correlated with overall reproductive success, promiscuity or extra-pair paternity in captive aviaries. However, manipulating the sex ratios in the aviaries was found to influence the correlations between neophilia

and the proportion of extra-pair paternity, suggesting that neophilia is tied in with variation in reproductive strategies, especially in males. Furthermore, exploratory behaviour has been shown to influence partner-selection specificity and consistency in the female zebra finch (David & Cézilly 2011). Two previous studies in birds have shown that socially monogamous pairs with more similar (assortative) levels of the personality traits exploratory behaviour and aggression, tended to raise foster offspring in better condition than pairs with dissimilar (disassortative) personalities (Both et al. 2005; Schuett et al. 2011a). Moreover, in one study when both members of a pair had high levels of exploration and aggression, they raised offspring in a better condition than any other pair combination (Schuett et al. 2011a). Such studies therefore indicate the potential importance of personality variation to reproductive success in the short-term. Any selection that captive conditions impose on individuals is likely to have been ongoing for several hundred generations in the domesticated zebra finches of North America and Europe.

Here, we examined the extent to which the breeding success of zebra finches in a common captive environment, a large outdoor aviary, was influenced by their exploratory behaviour. Prior to our breeding trial, we measured exploratory behaviour in a social foraging context in the same aviary environment, but in different social groups. Second, we measured the reproductive success of the behaviourally tested pairs. Following the previous work of Schuett et al. (2011a) and the predictions of the pace-of-life hypothesis (Réale et al. 2010), we predicted that the more exploratory individuals would have greater reproductive success in the aviary. Our work builds on previous work (Schuett et al. 2011a), by considering zebra finches breeding in a larger captive environment in which inter-individual competition and positive and negative social interactions can take place as they do in wild free-living populations of this species (Zann 1996; Mariette & Griffith 2013).

MATERIALS AND METHODS

Ethical Note

Animal welfare and methodological design were approved by the Animal Ethics Committee at Macquarie University (AEC reference number: 2010/059). The health and condition of all birds were monitored on a daily basis and no individuals were noted to be unduly distressed by the experimental procedures or housing conditions.

General Methods

Data were collected from July 2011 to June 2012 from domestic 'wild-type' zebra finches originally obtained from aviculturists in the Sydney region in 2005 and bred at Macquarie University for either three or four generations (Tschirren et al. 2009). All subjects were two to three years old at the time of the experiments, and had spent the majority of their lives in single-sex outdoor aviaries (8 x 10 x 2 m), with brief periods spent indoors in home cages with up to four individuals (77 x 48 x 40 cm). Individuals were provided with *ad libitum* commercial finch seed along with water, grit, cuttlefish and a daily provision of chopped spinach and peas. During experimental trials, aviaries and cages were supplied with water ad libitum, and featured a number of perches. Aviaries were also supplied with nest boxes during trials. Individuals were kept on an 11:13 h light:dark regime when housed indoors and at a constant temperature of 24 ºCelsius with 50% relative humidity. At the end of the experiment the birds were maintained in the same mixed sex flock in a similar large holding aviary.

Aviary Foraging Test and Data Analysis

For the methodology of this experiment and the subsequent data analysis, see Chapter 3 (Part 1: Aviary Foraging Test).

Aviary breeding experiment

The aviary breeding experiment was conducted for 72 days commencing in September 2011, and was run with 31 males and 25 females (3 males were not used in the breeding experiment as they expressed plumage colour mutations which we were trying to remove from our population). Before being introduced into the breeding aviary (8 x 10 x 2m), a small blood sample (<30µl) was taken from the brachial vein and stored in 95% ethanol. The previously sexually-segregated adults were simultaneously released into the aviary containing 34 nest boxes, each fitted with a single-coil antenna (5 cm diameter) connected to a PIT-tag detection system (LID-665 decoder; Trovan, UK) fixed inside the nest box around the entrance hole (to record bird identification and time and date (Mariette et al. 2011)). The contents of the nest boxes were inspected every 5-10 days between 10 a.m. and 3 p.m. to count the number of eggs and nestlings. When nestlings reached 12-15 days of age they were banded with a numbered plastic band and a blood sample was taken for parentage analysis. Putative parentage was assigned using a combination of decoder data and direct observation (using binoculars) of parents colour bands while they visited nest boxes from three to ten metres away. Individuals wore one of 15 randomly-allocated band colours with the PIT-tag attached from the aviary foraging test onwards, (the PIT-tag and it's glue obscured most of the band so little colour was showing), and also one of 45 different colour bands in the aviary experiment for identification. Although the issue of colour bands influencing attractiveness has been overstated in previous research (Seguin & Forstmeier 2012), we reduced any potential effect in this experiment by having no birds wear a red band and only one wear a green band (the two colours for which some effect has been shown). In only one case (where a male was not recorded to visit the nest)

were we unable to identify a social mother or father from either PIT-tag or observational data. We recorded the number of reproductive attempts made by each individual and the number of nestlings each individual successfully raised to banding age. All of the nestlings were left with their parents in the aviary until at least the end of the whole experimental period and until they had moulted into their adult plumage.

Molecular methods

We assigned parentage using ten fluorescently labelled microsatellite loci in two multiplex PCR reactions using a QIAGEN Multiplex Kit; reaction 1 included *Tgu*1, *Tgu*3, *Tgu*12 (Forstmeier 2007) and reaction 2 included *TG01-000*, *TG02-088*, *TG03-031*, *TG04-012*, *TG05-046*, *TG11-011*, *TG22-001* (Dawson et al. 2010). Samples were genotyped on an ABI3730 DNA Analyser (Applied Biosystems, Foster City, CA, U.S.A.) using GS-500 (Liz) in each capillary as a size standard. Allele sizes were estimated using GeneMapper version 3.7 (Applied Biosystems). All individuals were initially included in reaction 1 and paternity could be assigned to approximately half of the nestlings using these three markers. The remaining individuals were included in reaction 2, after which all parentage could be unambiguously assigned to most individuals. Two potential sires were identified for one offspring. In this case, the putative male matched and so was assumed to be the sire of this offspring. The overall final amplification failure rate across all loci was less than 1% and there was evidence of allelic dropout at 3 loci: *Tgu1* (1 offspring), *Tgu3* (4 offspring) and *TGU11-011* (2 offspring).

Statistical Analyses

Repeatability (*R*) values were calculated in R (R Development Core Team 2013) using the add-on package rptR (http://rptr.r-forge.r-project.org/), for males and females separately following the

methods described in Nakagawa & Schielzeth (2010). Repeatability was calculated for the exploration scores using Gaussian methods as this data was normally-distributed according to a Shapiro-Wilk test, although this method was not designed to be used with ordered data. These LMM-based methods utilized parametric bootstrapping and Bayesian methods for interval estimation and randomization for interval estimation (Nakagawa & Schielzeth 2010). All remaining data were analysed using the statistical software programme IBM SPSS v21.0 (IBM Corp 2012), and all data from the males and females were analysed separately. The exploration scores were compared with whether or not an individual was recorded engaging in putative reproductive activity (to at least the egg stage) using independent-samples t-tests. Spearman's rank-order correlations were used to compare the exploration score to the five breeding behaviour variables: 1) the number of breeding attempts made where at least one nestling hatched, 2) the number of successful breeding attempts made (where at least one nestling was banded), 3) the total number of nestlings raised, 4) the total nestlings raised in the first breeding attempt an individual made and 5) the number of genetic nestlings that were banded. To investigate whether the individuals that paired up with a partner in the aviary (we defined 'pairing up' as making at least one breeding attempt with a partner) did so assortatively or disassortatively (or neither) with respect to their exploratory behaviour, we conducted a Pearson correlation comparing male and female exploration scores. Finally, we conducted a generalized linear mixed model (GLMM) with a Poisson distribution and log link to analyse the variation in reproductive success of parents (total nestlings raised to banding age), with the covariates male exploration score, female exploration score and the interaction between them. Pair identity was included as a random effect.

RESULTS

Aviary foraging test

The exploration scores from the aviary foraging test were significantly repeatable in males ($R \pm$ SE $= 0.462 \pm 0.155$, N = 26, CI = 0.11, 0.726; Mean in hours $\pm$ SE (excluding all overnight non-feeding periods) = 18.346 ± 2.140) but not females ($R \pm$ SE = 0.291 ± 0.171, N = 25, CI = 0, 0.607; Mean in hours $\pm$ SE (excluding all overnight non-feeding periods) = 21.816 ± 2.492) between the first and second trials. As the results of the aviary foraging test were not significantly repeatable in females, the test and data should not be interpreted as a reliable measure of exploratory behaviour in females, however we included female exploration scores in subsequent analyses for completeness.

Reproductive success

There were three adult deaths of natural causes (one male and two females) recorded during the aviary breeding trials and these individuals were excluded from the data analysis (this number was to be expected over this period, considering individuals were two to three years old at the start of the experiments). There were also six males whose exploration scores were not successfully calculated during the aviary foraging test, and were excluded from the data analyses that featured this measure. From visual and PIT-tag observation data, 24 out of 30 males (80%) and 19 out of 23 females (82.6%) were putatively associated with a reproductive attempt (defined as tending a nest with eggs present), although parentage was only confirmed when offspring were successfully raised to banding age, blood sampled and genotyped. Whether or not an individual was recorded engaging in putative reproductive activity (to at least the egg stage) was not significantly related to an individual's exploration scores (male: $t(22) = -0.280$, $P = 0.782$; (20 yes, 4 no) female: $t(21) = -0.896$, $P = 0.381$ (19 yes, 4 no)). We found that the exploration scores of males were significantly

positively correlated with the number of breeding attempts they made and marginally not

significantly correlated with the number of nestlings they raised and the number of successful

breeding attempts they made (Table 5.1, Figure 5.1 and Figure 5.2). However, in females, there

were no significant correlations between their exploration score and the number of breeding

attempts made or the number of nestlings raised (Table 5.1). The number of nestlings raised in each

individual's first breeding attempt was not significantly correlated with their exploration scores in

either males or females (Table 5.1). During the trial, 21 males (70%) and 18 females (78.3%)

hatched at least a single nestling and 17 males (56.7%) and 17 females (73.9%) managed to

successfully raise at least one nestling to banding age. Of all individuals in the trial (except those

that died during the trial), males made a mean of 0.967 breeding attempts (range $= 0 - 2$) and raised

1.6 nestlings to banding age on average, while females made a mean of 1.174 breeding attempts

(range $= 0 - 2$) and raised 2.043 nestlings on average (range $= 0 - 7$). All individuals that made

more than one successful breeding attempt made their second breeding attempt with the same social

partner. There was no evidence that individuals paired assortatively or disassortatively with respect

to their exploratory behaviour ($rs = 0.167$, $N = 17$, $P = 0.523$). Finally, of those pairs that formed,

we found no evidence that the interaction between male and female exploration scores influences

the total number of nestlings raised by that pair, nor the female exploration score, but there was a

significant positive correlation with the male exploration scores (Table 5.2).

Genetic data

In total there were 29 nests where at least a single nestling hatched and 17 nests where at least one

nestling was successfully raised to banding age, resulting in a total of 50 blood sampled and banded

nestlings. The genetic data of one brood of two nestlings was lost due to a technical error. As there

were a relatively low number of adults in the aviary population we were able to determine the

parentage of all genotyped nestlings unambiguously with between three to 10 microsatellite loci, on

the basis of distinct genotypes. In cases where the three initial loci were insufficient to identify the parents, seven further loci were genotyped to identify the genetic parents of the offspring. In total, we genotyped 48 offspring, 20 of those at three loci and 28 at 10 loci. Of the 48 nestlings that were genotyped, 41 matched their social mother and 30 matched their social father (the social father was not identified from observations at one brood of two nestlings). There were seven out of 46 instances (15.2%) where nestlings were raised at a nest by neither the genetic mother nor father, with these identified as incidences of intraspecific brood parasitism by five different females, parasitizing six different broods. The genetic mothers and fathers of these individuals often bred successfully at other nests; however, in each case, they bred separately of one another. There were 39 nestlings that were produced in the nest of their genetic mother and of these 10 (25.6%), from seven broods, were sired by an extra pair sire (five males were responsible for these nestlings). The exploration scores of males or females were not significantly correlated with the total number of their genetic offspring banded during the experiment (the sum of those in their own nest and in the nests of other males; Table 5.1). From the genetic data, 12 out of 30 males (40%) and 14 out of 23 females (60.9%) were the genetic parent of at least one nestling that survived to banding age. Whether or not a male successfully engaged in extra-pair mating resulting in a nestling reaching banding age (overall: 5 males did, 25 did not; excluding those males missing an exploration score: 5 males did, 19 did not) was not significantly correlated with the exploration score of the genetic father ($t(22) = 0.602$, $P = 0.553$). Moreover, the tendency of a male to be cuckolded (overall: 7 males were, 23 were not; excluding those males missing an exploration score: 6 males were, 18 were not), was not significantly correlated with his exploration score ($t(22) = 0.089$, $P = 0.930$). Moreover, whether or not at least some of a female's genetic nestlings were raised by a different female (5 females did, 18 did not) was not significantly correlated with the exploration score of the genetic mother ($t(21) = 0.643$, $P = 0.527$), suggesting that the tendency of a female to lay an egg into the nest that was not her own (or desert eggs in a nest box) was not correlated with her exploration score. These correlations were qualitatively the same when those individuals that were

never associated with a reproductive attempt were removed from the dataset. From the observational and genetic data combined, no reproductive effort was recorded for 5 out of 30 males (16.7%) and 4 out of 23 females (17.4%). Only a single male was found to have sired offspring in another individual's nest despite not being associated with a reproductive attempt in his own right.

Table 5.1: Spearman rank correlations showing comparisons between exploration scores with four measures of breeding activity and success in males and females: 1) the number of breeding attempts an individual made where at least one nestling hatched, 2) the number of breeding attempts an individual made where at least one nestling made it to banding age, 3) the number of nestlings an individual raised to banding age from all breeding attempts, 4) the number of nestlings raised to banding age from only the first breeding attempt an individual made and 5) the number of an individual's genetic offspring raised to banding age by any individuals in the trial. Sample sizes were lower than the total number of individuals in the aviary as individuals were removed from the analysis if they died during the experiment (1 male, 2 females) or if their exploration scores were not successfully calculated during the aviary foraging test (6 males only), or for 'total nestlings raised in 1st breeding attempt', if they did not make any breeding attempts.

Correlations with exploration score	Male			Female		
	rs	*N*	*P* value	*rs*	*N*	*P* value
Number of breeding attempts	0.556	24	0.005	0.193	23	0.670
Number of successful breeding attempts	0.381	24	0.066	0.212	23	0.330
Total nestlings raised	0.393	24	0.058	0.282	23	0.193
Total nestlings raised in 1st breeding attempt	0.017	20	0.942	0.293	19	0.224
Total genetic nestlings	0.192	24	0.370	0.186	23	0.396
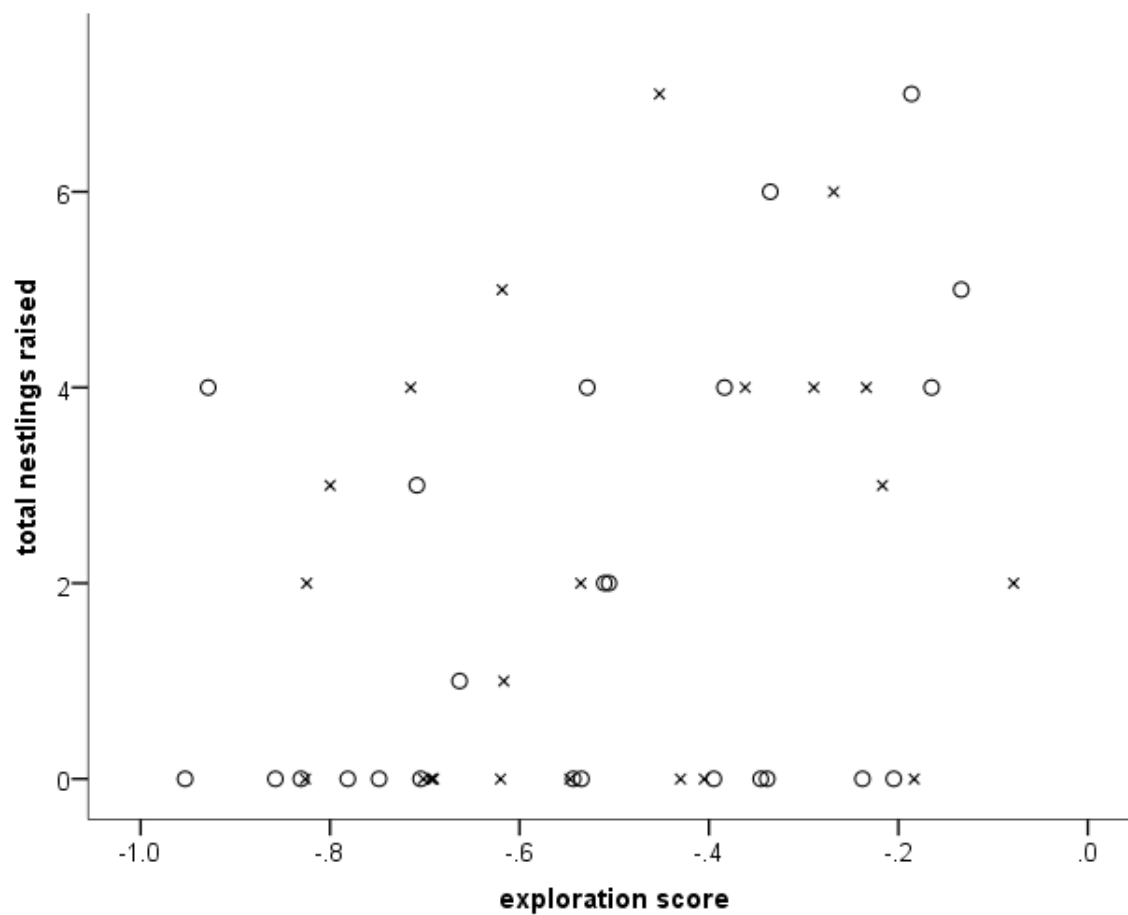
Figure 5.1: The correlation between exploration scores and the total number of nestlings successfully raised to banding age. A higher exploration score indicates a faster mean order to find two feeders in the two trials of the aviary exploration test. Males are shown with open circles and females with crosses.
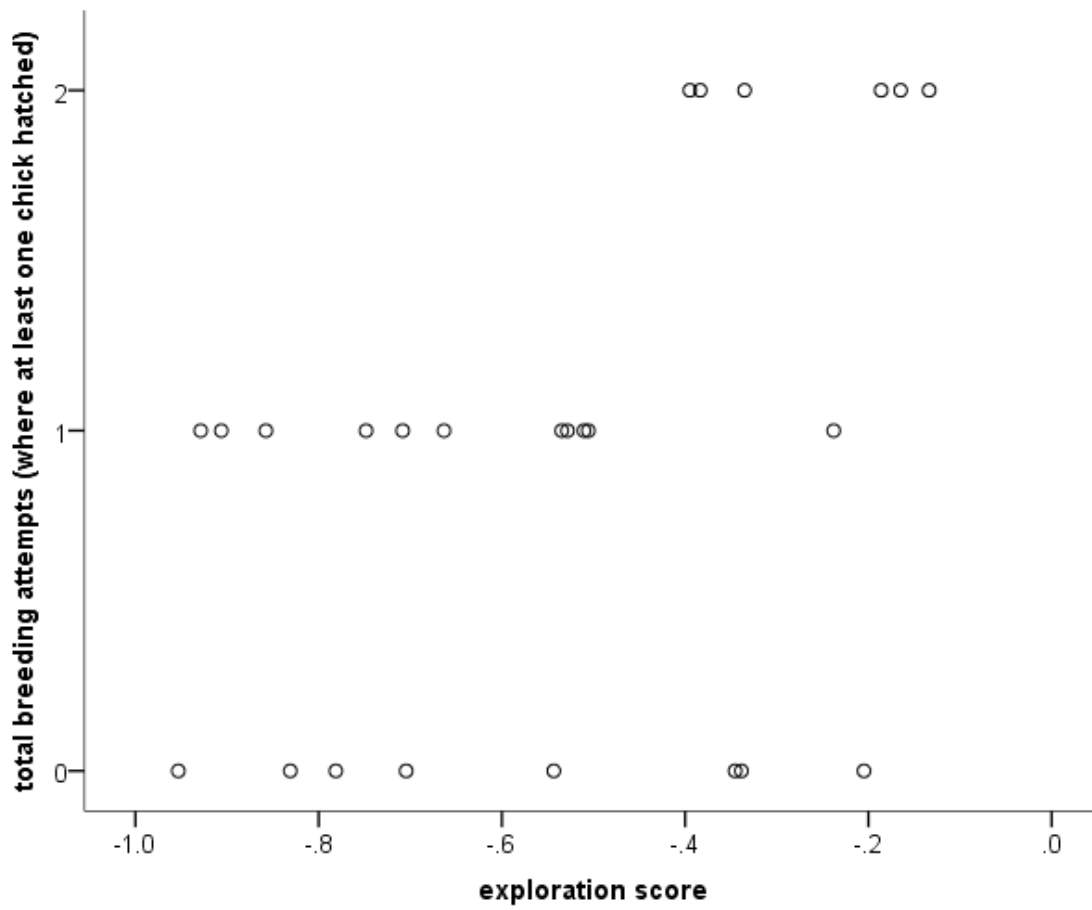
Figure 5.2: The correlation between exploration scores and the number of breeding attempts made (0, 1 or 2) during the aviary breeding experiment by males.

Table 5.2: Summary of Generalised Linear Mixed Models (GLMM) examining how the male and female exploration scores and the interaction between them influenced the total number of nestlings raised to banding age by that pair.

Term	Coefficient	SE	DF 1	DF 2	F-Value	P value	Upper CI	Lower CI
Male exploration	2.028	0.902	1	15	5.055	0.040	0.105	3.951
Female exploration	1.346	0.692	1	14	3.785	0.072	-0.138	2.829
Male exploration x female exploration	-3.771	4.526	1	13	0.694	0.420	-13.550	6.008
Pair identity	0.345	SD:0.587						

DISCUSSION

We found that for males, aspects of an individuals' exploratory personality were predictive of the degree to which they succeeded in producing and rearing offspring with their partner in captivity. More exploratory males made a greater number of breeding attempts where at least one nestling hatched. Moreover, for the males that attempted to breed with a partner (and marginally non-significantly for all of the males in the aviary), more exploratory males raised more nestlings successfully with their partner. However, exploratory behaviour did not affect the propensity of individual males to either breed or not breed. Furthermore, exploratory behaviour was not significantly related to the incidence of extra-pair paternity in either males or females. In contrast to males, the exploratory behaviour of females was not significantly repeatable and there was no significant relationship between this variable and measures of reproductive success.

There are a number of reasons why more exploratory males might have shown increased breeding behaviour in a captive aviary environment. One explanation is that the males with higher exploration scores were better able to provision their offspring with adequate food. In the wild, males are generally thought to be more likely than females to take on leadership roles in a foraging context (Zann 1996). In male zebra finches, both exploration and leadership are repeatable behaviours (Schuett & Dall 2009). Moreover, in randomly formed zebra finches pairs, the more active and exploratory individual was found to take on the leadership role in arriving at a foraging patch in nearly all cases (Beauchamp 2000). Hence, the males with higher exploration scores may have been more effective at leading their partners on foraging excursions to provision their offspring, as although food is provided ad libitum in an aviary environment, parents still have to make many foraging excursions to the feeders to feed their nestlings a sufficient amount of food for development (El-Wailly 1966).

Alternatively, the greater breeding activity of more exploratory males may have resulted from an increased desire to breed or a greater ability to breed successfully in a relatively short period of time. More exploratory males not only raised more nestlings successfully, they also made more breeding attempts (with several highly exploratory individuals attempting to breed twice over the 72 day period), suggesting they may be quicker to instigate or repeat breeding behaviour in an aviary environment. Previous work in another context has shown that established pairs are able to start a breeding attempt more quickly when given the opportunity (Adkins-Regan & Tomaszycki 2007). In this species, breeding in a highly unpredictable ecological context in the wild (Zann 1996), there is probably strong selection on the ability of individuals to quickly mobilize a reproductive effort when conditions are appropriate. In the context of our experiment, this may have occurred due to more exploratory males being quicker to establish partnerships in the aviary environment, or the short time span of the experiment (72 days) may have reduced the ability of less exploratory individuals to breed as effectively. A likely mechanistic route for such variation amongst individuals with respect to personality and reproductive activity is that prolonged elevated

stress in less exploratory individuals may have prevented or delayed breeding. Being introduced to a new environment and females for the first time as adults may have caused disproportionately more stress to those individuals less able to cope with it (Carere et al. 2003; Carere & Maestripieri 2013). However, we did not find that the number of offspring produced in an individual's first breeding attempt was correlated with their exploratory behaviour. Moreover, one study found that stress during handling was not significantly correlated with exploratory behaviour in the zebra finch (David et al. 2012b). Our results suggest that more exploratory males achieved greater breeding success through being more likely to breed repeatedly within the short trial. This result supports the hypothesis that more exploratory individuals are likely to maximise current over future reproduction (Wolf et al. 2007; Réale et al. 2010). Hence, we may have achieved different results if individuals were able to breed over a longer period of time, with less exploratory individuals potentially compensating for a slower start to breeding over time. However, only allowing a short window for breeding is ecologically relevant for this species as breeding windows can be short and close abruptly in the wild (Zann 1996; Griffith et al. 2008).

In contrast to males, the exploratory behaviour of females was not significantly correlated with any measure of their reproductive behaviour, nor the interaction between male and female exploration scores. Moreover, we found no evidence that males and females tended to pair assortatively or disassortatively with respect to their exploratory behaviour. Foremost, it is important to recall that the exploration scores of females were not themselves significantly repeatable, mirroring the result of separate studies, which found that females were less consistent in their exploratory behaviour than males (Schuett & Dall 2009; Mainwaring et al. 2011). However, significantly repeatable exploratory behaviour measures have been uncovered in female zebra finches in several different studies (Schuett et al. 2011a; David et al. 2012a). This implies either a) that exploratory behaviour is not a stable personality trait in females, b) the aviary foraging test (and our sample size) does not provide an adequate measure of exploration levels in females, or c) that

the relationship between exploratory behaviour and breeding behaviour in females is not present or more complicated than it is in males.

A high percentage of individuals in the breeding trial made at least some reproductive effort (minimally defined by the attendance at a nest with eggs). We are unable to rule out the possibility that the other individuals formed partnerships and made at least some attempt to breed, such as acquiring a nest box and building a nest. However, despite having over two months in which to breed and a small surplus of available males, only 78.3% of the females in the aviary managed to raise at least one nestling to banding age, and 70% of the males. Those individuals that did not breed successfully may have been suffering from elevated stress levels or other factors commonly experienced under artificial conditions that prevented them from exhibiting normal breeding behaviour (Carlstead et al. 1999; Wielebnowski 1999; Carere & Maestripieri 2013). Contrary to our predictions, the tendency of individuals to make some reproductive effort was not significantly correlated with their exploration scores, however, the low sample size of individuals that did not breed means that our tests likely suffer from statistical power issues, as only a large effect would be statistically significant, therefore our work does not rule out the possibility of such an effect in a larger sample. Moreover, it is possible that different personality attributes than exploratory behaviour, such as boldness or docility, may influence the tendency of zebra finches to instigate breeding behaviour in captivity, but further work is required to establish this link (Roberts et al. 2011).

The high levels of extra-pair paternity and intraspecific brood-parasitism recorded in our study were similar to other studies conducted in captive aviaries (Burley et al. 1996; Forstmeier et al. 2011; Tschirren et al. 2012; Schielzeth & Bolund 2010), and considerably higher than levels recorded in the wild (Birkhead et al. 1990; Griffith et al. 2010). This difference may be a further manifestation of the effects of stress on the usual breeding behaviour of birds in captivity, or an effect of the confined conditions resulting in a greater number of opportunities for extra-pair

breeding activity to occur (Griffith et al. 2010). Unlike a study in the great tit (Patrick et al. 2012), which found that the amount of extra-pair paternity was positively correlated with male exploratory behaviour, the tendency of males to successfully produce extra-pair paternity did not appear to be correlated to exploratory behaviour in our study. However, the sample size of the number of successful extra-pair copulations was quite low, and a larger study would be needed to rule out an effect definitively. Given that we only looked at the molecular signature of extra-pair paternity, rather than the copulation behaviour itself, we also feel unable to draw too many conclusions about this, and indeed do not know in this species and context whether extra-pair paternity is largely driven by female choice or male coercion (Griffith 2007).

Primarily we assayed parentage in this study for completeness to ensure that any results relating personality variation with reproductive success were not confounded by this alternative mating strategy. In contrast to the number of reproductive attempts made and nestlings raised, the number of an individual's genetic offspring successfully raised (by themselves or others) during the trial was not significantly correlated with an individual's exploration score. Therefore, instances of extra-pair paternity and egg-dumping appear to have at least partly compensated for the lack of reproductive attempts (at their own nest) made by less-exploratory males. This suggests that the specifics of the aviary environment (and the higher level of extra-pair paternity) may have diminished the effects of selection in captivity for increased exploratory behaviour over time in males. Hence, the effect of exploratory behaviour on the number of genetic offspring raised may be more prevalent in an environment (such as a cage) where these behaviours are prevented, or in the wild where such alternative mating tactics appear to be insignificant (Griffith et al. 2010). Finally, we found no evidence of individuals changing their social partner over the course of the trial, suggesting that the early mate choice decisions made by individuals were maintained over the 72-day trial.

Given that personality has a substantial genetic basis (van Oers et al. 2005a), the tendency of certain personality traits to have greater reproductive success in a typical captive environment may lead to changes in the average personality levels over many generations, or the production of new behaviours or personality types. This study provides partial evidence for that process occurring in captive populations of the zebra finch, with more exploratory males favoured over less exploratory males in their reproductive output from their social pair, but not in terms of overall production of offspring (pair and extra-pair offspring combined). A review by Smith & Blumstein (2008) on the links between personality and fitness across taxa found no evidence that exploratory behaviour was correlated with reproductive success, but there was a positive correlation with survival. Boldness, on the other hand, shows a positive correlation with reproductive success and a negative correlation with survival (Smith & Blumstein 2008). Boldness and exploratory behaviour have been shown to be correlated with one another in captive populations of the zebra finch, forming a behavioural syndrome (David et al. 2011a). It is conceivable that the increased reproductive success of bolder and more exploratory individuals, now freed from the negating influences of decreased survival due to predation and other factors generally encountered in the wild, could lead to an overall increase in these personality traits in the captive population over time. This result is supported by work in other species that found that boldness increased over several generations in captivity (Yoerg & Shier 1997; Roberts et al. 2011). However, other studies have found the effects of captivity on average levels of exploratory behaviour are not consistent between species (Price 1970; McPhee 2003).

To date, much of the work on personality has been conducted on captive populations, and model systems that are highly amenable to captive conditions such as the zebra finch, guppy *Poecilia reticulata*, and stickleback *Gasterosteus aculeatus*. The novel selective pressures imposed by captivity and the process of genetic drift are likely to affect the frequency and characteristics of the personality traits that individuals exhibit in captivity versus the wild (McPhee 2003; Lacy et al. 2013). As the conditions generally experienced by individuals in the wild are significantly altered in captivity, individuals with personality attributes that maximize reproductive success under captive

conditions are likely to flourish and produce offspring carrying the same traits (Price 1970; van Oers et al. 2005a). Our study finds that personality affects reproductive behaviour, which might suggest that the personality attributes of captive populations may not be representative of wild populations, especially after many generations of captive breeding or domestication. Hence, scientists should use caution when attempting to infer the characteristics of personality in the wild from captive populations, as these samples are likely to serve as biased representations of typical behaviour in the wild. As a result it may be very difficult to infer adaptive ecological explanations to explain variation in such traits as measured in captive populations, within which there may even be differences across social (aviary) and isolated (cage) contexts with respect to the relationship between personality and reproductive success.

Chapter Six

Personality in the wild zebra finch: exploration, sociality and reproduction

Prepared as:

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ABSTRACT

Although personality has been well-studied in a wide range of species, few studies have assessed whether behavior in standardized captive tests is predictive of behavior in the wild. We captured wild zebra finches at two breeding colonies (made up of nest boxes) and assayed their exploratory behavior with a novel environment test. Their wild foraging behavior was also measured with the use of a PIT-tag system to monitor their use of feeders we periodically moved at or around the colonies to assess their exploratory behavior and sociality levels. Individuals' reproductive success was also monitored at the nest boxes. We found that our measures of sociality and wild and captive exploration were all repeatable, but contrary to our predictions, exploration in the novel environment test was not significantly correlated to exploration of feeders in the wild. We failed to find a predicted negative relationship between exploration and sociality, instead finding a significant positive correlation between exploration in the novel environment and sociality. Finally, we found little evidence that any of our measured personality traits influenced reproductive success at the colony, either individually, or when the interactions between the personalities of both members of the pair were taken into account, except for a weak negative correlation between male brood size and novel environment exploration. Our results suggest that researchers should be careful when using tests conducted in captivity to make inferences about personality in wild populations, as tests like these might not be measuring what is expected.

Key words: Exploratory behavior, reproduction, fitness, sociability, novel environment.

INTRODUCTION

The existence of consistent individual differences in behavior, commonly referred to as personality, is well-established across a wide range of species. However, the majority of evidence for this has been obtained from individuals that were either briefly or permanently held in captivity (but see e.g. Herborn et al. 2010). One of the dangers of such work is that it has been conducted out of the ethological context of the natural evolutionary ecology of the species (Dall & Griffith 2014), and as such results may be misinterpreted. Our study species, the zebra finch, is a prime example of this. The zebra finch is a well-studied species, both in captivity and the wild for a variety of research areas in biology (Zann 1996). Over the past decade, the species has been well utilized for research into personality, with almost 30 journal articles already published on this area. However, to date, all of this work has been conducted on domesticated birds in captivity.

One of the most commonly utilized methods of assaying personality both in captivity and the wild across a range of species is an 'open-field' or 'novel environment' test (Montiglio et al. 2010). This test is usually interpreted to be a measure of exploratory behavior, although other personality traits, such as general activity or neophobia, can be measured within the same apparatus (Herborn et al. 2010). In this test, individuals are introduced to a novel environment (which varies greatly in size and structure between different studies/ species) and a measure of exploration is taken over time, such as the total number of movements made, the distance travelled or the total number of different areas visited (Montiglio et al. 2010). From the zebra finch literature, to date 17 journal articles have been published which featured some measure of 'exploratory behavior' or 'exploration', with this trait generally measured using some variation of the 'novel environment' or 'open-field' test (Table 6.1). From this work, authors have discovered not only that 'exploratory behavior' is repeatable long-term over time (David et al. 2012a) and constitutes a personality trait in the captive zebra finch, but also limited work has suggested that this trait is correlated with several different personality traits, such as activity, boldness and neophobia, forming a behavioral

syndrome (Martins et al. 2007; David et al. 2011a). However, no work has yet been conducted to test whether the 'novel environment' or 'open-field' test effectively predicts exploration of the real free-living environment in wild zebra finches.

To measure exploration of the real environment, previous studies of other avian species have used artificially-created food resources (such as feeder stations) coupled with detection systems such as PIT-tags to monitor the discovery of these patches (Herborn et al. 2010; Aplin et al. 2013). The thoroughness, speed or total area size of these discoveries are then used to evaluate an individual's exploratory behavior, and although the food patches are artificial, researchers attempt to emulate the way food patches would occur in the natural environment (Herborn et al. 2010; Minderman et al. 2010). Two species in particular in which wild exploratory behavior has been measured are the great tit *Parus major* and the blue tit *Cyanistes caeruleus*. The number of new foraging patches (feeders) found was shown to be positively correlated with exploratory behavior in a novel environment test in the blue tit (Herborn et al. 2010). In the great tit, one study found that personality in the wild was related to spatial and temporal changes in feeding behavior, with more exploratory individuals (as assessed in a novel environment test) more quickly switching to different more distant foraging areas when established artificial feeders were removed from the environment (van Overveld & Matthysen 2010). Moreover, another study found that exploratory behavior in captivity was correlated with dominance in a feeding context, and hence the monopolization of feeders by certain individuals (Dingemanse & de Goede 2004). A further study examined social networks and found that more exploratory individuals (assayed in captivity) form more weak temporally-unstable relationships with a greater number of conspecifics and move more between flocks (Aplin et al. 2013).

Table 6.1: A table illustrating all of the work published thus far which have attempted to measure exploratory behavior/exploration in the zebra finch, specifically with some form of novel environment test. Estimates of the repeatability of the trait measured (R value) are listed, except in those cases where the same experiment is referred to in several papers, along with the sample size, other personality traits measured in the paper and the dimensions of the apparatus (cage, box or aviary) in which exploratory behavior was measured.

R value	N	Other personality trait(s) measured	Dimensions of apparatus (length x width x height)	Reference
0.55-0.94	10	Activity	30 x 30 x 45 cm	Beauchamp 2000
Not repeated	57	Neophobia, Risk-taking behavior	150 x 150 x 150 cm	Martins et al. 2007
No estimate given	39	Boldness, Neophobia, Activity	30 x 45 x 40 cm	Donaldson 2009
Not repeated	26	None	185 x 185 x 185 cm	Krause et al. 2009
0.321	24	Leadership	65 x 110 x 93 cm	Schuett and Dall, 2009
0.81	41	Activity, neophobia, risk-taking behavior, obstinacy	140 x 140 x 70 cm	David, Auclair, et al. 2011
0.45	57	Mate choice	140 x 140 x 70 cm	David and Cézilly 2011
0.60	30	None	120 x 120 x 60 cm	David, Cézilly, et al. 2011
>0.21	52	None	185 x 185 x 185 cm	Krause and Naguib 2011
Males: 0.030 Females: 0.024	48	Boldness	250 x 250 x 250 cm	Mainwaring et al. 2011
Males: 0.291 Females: 0.414	77	Aggression	120 x 30 x 38 cm	Schuett, Dall, et al. 2011
Males: 0.401 Females: 0.447	102	None	120 x 40 x 45 cm	Schuett, Godin, et al. 2011
0.76	20	Struggling rate	140 x 140 x 70 cm	David, Auclair, and Cézilly 2012
See David, Auclair, & Cézilly, 2011	See David, Auclair, & Cézilly, 2011	Activity, Neophobia, Reaction to startle	140 x 140 x 70 cm	David, Auclair, Dechaume-Moncharmont et al. 2012
See David, Auclair, & Cézilly, 2011	See David, Auclair, & Cézilly, 2011	Activity, Neophobia, Reaction to startle	140 x 140 x 70 cm	David, Auclair, Giraldeau et al. 2012
Males: 0.441 Females: 0.404	113	Neophobia	250 x 250 x 250 cm	Mainwaring and Hartley 2013
0.277	154	None	120 x 30 x 38 cm	Schuett et al. 2013

Conversely, exploration speed in a novel environment test was not correlated with home range size in starlings *Sturnus vulgari*s, but spatial use within the chamber was (i.e. high perches or the floor) (Minderman et al. 2010). Moreover, Schuett et al. (2012) assessed whether jackdaws' exploration in a standardised novel environment test was predictive of their behavior towards a novel object in the wild, finding that, contrary to predictions, captive exploration and wild neophobia were positively correlated (more exploratory individuals tended to show greater latency to approach a novel object). In the zebra finch, previous work has found variation between individuals in the number and latency with which artificial feeding patches (feeders) are found in the wild; however, this work did not aim to measure personality directly (Mariette & Griffith 2013).

Several studies have found that sociality/sociability or the level of social behavior displayed by individuals within a species or population (i.e. the tendency to interact with or avoid conspecifics) may constitute a personality trait (Schmidt & Fox 1995; Cote et al. 2008; Koski 2011; Cote et al. 2012). Interestingly, it has been predicted that social contexts can select for individual differences in behavior due to social niche specialization (Bergmüller & Taborsky 2010) or social information influencing selection (Wolf et al. 2011; Dall & Griffith 2014). Individual differences in the level of social behavior may be caused by differences in personality traits such as boldness, neophobia or exploratory behavior resulting in individuals being more or less likely to aggregate in groups, rather than innate differences in social attraction (Webster & Ward 2011; Blumstein et al. 2013). In support of this idea, it has been found that the tendency to utilize producer or scrounger foraging tactics and to lead others to food patches are linked to personality traits such as activity and exploratory behavior in the zebra finch (Beauchamp 2000; David et al. 2011b). These relationships may also persist in the wild, and influence the tendency of different personality types to scrounge the feeder discoveries of others. Inter-individual variation in the tendency of breed socially or asocially have also been found in the wild zebra finch (Mariette & Griffith 2012). Moreover, sociality may be negatively correlated with exploratory behavior, as less exploratory zebra finches were found to spend more time with a social partner at a risky feeder than highly

exploratory individuals (Schuett & Dall 2009), and so may be more social in general, or just in risky foraging contexts, potentially to lower their risk of predation. Zebra finches have also been shown to be bolder in an asocial, rather than a social context (Mainwaring et al. 2011), which suggests that personality characteristics might be influenced by the social environment an individual happens to be in, or that the relationship between personality and sociality may be complex. Finally, the pace-of-life hypothesis predicts that sociability is negatively correlated with proactive personality traits such as fast (but superficial) exploratory behavior and boldness (Réale et al. 2010), although there is little evidence as of yet to support this relationship (Budaev 1997).

In a number of species, the personality traits under investigation have been shown to affect various traits that influence the fitness of individuals in the wild, such as survival (Dingemanse et al. 2004; Smith & Blumstein 2008) growth rate (Adriaenssens & Johnsson 2011; Heg et al. 2011) and reproductive success (Smith & Blumstein 2008; Betini & Norris 2012; Schuett et al. 2012). Moreover, in captive zebra finches links between reproductive behavior and personality have been found for both exploratory behavior (Schuett et al. 2011a) and neophilia (Schielzeth et al. 2011). A review of the personality literature found that overall, there is a positive correlation between survival and exploratory behavior; however, this relationship can vary from species to species or with fluctuating environmental conditions and may ultimately reflect trade-offs between different fitness variables such as growth and survival (Dingemanse et al. 2004; Stamps 2007; Smith & Blumstein 2008). In birds, reproductive success should be linked to a parent's ability to forage, which should furthermore be related to their ability to find food. This might explain the results of previous work in the wild zebra finch, which found that the quantity of food that parents deliver to broods differs between individuals (Gilby et al. 2011). Moreover, solitary breeders were shown to find novel food patches faster than colonial breeders and only these individuals were able to adjust the amount of food per nestling to reflect brood size, suggesting they were better parents (Mariette & Griffith 2013). The patterns of food patch use employed by individuals may also depend on their personality. For some individuals, the costs of continuing to feed from a well-established but

popular food resource over searching for novel food resources might outweigh the benefits, while others might be better off sticking to those resources that are well-established and following the lead of the social group. Potential advantages of sticking to a popular and reliable food resource are that individuals can conserve energy that would be spent travelling in search of new food resources and also potentially reduce their risk of predation by remaining in a group (Krause & Ruxton 2002). However, if that food resource should unexpectedly dry up, then individuals will have no knowledge of alternatives in the environment for them to rapidly switch to using. Hence, more exploratory individuals might have higher fitness during periods of food patch instability.

This study sought to address gaps in the personality literature and confirm the validity of some of the hypotheses that have come out of the work conducted on domesticated populations, in particular, whether personality differences might be driving variation in the discovery of food patches in the wild zebra finch. We attempted to determine 1) whether the results of a simple novel environment test commonly used to measure individual differences in exploratory behavior in captivity is reflective of the behavior of individuals in the free-living habitat. From previous research, we predicted that this would be the case, and that individuals with higher exploration scores in the novel environment test would discover a greater percentage of food patches over the course of our trials. We also attempted to measure 2) individual differences in sociality from the use of our artificial food patches and predicted that they would negatively correlate with our measures of exploratory behavior, as we expected that individuals that tend to avoid conspecifics at the most popular food patches would be more likely to seek out a number of quieter alternative food patches. Finally, 3) we measured the breeding success of individuals and contrasted this with their personality variables to investigate whether different personality types showed differing reproductive success over the course of the field season.

METHODS

Study population and site

The study site was located at the UNSW Fowlers Gap Arid Research Station in west New South Wales, Australia. The area is characterized by open chenopod shrub land containing sporadic stands of *Acacia* spp. (Griffith et al. 2008). The study population included two separate populations at very similar sites approximately 15 km apart (referred to as 'Saloon', located at 31º04'S, 141º50'E, and 'Sandstone', located at 31º01'S, 141º41'E). Both colonies featured a large breeding area of typical zebra finch habitat (*Acacia* spp. trees and shrubs) situated adjacent to a permanent dam. The two colonies were considered independent of each other as no movement of banded individuals between the two sites was recorded either during the field season in 2012 or previously by other researchers working at these sites. Each of these sites featured a number of nest boxes in the area immediately adjacent to the dam in which zebra finch pairs could breed. By the end of October 2012, the size of the area in which nest boxes were distributed and number of nest boxes available for breeding at these two sites was increased to 45 at Saloon (dispersed over an area of approximately 180 x 120 m) and to 74 at Sandstone (dispersed over an area of approximately 350 x 150 m). All nest boxes were fixed on individual steel stakes 1-1.8 m off the ground and within 2 meters of an acacia bush as previously described (Griffith et al. 2008).

Trapping of wild birds

From late September to mid- November, all adults were caught either at a walk-in trap at a single feeder at both colonies, or in nest boxes while breeding when nestlings were between six and twelve days old, and run through the novel environment test before being tagged. When individuals were captured at a feeder, they were extracted from the feeder by hand in groups of up to 5 individuals (if

more individuals than this were caught at once, the remainder were released) and immediately placed individually into a cotton bird bag to be transported to the location of the novel environment test 50 meters from the edge of the colony. Individuals were caught in groups rather than singly to reduce potential bias in the personalities of the individuals that were caught (as catching only the first individual to enter a feeder might inadvertently select for only bolder, more exploratory or socially dominant individuals) (Garamszegi et al. 2009; David et al. 2011a; Carter et al. 2012; Biro 2013). When individuals were caught with nest traps they were immediately transferred to a bird bag and transported to the location of the novel environment test. Individuals were run through the novel environment test as quickly as possible after capture, but some individuals remained in the bird bags for up to 45 minutes before they could be tested.

Novel environment test

There were two novel environment tests conducted. All individuals were run through the novel environment test following their first capture. Additionally, a subset of individuals were run through the novel environment test at the end of the field season to allow for within individual comparison. The set-up of the novel environment test was similar to the open-field test commonly used in small mammal research (Montiglio et al. 2010), being conducted in a purpose-built box that functioned as a novel arena. This box (120 cm long x 42 cm wide x 60 cm high) was constructed from wood except for the lid, which was made from white opaque Perspex and enabled natural light to illuminate the interior of the chamber. To begin with, each individual was removed by hand from the bird bag and placed directly into a small carry box (20 cm long x 15 cm wide x 15 cm high) attached to the outside of the main box to habituate individuals to a box environment and allow them time to calm down after being in a bird bag. After two minutes, the experimenter removed a wooden door that connected the carry box to the main chamber, and allowed the bird to enter the test arena without seeing the experimenter. In most cases (190 out of 231), individuals flew directly

into the main box when the door was removed, but in cases where they did not enter after 15 seconds, the experimenter tapped on the back of the box for five seconds then, if this did not work, put their fingers through the external door of the carry box to scare the bird into the main box. The main box contained four wooden 'trees' of the same size and shape which each had two intersecting perches at the middle and near the top, allowing 4 places per tree that an individual could land on. Moreover, the floor of the box was split into 12 equally-sized rectangular areas marked with a vivid marker, and also had 9 wooden blocks on the floor of the cage, at the intersection of the floor and walls, which were used to hold it together, but on which the birds could also perch. In total, the perches, blocks and sectioned floor provided a total of 37 distinct places that could be scored as being visited. The interior of the box was filmed with two video cameras (High Definition Video Camera HDC-HS20, Panasonic, http://panasonic.net) through two holes at opposite ends of the box that were cut to fit the lens of the video camera. With these two video cameras the birds were filmed at all times while they were in the box. During the entire process the experimenter sat silently on a chair next to the box monitoring a stopwatch, visually isolated from the subjects at all times.

Behavior scoring

For the novel environment test, video analysis was conducted on the five minutes after each individual exited the confines of the small holding box and entered the main experimental chamber. The total number of flights or hops between different areas during the five minutes was recorded. A movement was defined as any flight or series of hops that resulted in an individual moving between two different areas (the 37 distinct places in the apparatus), or any flight which resulted in an individual landing back in the same area (this behavior occurred frequently with individuals flying to the top of the box as if searching for an exit and then landing back in the same area). Hops within the same area were infrequent and difficult to quantify, so were not measured. The total number of different areas visited during the five minute period was also recorded. However, when we later

investigated the relationship between these two variables (total movements and total areas) we found that they were highly positively correlated with one another ($r = 0.896$, $N = 230$, $P < 0.001$). Therefore, we dropped total areas from further analysis and instead only total movements were recorded as our measure of an individual's level of exploratory behavior in the novel environment test (*novel environment exploration*), as this measure is commonly used in the literature (Table 6.1). Finally, we conducted a *t*-test to determine whether the method of capture (from the central feeder or a nest box) affected *novel environment exploration* scores and a Spearman rank-order correlation to investigate whether the time and individual spent in a bird bag before the start of the novel environment test affected their *novel environment exploration* scores (unfortunately information about the time spent in a bird bag for many individuals was not available due to a logistical error).

PIT-tagging for wild behavior assaying

After five minutes in the main box, the subjects were caught by hand through a flap in the side of the box. On being removed from the experimental chamber birds were taken to a nearby vehicle to be tagged, measured, blood sampled and then released. Birds were implanted with a passive integrated transponder (PIT) tag (11 x 2 mm; Trovan; Hessle, UK), banded with an individually numbered metal band (Australian Bird and Bat Banding Scheme) and two uniquely identifiable color bands. A blood sample was also taken from each bird (of about 10µl) before they were released for a separate study.

Distribution of sampled individuals

At Saloon, 44 males and 22 females were captured at the central feeder and 15 males and 22 females were captured at nest boxes, while at Sandstone, 33 males and 28 females were captured at the central feeder and 24 males and 23 females were captured at nest boxes. All of these individuals were fitted with a PIT-tag after capture. As several individuals were re-caught over the course of the

season at nest boxes, these individuals were not run through the novel environment test on the occasion of this second capture, but we checked whether each individual's PIT-tag had been lost with a scanner and replaced it if necessary (this was required for 7 out of 17 individuals). During the final two weeks of the field season, the three most popular feeders at each colony from the feeder experiment (described below) were left open and fitted with traps which automatically closed when a PIT-tagged individual entered the feeder. Over this period, we recaptured as many tagged individuals as possible to be run for a second time through the novel environment test. The set-up of this latter novel environment test was identical to the test that had been conducted earlier (there was an average of 59.2 days between the two trials for those individuals that completed a second test). Despite an equivalent effort at both colonies, we only recaptured and tested 3 males (5.1 %) and 5 females (11.1 %) at Saloon, but 22 males (39.0 %) and 19 females (37.3 %) at Sandstone, as it appeared individuals at Saloon were less inclined to use the feeders during this period.

Assessment of wild foraging: feeder experiment

The feeder experiment was run from mid-October to mid-December. To begin with a single feeder (a wire finch holding cage with dimensions of 70 x 40 x 50 cm) was placed near the center of both colonies at the beginning of September containing a seed tray (50 x 30 cm) which was kept full of commercial mix finch seed for the entire season. These central feeders were also used for trapping birds over the course of the season. Initially, to encourage birds to use the feeder the large door of the cage was wired open (20 cm x 20 cm) allowing easy access. This entrance was later modified through the addition of a powered antenna (around an 11 cm opening) connected to a PIT-tag detection system (LID-665 decoder; Trovan, UK) that automatically recorded the unique identification of any tagged bird going through the entrance along with date and time. From previous work, the detection rate of the PIT-tag system was estimated at 94% each time a tagged individual visited the feeder. Beginning in mid to late October (Saloon and Sandstone respectively)

six other feeders were set up with PIT-tag detection systems in the environment at varying distances from the central feeder and their locations changed at 2-10 day intervals. However, for our analysis of exploration in the field we focused solely on data collected from the feeders immediately following a 3-day period of heavy rainfall in mid-November (when all of the feeders stopped working as we were unable to access the colonies), hence, individuals at the colonies had approximately one month before this to adjust to using the feeders at the colonies. Two or three days respectively after this rainfall at Saloon and Sandstone, we set up nine additional feeders (along with removing the previous six) to the central feeder. To choose their location, each feeder was allocated one of 16 compass directions to follow at random from the central feeder along with a distance, with two feeders allocated a random distance 10-50 m from the central feeder, two 50-200 m, two 200-400 m, two 400-1500 m and one 1500-3000 m. Feeders were usually relocated to a new random position every four days for the closer feeders (400 m or less from the central feeder) and every 8-10 days for the far feeders (though in a few cases these lengths varied by two days due to logistical reasons) for a total of 28 days at each colony. However, the central feeder remained open and in the same location for the duration of the field season so that individuals had a reliable and plentiful food source even if they chose not to explore the environment in search of new feeders at new locations. The PIT-tag data from each feeder was downloaded to a laptop every two days when logistically possible, and batteries were changed every two to four days.

Reproductive success

Nest boxes were checked at least every two days for breeding activity, and from this data we extracted two variables of breeding success for each individual's first known breeding attempt of the season from day 12 data (days after the first nestling hatched): the number of nestlings alive (*brood size*), and the mean mass of the nestlings in the nest (*mean nestling mass*). Over the field season, we recorded 31 breeding attempts at Saloon and 38 at Sandstone where at least one of the

parents was identified as a PIT-tagged individual. In total, at least one breeding attempt was recorded for 45 tagged individuals at Saloon (20 males and 25 females) and 57 at Sandstone (28 males and 29 females). Both of the parents were PIT-tagged for 17 recorded breeding attempts at Saloon, and 22 at Sandstone. Overall, no males and two females at Saloon, and three males and five females at Sandstone, aborted breeding attempts where nestlings had hatched (we only attempted to identify parents once nestlings had hatched). Only 12 individuals at Saloon and 23 at Sandstone, for which we recorded at least one breeding attempt, successfully completed the feeder experiment (visited the feeders or at least 25 out of 28 days, as described in the *Data analysis* section). The majority of these individuals (27 out of 35) were run through the novel environment test and tagged for the first time between days 6-12 after the first nestling hatched during their recorded breeding attempt. However, in the remaining cases (8 out of 35), their capture during their breeding attempt was a recapture, as they had already been captured and run through the novel environment test previously, so these individuals were released after capture after checking their PIT-tags were still in place. As we considered that all individuals that completed the feeder experiment were unlikely to be transient to the area, and would very likely have bred in the nest boxes if they had made a breeding attempt during the field season (no other active nests were found in the surrounding area), we included these individuals in our analysis of *brood size*, allocating them a *brood size* of '0'. For all the breeding attempts, we assumed that our nest box capture attempts had little effect on *brood size* or parental feeding rates and hence *mean nestling mass*, but even if they did, most individuals were exposed to roughly the same number of nest box trapping attempts so the influence would likely have been similar for all parents. We conducted two separate Mann-Whitney U tests to compare the *brood size* and *mean nestling mass* of the two colonies (Saloon, Sandstone) for all breeding attempts, except for those where at least one of the parents was known to be attempting to breed a second time (or more) that season.

Over the whole season we caught and PIT-tagged 59 males and 44 females at Saloon and 57 males and 51 females at Sandstone. For the feeder data, we focused only on those tagged individuals who visited the feeders on at least 25 days out of the 28 days the feeder experiment was run. However, as a number of individuals stopped being recorded as using the feeders before or during this period (they may have lost their PIT-tags, left the area, died or simply ceased visiting the feeders), the size of the dataset was reduced considerably, to 11 males and 9 females at Saloon and 23 males and 19 females at Sandstone. We conducted a *t*-test to compare *novel environment exploration* of those individuals that were included in the dataset versus those that were not. From the feeder experiment data we extracted four separate variables, *feeder visits*, *feeder exploration*, *feeder sociality*, and *territory size*. To calculate an estimate of the mean feeder visits made per day for each individual, any visit made to a feeder within 10 minutes of another visit to the same feeder was considered part of the same visit. This was divided by the total number of days each individual was known to be tagged (which varied between 25 and 28, as some of the included individuals were not recorded using the feeders for the last few days of the period and so may have lost their PIT-tag) to obtain the feeder visits score (*feeder visits*). Secondly, we calculated a feeder exploration score for each individual, which was defined as the total number of different feeders found over the entire 28 day period (*feeder exploration*). Thirdly, we calculated a measure of sociality, *feeder sociality*, from the tendency of individuals to use the most popular feeder (on that day) over less popular feeders. To calculate this, we narrowed our dataset down to only days at Saloon and Sandstone where the position of feeders were stable (no feeders changed position on that day), and one feeder had both the most different individuals visiting that feeder and the highest total number of visits on that day (it was the most popular feeder on that day), which left nine days at each colony (the central feeder was the most popular feeder on only two of these days at Saloon, and one at Sandstone). For each individual, the proportion of visits made to the most popular feeder was compared to their total feeder visits made on that day to any feeder and averaged over the nine separate days to obtain

feeder sociality, with higher scores indicating a tendency to preferentially visit popular feeders. While we can be relatively certain that individuals using the most popular feeder were being social in their behavior, unfortunately due to the presence of untagged individuals in the environment we cannot be sure they were being asocial in their behavior at other feeders, only that this is likely. Hence, we felt that the best sociality measure we could calculate was one that compares visits to a feeder we know is social versus all of the others which may be either social or asocial, averaged over many days (the likelihood that a highly social individual would avoid making visits to the most popular feeder, while still being social, is reduced by using data from many different days). An estimate of territory size (*territory size*) was obtained from the feeder use of each individual in R (R Development Core Team 2013, R Foundation for Statistical Computing, Vienna, Austria) using the package adehabitatHR, by calculating the minimum convex polygon that encloses all data points (feeders visited) over the feeder experiment period and determining the area of this polygon. To avoid pseudoreplication, for all statistical analyses except when calculating the repeatability of variables, only a single value was used per individual as each score (*novel environment exploration, feeder exploration, feeder sociality, feeder visits* and *territory size*). In the case of *territory size* and *feeder exploration*, these were only single value scores, for *novel environment exploration*, only the score from the first test each individual participated in was used, and for *feeder sociality* and *feeder visits*, mean scores were calculated from the different days of data. Finally, we calculated how distance from the central feeder affected the popularity of feeders by calculating Pearson correlation coefficients of the distance of each feeder from the central feeder at the colony with the total number of individuals that found it and the total number of individual visits it received for Saloon and Sandstone separately.

Repeatability

Using a method employed by a number of studies, we assessed repeatability based on our two (or more, depending on the variable) repeated behavioral assays for each variable to extract an *R* value, with *R* values closer to one indicating greater repeatability (Bell et al. 2009). Repeatability (*R*) values were calculated in R (R Development Core Team 2013) using the add-on package rptR, following the methods described by Nakagawa & Schielzeth (2010). For the novel environment test, we were only able to calculate the repeatability of the test for those 47 individuals which we were able to capture and re-run through the test at the end of the season. For the feeder experiment, repeatability of the number of feeder visits was calculated for all days that the 63 individuals for which we had at least 25 days of data were known to be tagged. To calculate the repeatability of *feeder exploration*, we compared the number of feeders found during an early subset of the feeder experiment period with a latter subset (both covering approximately 12 days). To calculate the repeatability of *feeder sociality*, we compared the proportional use of the most popular feeder over the nine days they were measured in each individual. To account for differences in average score between colonies, we also calculated the feeder experiment repeatability for Saloon and Sandstone separately. Repeatability was calculated for *feeder exploration* using Gaussian LMM-based methods as this data had a Gaussian error structure. These LMM-based methods utilized parametric bootstrapping and Bayesian methods for confidence interval estimation and randomization for significance testing (Nakagawa & Schielzeth 2010). The data recorded for *novel environment exploration* and *feeder visits* were typical of count data, so repeatability was calculated using the methods described for count data for these variables. These methods utilized multiplicative dispersion GLMMs (in which the overdispersion is modelled as a further parameter of the distribution from which the original responses are assumed to be derived) with a log link for estimating repeatability on the original scale (Nakagawa and Schielzeth 2010). Finally, as *feeder sociality* was proportion data, repeatability was calculated with multiplicative-overdispersion model GLMMs with variance-stabilizing logit link (Nakagawa & Schielzeth 2010). For all of these

methods, due to discrepancies between LRT *P* values and 95% confidence intervals (as is often the case the LRT *P* values were too small, see Nakagawa & Cuthill 2007), the estimates of *P* values were unreliable. Hence, they were not reported, and instead instances where the lower confidence interval was below 0 were considered non-significant (following Nakagawa & Cuthill 2007).

Statistical analyses

Further analyses were conducted with the statistical software program IBM SPSS Statistics for Windows, v21.0 (IBM Corp, Armonk, NY). Firstly, we calculated Spearman rank-order correlation coefficients between each of the four feeder experiment variables (*feeder visits*, *feeder exploration*, *feeder sociality* and *territory size*). Secondly, we ran a Generalized Linear Model with a negative binomial error structure with *novel environment exploration* as the dependent variable, *feeder exploration*, *feeder sociality, feeder visits* and *territory size* as fixed covariate terms and *sex* (male, female) and *colony* (Saloon, Sandstone) as fixed factorial terms. Thirdly, we ran General Linear Models for both sexes separately with *brood size* as the dependent variable and *colony* (Saloon, Sandstone) as fixed factorial terms, and each of the four potential predictors from the feeder experiment (*feeder exploration*, *feeder sociality, feeder visits* and *territory size)* tested in turn as a fixed covariate term in separate models (we ran separate models for each predictors to avoid potential collinearity problems). We did the same for *mean nestling mass*, except *brood size* was included as a fixed covariate term in each model. As we could not be certain that individuals that did not breed in the next box colonies did not breed somewhere else (a number active nests were noted in the vicinity of the colony over the course of the field season), we excluded all individuals from the analysis that did not make a known nest box breeding attempt. Moreover, the *mean nestling mass* models excluded all individuals with a brood size of zero on day 12 as there were no mean mass scores available for these individuals. We also ran two identical models with *brood size*, and *mean nestling mass*, respectively, as the dependent variables, except that *novel environment*

exploration was the predictor. For these models we included all individuals for which we had obtained breeding data that had also completed the novel environment test at least once (i.e. not just those for which we had full feeder experiment data). This increased the sample sizes to 48 males (20 from Saloon, 28 from Sandstone) and 44 females (20 from Saloon, 24 from Sandstone) and for the *brood size* analyses, and 38 males (14 from Saloon, 24 from Sandstone) and 36 females (17 from Saloon, 19 from Sandstone) and for the *mean nestling mass* analyses. We also ran separate GLMs under the assumption that all those individuals that completed the feeder experiment but did not make a known breeding attempt in the next boxes were unsuccessful breeders and therefore they were allocated a *brood size* of '0'. For the six pairs (three at Saloon, three at Sandstone) where both the male and female completed the feeder experiment, we conducted Spearman rank-order correlations to compare male and female *feeder exploration*, *feeder sociality*, *feeder visits* and *territory size* scores. Next, for the 33 known pairs for which we had both novel environment test scores (*novel environment exploration*) and breeding attempt data, we conducted a Spearman rank-order correlation to determine whether individuals were likely to pair assortatively, disassortatively or neither with respect to *novel environment exploration*. Finally, we ran two separate GLMs: the first had *pair brood size* as the dependent variable with *colony* (Saloon, Sandstone) as a fixed factorial term, and male *novel environment exploration* and female *novel environment exploration,* and the interaction between them as fixed covariate terms; the second had *pair mean nestling mass* as the dependent variable with *colony* (Saloon, Sandstone) as a fixed factorial term, and male *novel environment exploration* and female *novel environment exploration,* the interaction between them, and *pair brood size* as fixed covariate terms.

RESULTS

Table 6.2: Mean values and repeatability (*R*) of individuals' behavior in the (a) novel environment test and (b) feeder experiment. The *novel environment exploration* value was calculated from all 47 individuals who completed the novel environment test twice out of the 231 total tests run over the course of the season, while the mean *feeder visits*, *feeder exploration* and *feeder sociality* values were calculated from the 62 individuals who completed the feeder experiment.

Component	Mean ± SE	*R* ± SE	N	Lower CI	Upper CI
(a) Novel environment test					
Novel environment exploration	5.221 ± 0.476	0.424 ± 0.103	47	0.269	0.675
(b) Feeder experiment					
Feeder visits	6.995 ± 0.337	0.462 ± 0.051	62	0.356	0.549
Feeder exploration	0.559 ± 0.016	0.439 ± 0.101	60	0.212	0.610
Feeder sociality	0.451 ± 0.028	0.192 ± 0.046	62	0.089	0.266
Feeder exploration - Saloon		0.429 ± 0.181	19	0	0.738
Feeder exploration - Sandstone		0.271 ± 0.140	41	0	0.541

Repeatability of behavior

Individuals' behavior as assayed by our different variables was stable throughout our study. *Novel environment exploration*, *feeder visits*, *feeder exploration* and *feeder sociality* were significantly repeatable; however, when we split the *feeder exploration* scores into separate Saloon and Sandstone datasets the results were still repeatable but not significantly so (all results are shown in Table 6.2).

Novel environment test

Performance in the novel environment test (*novel environment exploration*) was not influenced by place of capture (whether an individual was captured from a feeder or a nest box) (t_{181} = -1.427, P = 0.155). Similarly, the amount of time that individuals spent in a bird bag before the start of the novel environment tests was not significantly correlated with their novel environment exploration scores (*rs* = 0.001, N = 55, P = 0.994). Moreover, whether or not an individual was included in the dataset (visited the feeders for at least 25 days) was not significantly correlated with *novel environment exploration* ($t_{75.9}$ = -1.543, P = 0.127).

Feeder experiment

Feeder visits were significantly positively correlated with *feeder exploration* (Table 6.3). Moreover, *feeder sociality* was negatively correlated with *territory size* (Table 6.3). However, neither *feeder sociality* nor *territory size* was significantly correlated with either *feeder visits* or *feeder exploration* (Table 6.3). We found that both the number of individuals that found a feeder (Saloon: r = -0.555, N = 42 feeder locations, P < 0.001; Sandstone: r = -0.547, N = 46 feeders locations, P < 0.001) and the total visits to a feeder (Saloon: r = -0.443, N = 42 feeder locations, P = 0.003; Sandstone: r = -0.353, N = 46 feeder locations, P = 0.016) were significantly negatively correlated to the distance of that feeder from the central feeder in the colony. We did not find a significant effect of *sex*, *colony*, *feeder exploration*, *territory size* or *feeder visits* on *novel environment exploration* (Table 6.4 and Figure 6.3a). However, *novel environment exploration* was significantly positively correlated to *feeder sociality* (Table 6.4 and Figure 6.3b).

Table 6.3: Spearman rank-order correlations between four variables measured from the feeder data, *feeder visits*, *feeder exploration*, *feeder sociality* and *territory size*, listed as *r*, *N*, *P* value.

Variable	Feeder exploration	Feeder sociality	Territory size
Feeder visits	0.479, 62, <0.0001**	0.003, 62, 0.979	0.026, 62, 0.843
Feeder exploration	-	0.161, 62, 0.213	0.206, 62, 0.109
Feeder sociality	-	-	-0.386, 62, 0.002**

Table 6.4: Summary of a Generalized Linear Model with negative binomial error structure examining variation in the exploration of a novel environment by zebra finches in relation to feeder exploratory behavior, feeder sociality behavior, the mean daily number of feeder visits, territory size based on feeder use, sex and colony identity.

Term	Unstandardized coefficient	SE	DF	Wald Chi-Square	*P* value	Upper CI	Lower CI
(Intercept)	1.979	0.8580	1	6.466	0.011	0.297	3.661
Feeder sociality	2.627	0.7718	1	11.587	0.001	1.115	4.140
Feeder exploration	-0.080	0.0599	1	1.794	0.180	-0.198	0.037
Colony (Saloon)	-0.200	0.3732	1	0.287	0.559	-0.931	0.532
Sex (male)	0.148	0.2976	1	0.249	0.643	-0.435	0.732
Feeder visits	-0.022	0.0716	1	0.093	0.798	-0.162	0.118
Territory size	0.001	0.0163	1	0.008	0.932	-0.031	0.033

(a)
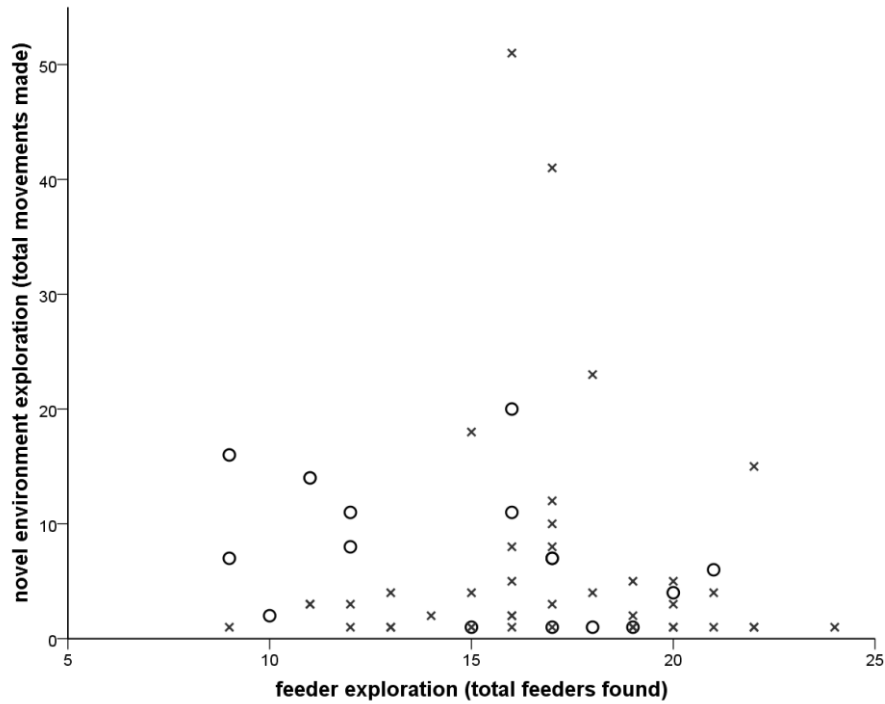
(b)
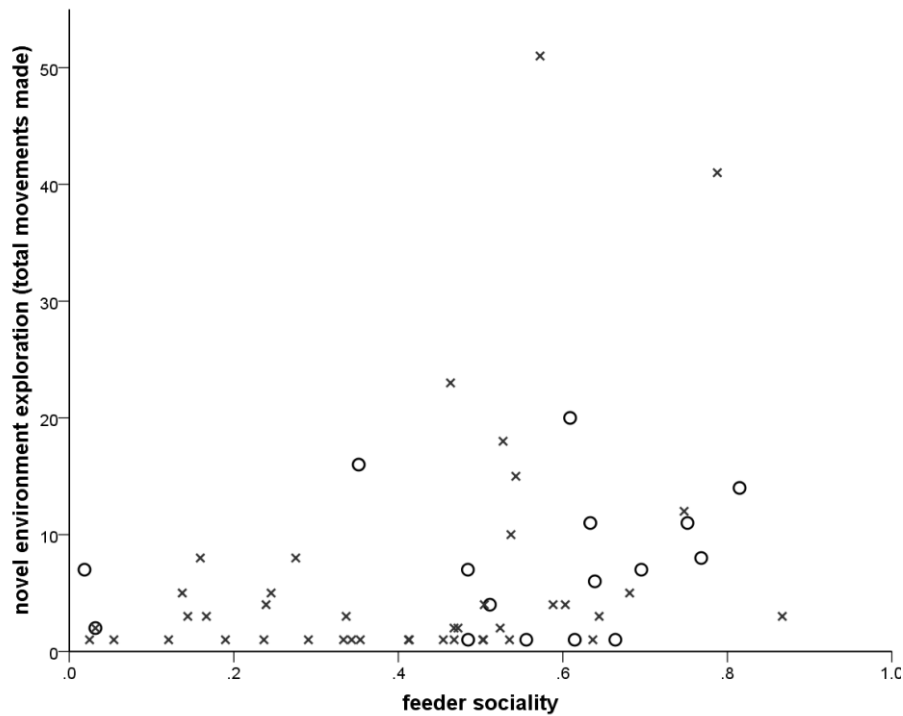
Figure 6.1: The correlation between *novel environment exploration* and (a) *feeder exploration* and (b) *feeder sociality*. A higher *novel environment exploration* score indicates a higher number of movements made during the novel environment test. A higher *feeder exploration* score indicates a greater number of feeders found, while a higher *feeder sociality* score indicates a greater mean proportion of use per day of the most popular feeder during the feeder experiment. Individuals from Saloon are shown with open circles and individuals from Sandstone with crosses.

Reproductive success

We found that *brood size* significantly differed between the two colonies ($U = 343.500$, $Z = -2.418$, $P = 0.016$), with larger brood sizes on average occurring at Saloon (Saloon mean = 4.28, SD = 1.58, $N = 29$, Sandstone mean = 3.42, SD = 1.78, $N = 36$). This was likely driven by both a larger number of failed breeding attempts with a recorded brood size of 0 at Sandstone (five) than Saloon (two), and a larger peak brood size at Saloon (13 broods of 5) than Sandstone (12 broods of 4) (Figures displaying this data are included as Supplementary materials). However, *mean nestling mass* did not significantly differ between the two colonies ($U = 289.000$, $Z = -0.020$, $P = 0.984$; Saloon mean = 9.24, SD = 1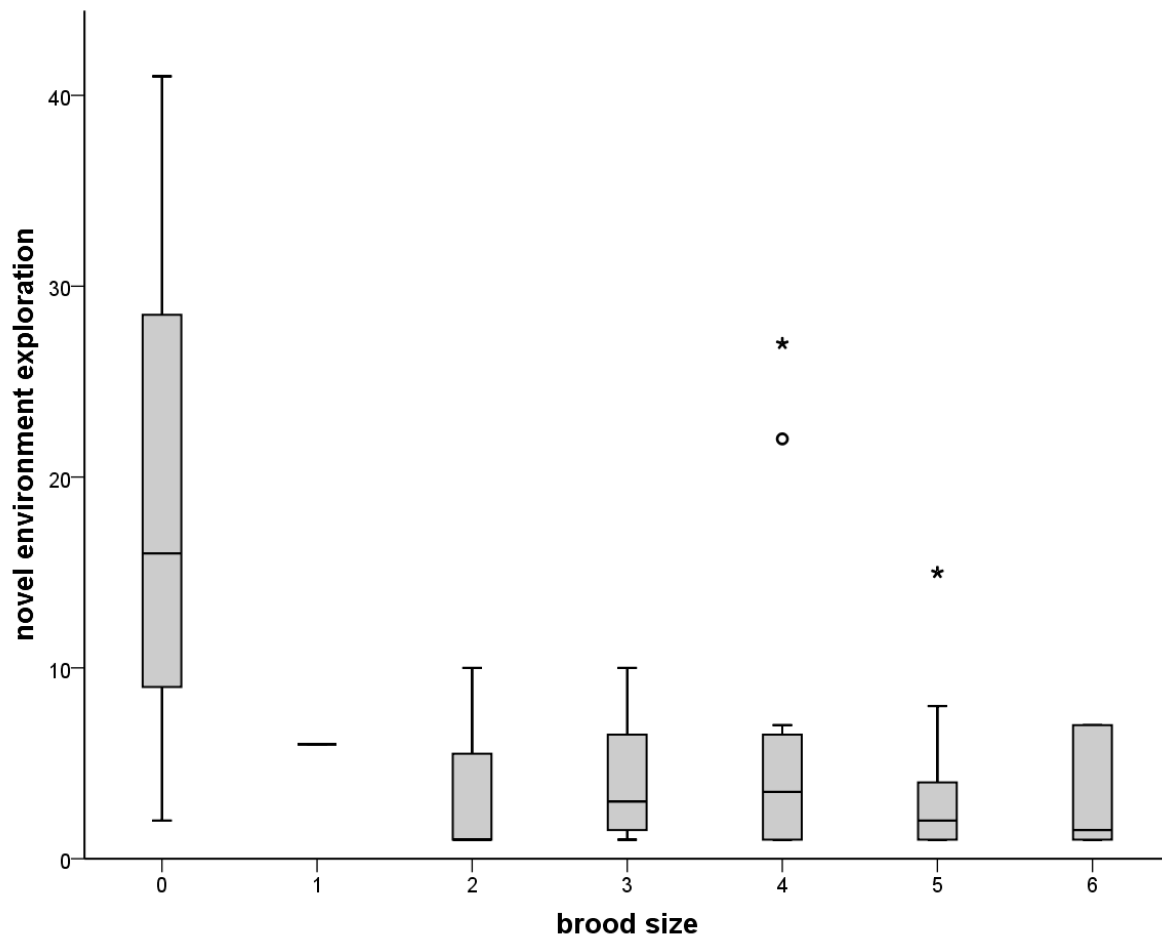.00, $N = 20$, Sandstone mean = 9.20, SD = 0.82, $N = 29$). Overall, the only significant relationship between reproductive success and personality we found was a negative correlation between *brood size* and *novel environment exploration* for males (Table 6.5 and Figure 6.2). We also recorded a non-significant positive trend between male brood size and territory size, again for males only (GLM: Coefficient = 0.102, $SE = 0.049$, $F = 4.399$, $df_1 = 1$, $df_2 = 15$, $P = 0.053$) (Figure 6.3). Apart from this, we did not find any significant relationships between either male or female *brood size* and *novel environment exploration*, *feeder exploration, feeder visits, territory size* and *feeder sociality* (results of these statistical tests can be found in supplementary materials). However, when we included all individuals that completed the feeder experiment in our analyses (not only the individuals that were recorded as making at least one breeding attempt) by allocating non-breeders a *brood size* score of '0', we found significant positive correlations between *brood size* and *feeder visits* for both males (GLM: Coefficient = 0.551, $SE = 0.118$, $F = 21.908$, $df_1 = 1$, $df_2 = 31$, $P = <0.0001$) and females (GLM: Coefficient = 0.361, $SE = 0.155$, $F = 5.441$, $df_1 = 1$, $df_2 = 25$, $P = 0.028$) (Figure 6.4). Apart from this, we did not find any significant relationships between either male or female *brood size* and *feeder exploration, territory size* and *feeder sociality* (detailed results of these statistical tests can be found in supplementary materials). Similarly, we did not find any significant relationships between *mean nestling mass* and *novel environment exploration*, *feeder exploration* or *feeder sociality* for either males or females (results of these statistical tests can be

found in supplementary materials). For all 33 pairs where both the male and female went through the novel environment test, we found no evidence that individuals paired assortatively with respect to *novel environment exploration* ($rs = -0.045$, $N = 33$, $P = 0.804$). For the six pairs where both individuals completed the feeder experiment, we found that *feeder sociality* ($rs = 0.886$, $N = 6$, $P = 0.019$) and *territory size* ($rs = 0.943$, $N = 6$, $P = 0.005$) were significantly and *feeder exploration* ($rs = 0.754$, $N = 6$, $P = 0.084$) marginally significantly positively correlated between the male and female, but *feeder visits* was not ($rs = 0.348$, $N = 6$, $P = 0.499$). Moreover, we did not find any significant relationships between *pair brood size* and *male novel environment exploration*, *female novel environment exploration*, or the interaction between male and female *novel environment exploration,* but there was a significant effect of *colony* (Table 6.6). Finally, we did not find any significant relationships between *pair mean nestling mass* and *male novel environment exploration*, *female novel environment exploration*, the interaction between male and female *novel environment exploration*, *colony* or *pair brood size* (Table 6.7).

Table 6.5: Summary of a General Linear Model examining variation in *brood size* in relation to *novel environment exploration* and *colony* (Saloon, Sandstone) for males only.

Term	B	SE	df1	df2	F	*P* value	Upper CI	Lower CI
(Intercept)	3.836	0.333	1	45	293.641	<0.0001	3.164	4.507
Novel environment exploration	-0.059	0.028	1	45	4.391	0.042	-0.116	-0.002
Colony (Saloon)	1.000	0.433	1	45	5.349	0.025	0.129	1.872

Figure 6.2: The relationship between male *brood size* during the first recorded breeding attempt and *novel environment exploration* scores. Outliers are denoted with circles if they are farther than 1.5 interquartile ranges yet closer than 3 interquartile ranges from the nearer edge of the box, and a star if they are farther than 3 interquartile ranges from the nearer edge of the box. As there were only three individuals with a *brood size* score of 0, the highest *novel environment exploration* score recorded (41 movements) does not appear as an outlier on the plot.
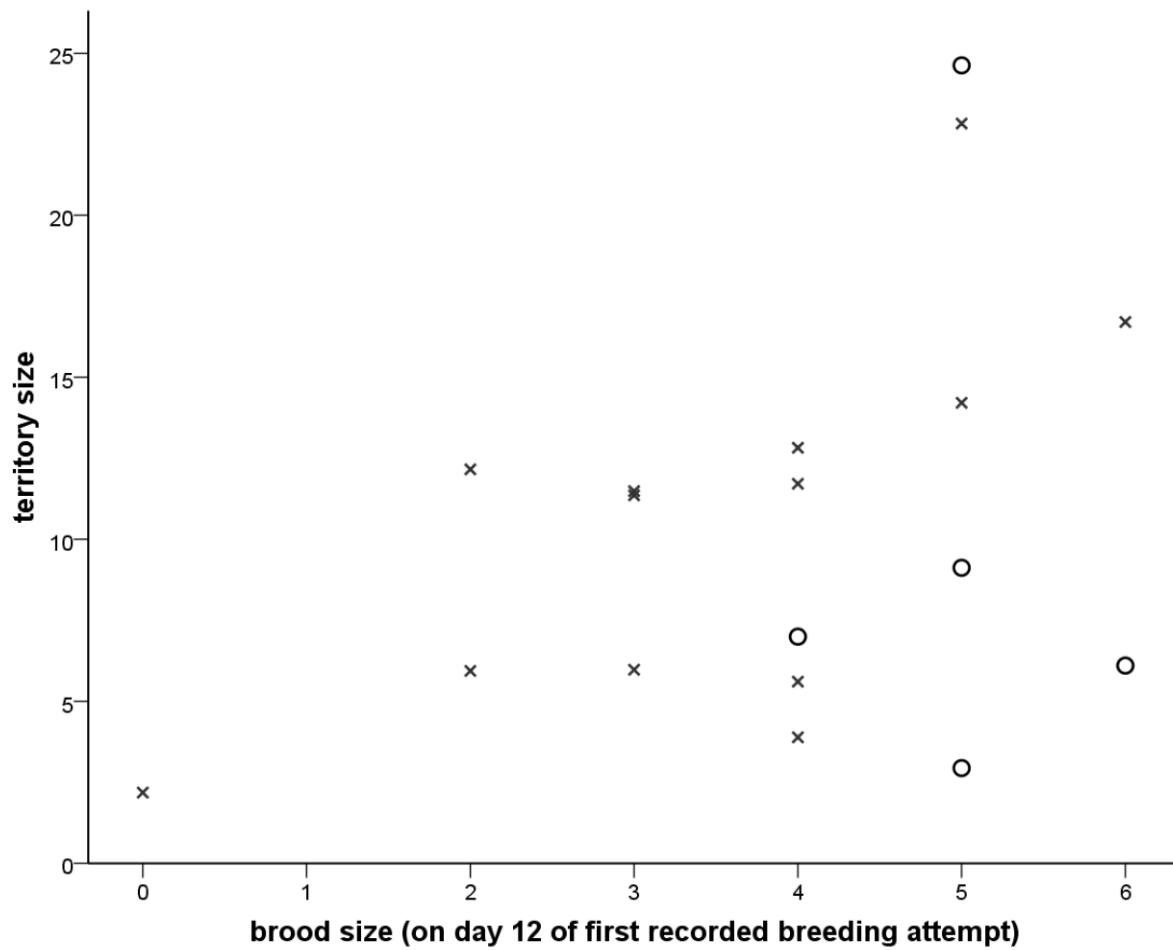
Figure 6.3: The relationship between male *brood size* during the first recorded breeding attempt and *territory size* during the feeder experiment. Individuals from Saloon are shown with open circles and individuals from Sandstone with crosses. Any individuals that did not make any known breeding attempt in the nest boxes during the field season are excluded from the figure.
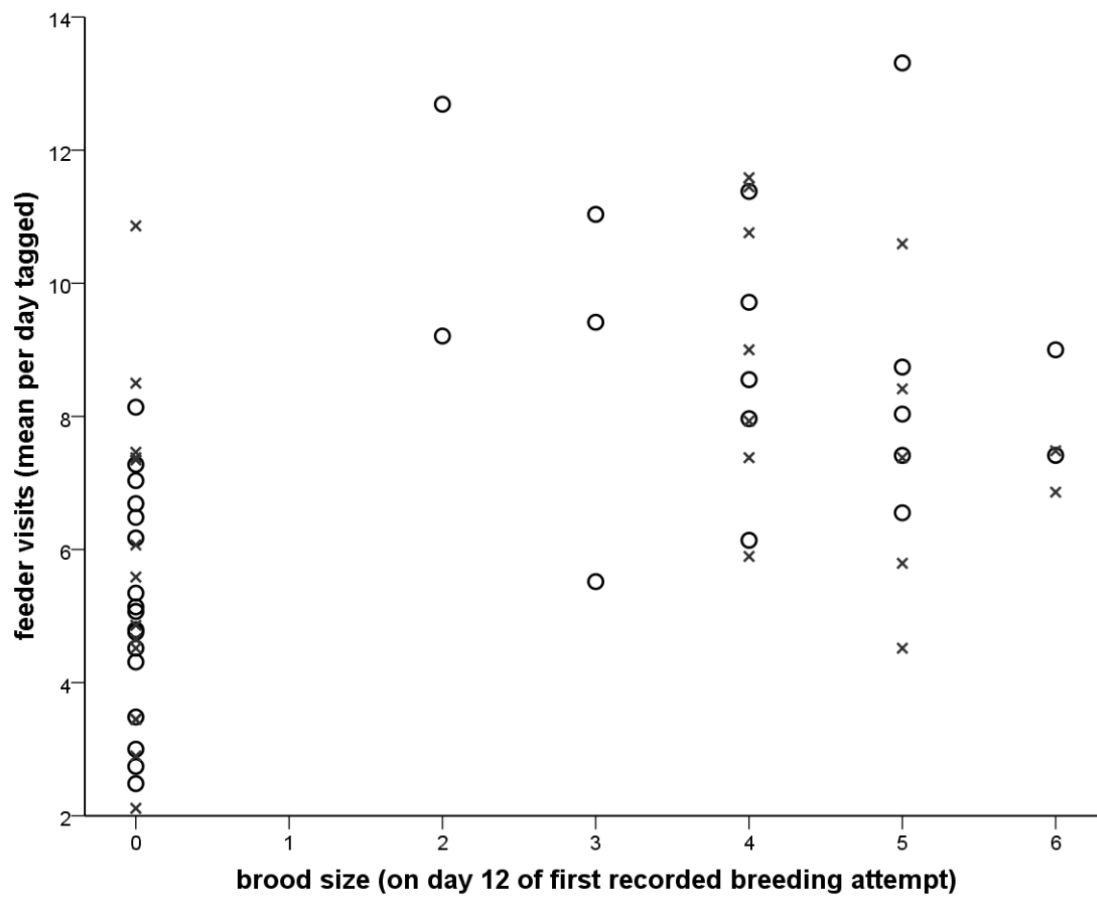
Figure 6.4: The relationship between male *brood size* during the first recorded breeding attempt and *feeder visits* during the feeder experiment. Individuals from Saloon are shown with open circles and individuals from Sandstone with crosses. For this analysis, all individuals that completed the feeder experiment but did not breed were allocated a *brood size* score of '0'.

Table 6.6: Summary of a General Linear Model examining variation in *pair brood size* in relation to the *novel environment exploration* scores of both parents, their interaction and *colony* (Saloon, Sandstone). *Novel environment exploration* is abbreviated to *N.E.E.*

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	3.657	0.516	1	28	83.253	<0.0001	2.601	4.714
Colony (Saloon)	1.234	0.584	1	28	4.465	0.044	0.038	2.431
Male N.E.E.	-0.051	0.058	1	28	0.755	0.392	-0.170	0.069
Female N.E.E.	0.016	0.067	1	28	0.058	0.811	-0.121	0.154
Male x *female N.E.E.*	0.001	0.005	1	28	0.083	0.775	-0.009	0.012

Table 6.7: Summary of a General Linear Model examining variation in *pair mean nestling mass* in relation to the *novel environment exploration* scores of both parents, their interaction, *pair brood size* and *colony* (Saloon, Sandstone).

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	8.865	0.879	1	22	80.737	<0.0001	7.043	10.687
Colony (Saloon)	0.036	0.496	1	22	0.005	0.943	-0.994	1.065
Pair brood size	0.016	0.199	1	22	0.006	0.937	-0.396	0.427
Male N.E.E.	0.016	0.043	1	22	0.139	0.713	-0.072	0.104
Female N.E.E.	0.010	0.046	1	22	0.048	0.829	-0.086	0.106
Male x *female N.E.E.*	-0.002	0.004	1	22	0.238	0.631	-0.009	0.006

DISCUSSION

Feeder exploration

The number of feeder visits made per day and our two measures of personality traits – exploratory behavior and sociality – were all significantly repeatable, except when the exploratory behavior was split into data from the two separate colonies, but this was likely just due to a reduction in sample size. Consequently, this suggests that as exploratory behavior and sociality represent consistent individual differences in behavior, they may potentially be considered as repeatable personality traits, similar to those found in other studies of species in the wild (Bell et al. 2009). However, the significant repeatability of the number of feeder visits made per day highlights a potential problem with estimating exploratory behavior from feeder use: that individuals that found less feeders may have been relying on feeders less for their source of food than other individuals and hence less likely to search for them, rather than being less exploratory in their innate personality. This is reflected in the significant positive correlation between feeder exploration score and mean feeder visits made per day. Moreover, individuals who found less feeders may actually be more exploratory, as they may be able to locate more and potentially higher quality food sources in the natural environment, rather than relying mostly on the feeders as their main source of food. However, the large amount of food easily accessible at feeders compared with natural foraging patches should hopefully have motivated individuals with both high or low exploratory behavior to seek out the feeders, and at least visit them a few times, even if some individuals did not rely on them as a major food source. We did not find any significant correlations between an individual's estimated territory size and their level of exploratory behavior or mean feeder visits made per day. This suggests that individuals that found more feeders and/or used feeders more frequently did so within the same area rather than seeking out feeders further away from the colony. However, we did find a significant negative correlation between an individual's estimated territory size and their level of sociality in feeder use. This suggests that individuals that tended to use the most popular

feeder (the feeder that received the most visits on that day) more on average were less likely to find feeders far away from the center of the colony (which greatly increases their estimated territory size). This result might be expected as most of the most popular feeders on a given day were near the center of the colonies rather than on the outskirts.

Sociality

We did not find the expected negative correlation between our measure of exploratory behavior in the wild and our measure of sociality (mean proportion of visits to the most popular feeder per day). This result contrasts with work which found that the use of social information to discover food patches is linked to exploratory behavior (Marchetti & Drent 2000; Kurvers et al. 2010) and an earlier study in the zebra finch, which found that more asocial breeders at Fowlers Gap were quicker and more likely to discover new feeders than more colonially-breeding individuals (Mariette & Griffith 2013). However, we did not attempt to include asocial breeders (with nest boxes set up far from the main colony) so it is possible that these individuals were not represented in our study. Furthermore, as the zebra finch is a highly social species, it is likely that new food patches might often be first discovered by groups of individuals (or at least pairs) rather than lone birds, and that individuals in these groups would consist of a range of personality types. This would have weakened any obvious trends between feeder discovery rates (*feeder exploration*) and our other measured variables. This idea is supported by the strong positive correlations we found for the feeder experiment variable scores (*feeder exploration*, *feeder sociality*, *territory size*) between the members of known breeding pairs. It is also likely that individuals utilize social information, networks and learning to bolster their rate of discovery of food patches (Benskin et al. 2002; Rands et al. 2008; Krause et al. 2010; Webster & Ward 2011; Aplin et al. 2012; Wilson et al. 2013). Hence, even if an individual discovered a new food patch alone or with its partner, it might then pass this information on deliberately to other members of the colony and vice versa, resulting in a

mutual benefit of all members of the social group, or inadvertently through the scrounging behavior of conspecifics, a behavior that is particularly favored by individuals with low foraging efficiency or environmental sampling rate (Beauchamp 2006; Giraldeau & Dubois 2008; Pike et al. 2008; Minderman et al. 2009; Rosa et al. 2012). In support of this argument, in three species of tits it was shown that individuals that occupied more central positions in social networks, i.e. they had social associations with a large number of individuals, were more likely to discover novel food patches in the environment and tended to arrive at these food patches sooner (Aplin et al. 2012), hence this study found the opposite result to our prediction of a negative correlation between sociality and exploration.

Novel environment test

While we found that behavior in our novel environment test was significantly repeatable, the results failed to be positively correlated with exploration in the wild from our feeder experiment as predicted based on the results of a few previous studies (Herborn et al. 2010; van Overveld & Matthysen 2010). Instead, we found a significant positive relationship between feeder sociality and the novel environment exploration scores. However, this is not the first study that failed to find a predicted correlation between behavior in captive personality tests and behavior in the wild (Schuett et al. 2012). This may have occurred due to shortcomings in the set-up of the novel environment test, resulting in a failure of our standardized test of novel environment exploration to reflect underlying personality differences. Firstly, it is possible that due to focusing on the measure of 'total flights/hops between areas' that this was measuring activity more so than exploratory behavior; however, the two have been shown to be positively correlated in this species in previous studies so this could still have resulted in a significant positive correlation (Beauchamp 2000; David et al. 2011a). Secondly, stress is a confounding factor and could have influenced the results of the novel environment test. Moreover, this is a factor that has previously been linked to exploratory and

risk-taking behavior in the zebra finch (Martins et al. 2007). Due to logistical infeasibility caused by the fact that many individuals were breeding at the time of capture, we were unable to maintain individuals in captivity for a considerable length of time before testing their personality, which may have influenced the results of the assays by not allowing sufficient time for individuals to habituate (Butler et al. 2006). Almost all previous studies have involved holding individuals temporarily in an environment similar to the novel environment (rather than a handling/bird bag) for periods ranging from 10 minutes (Kluen et al. 2012) to days (Dingemanse et al. 2004; Herborn et al. 2010) before the onset of the novel environment test to give individuals time to 'settle down' and for stress levels to lower. Unfortunately, zebra finches show increased levels of stress (as evidenced by corticosterone levels) when exposed to social isolation, handling and restraint (Breuner et al. 2006; Banerjee & Adkins-Regan 2011; Perez et al. 2012), all of which individuals would have experienced during our novel environment test. However, exploration/activity during stress could potentially constitute a personality trait on its own, or be intrinsically linked to other personality traits such as boldness or exploratory behavior (Carere et al. 2003; Baugh et al. 2012). Unfortunately the stress levels experienced by subjects in our tests could not be properly standardized, with individuals being held for differing amounts of time prior to the start of the novel environment test. However, we did not find an obvious correlation between the time individuals were held before the start of the novel environment test and their scores in the test, which appears to contradict this notion that handling time, at least, significantly affected behavior in the novel environment tests. Moreover, although breathing rate during handling does not appear to be correlated with personality in the zebra finch (David et al. 2012b), increased 'perch-hopping' following stress has been shown to occur at higher rates in slow explorers rather than fast explorers in the great tit which may explain why individuals that produced the most movements in the test actually showed lower exploratory behavior on average (but not significantly so) in the wild (Carere et al. 2003). This might also explain why we found a positive correlation between feeder sociality and total movements in the novel environment tests, as individuals that are more accustomed/prefer

to live in a group may have been more stressed than more asocial individuals by the social isolation incurred during the test, and so made a greater number of movements during the test (in this case reflecting escape behavior rather than exploration). Finally, the lack of a link between our measure of exploration in the novel environment test and in the wild might suggest that our test or the aspect of the test we measured is not reflective of general personality traits in the wild. This trait (total flights or hops between different areas) may be linked to a physiological trait (Biro 2012) or some other aspect of an individual's personality, and exploration may instead be better reflected by some other measure, such as which areas of the apparatus that were preferred by individuals (perches vs. floor), which has been shown to correlate with home range size in wild starlings (Minderman et al. 2010). However, as most individuals did not spend any time on the perches and only made a few flights towards the ceiling of the box (as if attempting to escape) during the entire five minute period, this measure would not be useful for our test. Moreover, their behavior in the test differed considerably in our work with similar novel environment tests with domesticated zebra finches, where individuals made far fewer escape behaviors and spent a considerably greater time exploring perches rather than simply sitting on the floor of the apparatus (McCowan & Griffith 2012, unpublished research). This may have occurred due to individuals not being accustomed to captive conditions and/or heavily affected by stress.

Individuals at Sandstone colony made greater mean movements than individuals at the Saloon colony, which may suggest that population-level differences in personality exist in this region, as has been previously been suggested (Réale et al. 2010; Magnhagen et al. 2012). In contrast, the specifics of the location and the time individuals were in holding bags before the onset of the test may have varied to a small degree between the colonies which may have produced this small significant difference. Moreover, the number of birds breeding was generally greater at Sandstone, thus breeding density may have affected the mean novel environment exploration scores.

Reproductive success

We uncovered no significant relationships between our two measures of reproductive success (total brood size and mean nestling mass at pre-fledgling on day 12) and any of our measures of feeder behavior. However, we did find a non-significant positive trend between male brood size and territory size (as estimated from the specific feeders visited during the feeder experiment) and a significant negative correlation between male brood size and their scores in the novel environment test. These first of these results suggests that males that raised more nestlings successfully tended to find more distant feeders from the center of the colony, thereby increasing their estimated territory size. This might be explained by higher quality, more wide-ranging males being better able to provision their nestlings with adequate food for survival (or females being more likely to lay large clutches when paired with such males). The second result suggests that males that raised more nestlings successfully also tended to make less movements during the novel environment test. Novel environment exploration was positively correlated to sociality, which suggests that more asocial males might have had greater breeding success; however, no direct link between the two variables was found. Instead, this correlation may have been caused by breeding males conserving their energy during their capture (in many cases individuals were captured from nest boxes with active clutches) to provide for their young rather than actively exploring the novel environment test. However, it might be expected that actively breeding males would be the most motivated to find a way out of the box to return to their nests, which contradicts this notion. Instead, this latter of the two correlations may be mostly driven by a few outliers in the data, especially one male in particular that recorded a brood size of 0 for his first breeding attempt, along with the highest novel environment score (for a male) of 41 (the mean *novel environment exploration* score for males was only 5.26). When this male is removed from the data the correlation between novel environment exploration and brood size becomes non-significant. We also looked at the novel environment exploration scores of both parents combined, at those nests where we managed to capture them both, to assess whether pairs that were mated assortatively or disassortatively obtained greater

brood sizes, but found no effect. Moreover, we found no evidence from the pairs that we captured that individuals preferentially paired assortatively or disassortatively with respect to their novel environment test scores. When we analyzed our data with all individuals that completed the feeder experiment but did not record a breeding attempt in the nest boxes allocated the brood size of '0', the only significant correlations we found were positive correlations between the mean feeder visits made per day and brood size. This relationship might be expected since breeding individuals need to acquire more food to feed their young as well as themselves and the feeders provided a plentiful, easy to access supply of food close to the nest boxes and so would likely have been a useful resource for breeding individuals. Moreover, the greater the number of young that need to be fed in a brood, the more food that needs to be acquired, at least for nestlings to be raised in equal condition (and a parent can only carry so much food from a feeder to a nest box in a single trip). However, Mariette & Griffith (2013) found that colonially-breeding zebra finches (rather than asocial breeders) tended to provide their broods with an equal total amount of food overall irrespective of brood size, which suggests that all individuals that made a breeding attempt would likely have elevated their total food acquired/transported to the nest boxes by a roughly similar amount. This might explain why the correlation between brood size and mean feeder visits only became significant when non-breeding individuals were included in the analysis and allocated a brood size of '0'.

These results either suggest no obvious links between personality and reproductive success during our study (Patrick & Browning 2011), or that the way we measured reproductive success masked these effects (territory size and mean feeder visits made were not considered to be 'personality' traits). Firstly, zebra finches can make more than one breeding attempt per year (Zann 1996), and so this may have increased the reproductive success of some individuals while reducing it in others. As we only focused on the first breeding attempt made by an individual (there were only a few cases where we recorded individuals breeding twice), we could not be certain that we were monitoring the first breeding attempt made by an individual in that season. Secondly,

reproductive success is higher in the nest boxes in our colony than the surrounding natural nests (Griffith et al. 2008). Hence, reproductive success may have been artificially inflated for all individuals by the artificial nest boxes, which may have masked potential effects on fitness of processes such as predation (Jones & Godin 2010) and the associated links between personality and nest defense (Hollander et al. 2008). Thirdly, previous research has suggested that the combination of personality traits of both of the parents rather than just one or the other influence reproductive success (Both et al. 2005). In domesticated zebra finches, highly exploratory females were shown to exhibit a preference for highly exploratory males, while less exploratory females showed no preference (Schuett et al. 2011b). Moreover, assortative pairs with respect to exploratory behavior were found to have greater reproductive success than disassortative pairs (Schuett et al. 2011a). We found no significant evidence for a preference for assortative or disassortative mating with respect to novel environment test scores or greater reproductive success for one tactic or the other. However, considering the difficulties of identifying what the novel environment test was actually measuring due to its lack of a link to wild exploratory behavior, this lack of a result does not rule out potential interactions between personality types in influencing reproductive success. Fourthly, it may have been difficult to identify significant correlations between the personality traits we measured and reproductive success due to unidentified fluctuating environmental conditions resulting in changes to selective pressures on the traits over the course of the field season (Dingemanse et al. 2004), or the most adaptive personality types may even have varied dependent on the specific nest box locations in which the parents chose to breed due to slight habitat differences between them (Hensley et al. 2012). However, as our length of study was relatively short (just two and half months), compared to previous work that has provided evidence of fluctuating selection (Dingemanse et al. 2004), and the nest box colonies relatively small and consistent (all nest boxes were placed within a few meters of an *Acacia* spp. tree and no two nest boxes within a colony were more than 350 m apart), we feel that either of these potential influences having a strong effect on our results is unlikely. Fifthly, while Schielzeth et al. (2011) found no

significant correlations between neophilia and various measures of reproductive behavior (reproductive success, promiscuity and extrapair paternity) in captive zebra finches, their results suggest that this personality trait is related to the use of different reproductive strategies. This may also be true of wild zebra finches with regards to their feeder exploration behavior, rather than there existing a direct link with reproductive success. However, as we did not compare reproductive strategies in our study this is entirely speculative. Finally, females might have used compensatory investment to offset the effects of being paired with a less attractive male (Bolund et al. 2009), or in the case of our study a less than desirable personality type, which may have masked the effects of personality on reproductive success, preventing us from obtaining a significant result.

Mean brood size tended to be larger at Saloon than Sandstone (all individuals that made no known breeding attempt were excluded from this analysis). This was likely driven by both a larger number of failed breeding attempts (with all of the nestlings that hatched dying by day 12) at Sandstone than Saloon, and a larger peak brood size at Saloon (a peak brood size of five) than Sandstone (a peak brood size of 4). This suggests that breeding success was greater in general at Saloon, however, the mean nestling mass at day 12 did not significantly differ between the two colonies, which suggests that those nestlings that were successfully raised to this age received similar amounts of nutrition. The differences in breeding success at the two colonies may have occurred due to a variety of unidentified real or perceived differences in the two environments resulting in a greater likelihood of nest desertion at Sandstone, or differences in parental quality between the two populations.

Despite there being a wealth of work on personality in captivity across different species, the amount of studies examining personality in the wild is more scant. Our work provided the first investigation into the personality of the zebra finch in the wild. From this work we found that although the commonly used 'novel environment' or 'open-field' test is repeatable in the wild zebra finch (in a similar manner to this and other species in captivity and the wild), we did not find that it

predicted exploratory behavior of feeders in the wild. Instead, we found a weak positive correlation between exploration in this test, as it is generally defined, and sociality in their feeder use. Future work attempting to assess the personality in the wild with a novel environment test should focus on allowing individuals adequate time to adjust to captivity before assessing their personality; however, work would need to be conducted to establish the amount of time required. However, it is likely more biologically meaningful to measure personality from the use of natural resources or approximations of them, such as feeders, to properly assess the mechanisms driving the production of those behaviors in the wild.

Ethical note

Animal welfare and methodological design were approved by the Animal Ethics Committee at Macquarie University (AEC reference number 2011/041).

Chapter Seven

General Discussion

"Both subspecies of Zebra Finches must be considered successful in their respective environments because both are relative1y numerous, wide-spread in distribution, and persistent in a rapidly changing environment. Understanding their life histories is the key to understanding why they are successful."

Richard Zann (Zann 1996)

Individual assays in a social species: the role of stress

This thesis investigated personality in the zebra finch from several new perspectives. The majority of previous personality work not only in this species, but in all animal species, generally assays personality traits in individuals that are alone, rather than in social groups (Webster & Ward 2011). While I do not seek to discredit this method as a valid measure of personality traits, in the wild, zebra finches are rarely on their own (**Chapter Two**) and complete most common tasks such as foraging, watering and travelling as part of a pair (which represents the sexual partnership) or in small (or more rarely, large) social groups. This method also fails to directly investigate whether an individual's propensity to move and feed alongside others is related to personality. Moreover, zebra finches that are forced to endure social isolation in captivity have been shown to exhibit increased stress levels (Banerjee & Adkins-Regan 2011; Perez et al. 2012). We obtained similar results, with those wild-caught individuals that we socially isolated for our novel environment test behaving as if highly stressed (**Chapter Six**). Unfortunately, as stress may modify or change behaviour (Moberg & Mench 2000; Blanchard et al. 2001), assaying individuals' behaviour while exposed to stress (the level of which may vary from individual to individual) can introduce bias into the results.

Stress has also been shown to be linked to personality traits such as exploratory behaviour and risk-taking behaviour and in fact, the levels of these behaviours exhibited in assays can be manipulated by selecting for the amount of corticosterone produced in response to a manual restraint stressor in artificial lines (Martins et al. 2007). We considered the potential for these biases, and in our captive work we tried to reduce the stress levels experienced by individuals in our assays of personality as much as possible, by testing individuals in social groups or pairs rather than alone to reduce the stress of social isolation (Blanchard et al. 2001), and over longer periods of time than usual (days rather than minutes) following handling and restraint, as these are also well-known stressors (Banerjee & Adkins-Regan 2011), to give individuals' stress levels time to return to baseline.

Aside from the impacts of stress on behaviour, it has been suggested that it is difficult to obtain clear a priori theoretical predictions from the results of a novel environment or open-field test (Dall & Griffith 2014), as it is difficult to determine what aspect of behaviour it is testing. This is likely especially true in the wild zebra finch, as individuals would rarely have encountered a similar environment in the wild. Exploration in the wild in the zebra finch is likely conducted from the air and over much larger distances than that available in the small novel environment test apparatus. When individuals do explore on the ground it is likely mostly related to searching for grass seeds or nesting materials, neither which an individual would be motivated to do while in a highly-unusual foreign and stressful environment, following an event (capture and handling) that likely simulates predation, and may inspire attempted escape behaviour. However, these factors are also a problem in other avian species, such as the great tit (*Parus major*) and blue tit (*Cyanistes caeruleus*), but studies that have implemented novel environment tests in these species have obtained positive correlations between exploration in these environments and their exploration of feeders in the wild (Herborn et al. 2010; van Overveld & Matthysen 2010).

When we attempted the most commonly used method for measuring exploratory behaviour, the 'novel environment' or 'open-field' test in our captive experiments, we found only a weak link between behaviour in this apparatus and exploration in social groups, and no correlation with general activity levels of individuals in a social pair (situations in which individuals likely experience low levels of stress). Interestingly, when we used this test on wild birds at Fowlers Gap (**Chapter Six**), we failed to find the expected link between this assay and exploratory behaviour in the wild, despite the previously mentioned work in other species which has confirmed a positive relationship between the two methods (Herborn et al. 2010; van Overveld & Matthysen 2010). We expected that rather than our exploration test not providing a suitable environment to measure exploratory behaviour, stress was the more likely culprit producing such counter-intuitive results, as individuals were exposed to several stressors during our assays, namely social isolation, handling and restraint, which likely raised their stress levels above those experienced on a day-to-day basis.

In contrast to these novel environment test results, in our other captive experiments we attempted to reduce the amount of stress individuals experienced by assaying individuals in social pairs or groups, and focused on much larger and more naturally-representative tests of behaviour. We also measured the repeatability of activity levels over an individual's lifespan, finding that at least in males this personality trait appears to be formed and remain stable from as young as five days of age till near the end of their lifespan (**Chapter Four**). Moreover, we found that exploratory behaviour in a social foraging context in small to large single-sex groups, which may or may not have been influenced by leadership and following behaviour, was positively correlated to general activity levels of individuals kept in pairs (sexual partnerships) (**Chapter Three**). This relationship occurred despite the different physical and social environments of the two tests (large aviary versus home cage). Moreover, we also found that more active/exploratory males were less social in their feeder use, suggesting either that they actively avoid using the most popular spots, or that less active/exploratory males seek out the popular feeding spots (or are unable to find alternatives). Hence, the degree of sociality that individuals exhibit – which could alternatively be defined as their gregariousness or sociability, or the intrinsic propensity with which individuals interact with and coordinate their activity with conspecifics – either functions as an important component of personality or constitutes a personality trait in itself. In past research individual differences in social niche specialisation or sociality have been suggested as a possible mechanism for the evolution of personality (Bergmüller & Taborsky 2010). We looked for possible fitness benefits of sociality by investigating the same two traits in the wild using a PIT-tag monitoring systems (**Chapter Six**). We failed to uncover the expected negative correlation between exploratory behaviour and sociality in the way individuals used feeders. There are a number of reasons why this link between exploratory behaviour and sociality may have failed to manifest in the feeder use of wild birds. As zebra finches are a highly social species, the effects of differences in exploratory behaviour between individuals on fitness are likely to be mitigated or at least influenced by the use of social networks, social information and scrounging behaviour in the discovery of resources in the environment (Giraldeau

& Dubois 2008; Aplin et al. 2012; Aplin et al. 2013). However, as zebra finches are so social, it is difficult to isolate an individual's own personality from that of other members of its social group or partnership by their behaviour in a social context. In other words, less exploratory individuals may have obtained inflated exploration scores by following more exploratory individuals to feeders in the environment via the use of social information or simply by allowing more exploratory individuals to play a leadership role. Personality has previously been linked to the adoption of a leadership role in both the zebra finch (Beauchamp 2000) and other species (Kurvers et al. 2009). We also found that more active females were more likely to play the leadership role in our social aviary foraging experiment (**Chapter Three**). Alternatively, a meta-analysis of behavioural syndromes has shown that correlations between different personality traits are weak on average (Garamszegi et al. 2012), so we may have failed to find significant correlations between wild personality traits due to an insufficient sample size. Moreover, the selection of work on the captive zebra finch showing significant relationships between personality traits may have been influenced by publication bias, with significant results more likely to be published than non-significant results (Garamszegi et al. 2012). This would suggest that the actual correlation sizes between traits are weaker than those predicted based on the published literature, and therefore it would have required a larger sample size for us to demonstrate similar effect sizes.

Personality and reproductive success

A number of studies have previously examined the link between various personality traits and fitness traits, such as growth rate (Adriaenssens & Johnsson 2011), survival (Archard & Braithwaite 2011) and reproductive success (Vrublevska et al. 2014). Moreover, according to the pace-of-life hypothesis, an individual's behavioural type (proactive or reactive) may be linked to different behavioural strategies (Wolf et al. 2007; Réale et al. 2010), or reflect trade-offs between different life-history fitness traits (e.g. some individuals might favour current reproduction over long-term

survival) (Stamps 2007; Smith & Blumstein 2008). However, little work has yet investigated the relationship between personality and fitness in the zebra finch, despite the zebra finch being one of the key model species for the study of personality. Unfortunately, fitness is difficult to measure in the wild zebra finch for a number of reasons. Firstly, it is difficult to gauge survival rates by monitoring populations at only a single study site, as dispersal to other areas is frequent in this semi-nomadic species, and the tendency to disperse may be related to an individual's personality (Cote et al. 2010; Chapman et al. 2011; Quinn et al. 2011; Rasmussen & Belk 2012). Secondly, as zebra finches are opportunistic breeders it can be difficult to monitor annual breeding success without monitoring all breeding attempts individuals make, which especially in central Australia, can occur year-round and may be linked to difficult-to-predict patterns such as rainfall or the levels of nest predators in the area (Zann et al. 1995; Zann 1996). Moreover, it may be necessary to monitor the entire lifespan of individuals to investigate how personality influences lifetime reproductive success (Armitage & Van Vuren 2003), which is difficult as individuals may disperse to different areas between breeding seasons, particularly if conditions are not favourable (Zann 1996). Thirdly, breeding success in captive environments such as aviaries may not provide an entirely valid simulation of breeding in the wild, due to the reduced or altered resources and stressors in captivity.

Despite these limitations we attempted to assess the relationship between personality and reproductive success in the short term both in captivity (**Chapter Five**) and in the wild (**Chapter Six**). Our findings were mixed, with exploratory behaviour appearing to have an effect on at least one aspect of reproductive success in males in captive aviaries, namely the number of breed attempts made, and a marginally significant effect on the total number of nestlings he raised with his social partner (though some of these nestlings may have been sired by other males). Conversely, we did not find any significant correlations between reproductive success and the personality traits we measured in the wild, exploratory behaviour and sociality. Unfortunately, we were only able to measure one fitness attribute over a relatively short period of an individual's lifespan (a couple of

months of breeding activity in captivity, only a single breeding attempt per individual in the wild). However, studies must be conducted over the long-term to investigate whether disruptive or fluctuating selection influence fitness (Bergeron et al. 2013), as the relationship between personality traits and fitness may be altered under different seasons, weather and environmental conditions. Moreover, an experimental approach might be better for demonstrating a relationship which is less feasible in the wild than in a controlled aviary environment.

Methods for assaying personality in the future

This thesis sought to broaden our understanding of various aspects of zebra finch personality, while approaching personality research from an ecological point of view, and assaying personality in the wild zebra finch for the first time. However, this work also raised several questions to be addressed in the future. Firstly, we established a link between zebra finch activity during food begging at a very young age (five days old) and adult general activity levels (**Chapter Four**). However, we did not examine which factors resulted in this correlation. Hence, future work is needed to assess whether this relationship is caused by physiological factors, such as differences in metabolic rate between individuals (Bouwhuis et al. 2014) or tied in to environmental or ontogenetic factors, or a combination of both. Moreover, repeated tests are required to confirm whether or not activity can reliably be assayed at such a young age as this could provide an extremely useful method of assaying personality. This method would be particularly useful in the wild, as adult birds would not need to be captured, which may affect the way they behave, or result in their desertion of the area.

Although our work focused on measuring individual differences in behaviour under group-living conditions more reflective of the natural environment in which zebra finches live than previously used individual assays (**Chapters Three, Five, Six**), it would also be useful to find methods of assaying sociality under more controlled conditions. One possible method of assaying an individual's sociality levels might be via an apparatus such as those commonly used for mate-

choice tests. Though their work was not focused on personality, Goodson et al. (2009) assayed the sociability of individuals, by placing them in the central chamber of an apparatus with differing numbers of conspecifics in separate cages at either end. The amount of time an individual chooses to spend at the different ends of the apparatus could then be quantified to measure of their sociality. However, further work on this test would need to be conducted to assess what set up best assays highly social/asocial personality types. For instance, asocial zebra finches might be attracted to only one or two zebra finches over a large group, but avoid an area of the apparatus that is completely devoid of conspecifics, as all individuals might prefer to have some company rather than be on their own. Moreover, results of the test should be compared to behaviour under more natural conditions, such as social behaviour in an aviary or in the wild, as it is difficult to make inferences about the ecology and behaviour of wild zebra finches from personality assays alone.

Whilst my work provided the first experimental analysis of personality in the wild zebra finch (**Chapter Six**), further work is necessary to confirm the links between traits. In particular, to more thoroughly assess the relationship between personality traits and fitness, it would be useful to capture and tag the majority of the zebra finches present in a region, and to follow these individuals over their entire lifespan to assess not only reproductive success but other life-history traits, such as growth rates and survival, which are known to be tied to personality in other species (Smith & Blumstein 2008). However, due to their nomadic nature, this might not be logistically feasible in the zebra finch until economical GPS tags small enough to be attached to zebra finches become commercially available. Moreover, the use of these sorts of active rather than passive tags will likely prove useful in determining the social nature of individuals, by allowing researchers to calculate the average number of conspecifics individuals spend their time with. However, the currently-used PIT-tag system may still provide fruitful data about the relationship between personality and social relationships from social network analyses, by examining whether or not individuals make concurrent visits to feeders and/or nest boxes. Similar work in several tit species has found links between exploratory behaviour and the types of relationships individuals work with

conspecifics, with some individuals forming many weak relationships and some fewer but stronger relationships (Aplin et al. 2012; Aplin et al. 2013). Similarly, it would be interesting to see similar studies conducted on the zebra finch, especially to examine more nuanced forms of individual differences in social behaviour separate from preferences for different group sizes, which is an area of research this thesis did not address.

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SUPPLEMENTARY MATERIALS

(for Chapter Six)
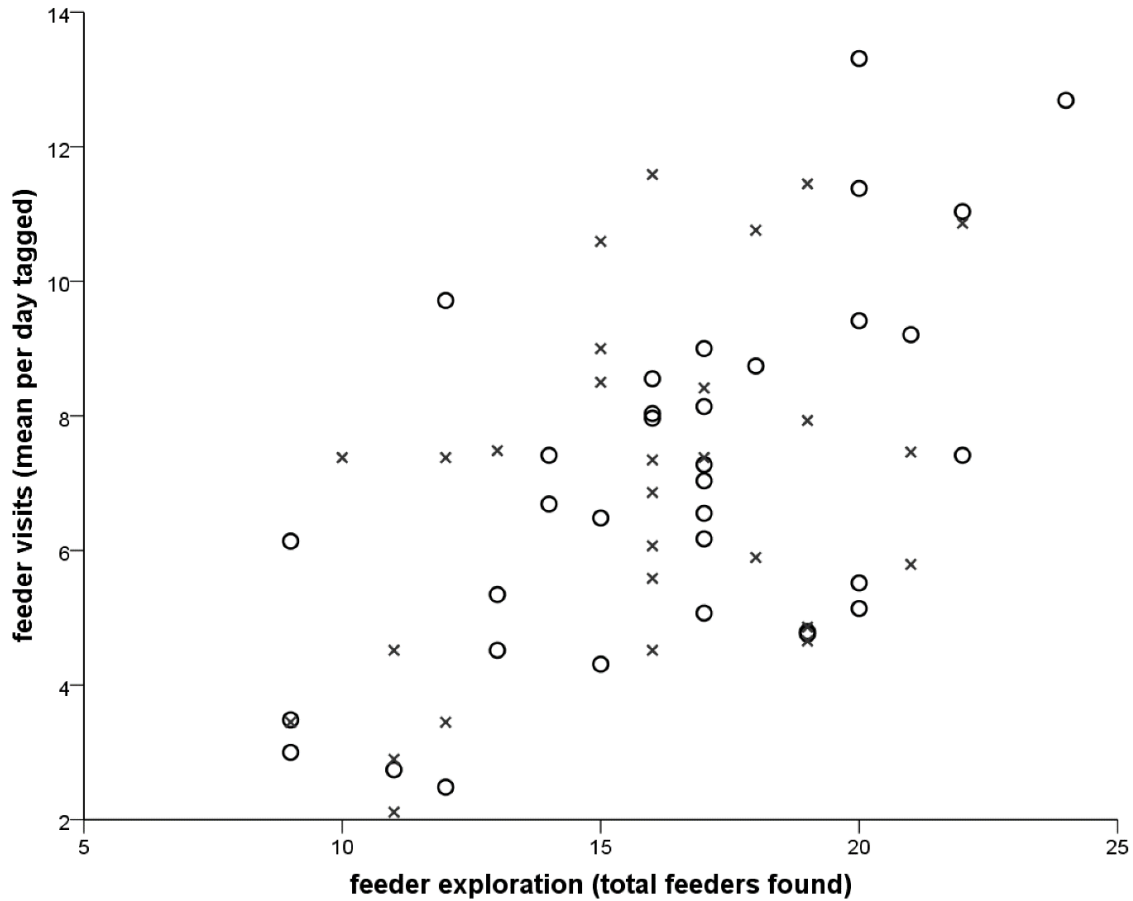
Figure 6.5: The correlation between *feeder exploration* and *feeder visits* (the mean number of feeder visits made per day, only including those days individuals were known to be tagged). A higher exploration score indicates a greater number of feeders found during the feeder experiment. Males are shown with open circles and females with crosses.
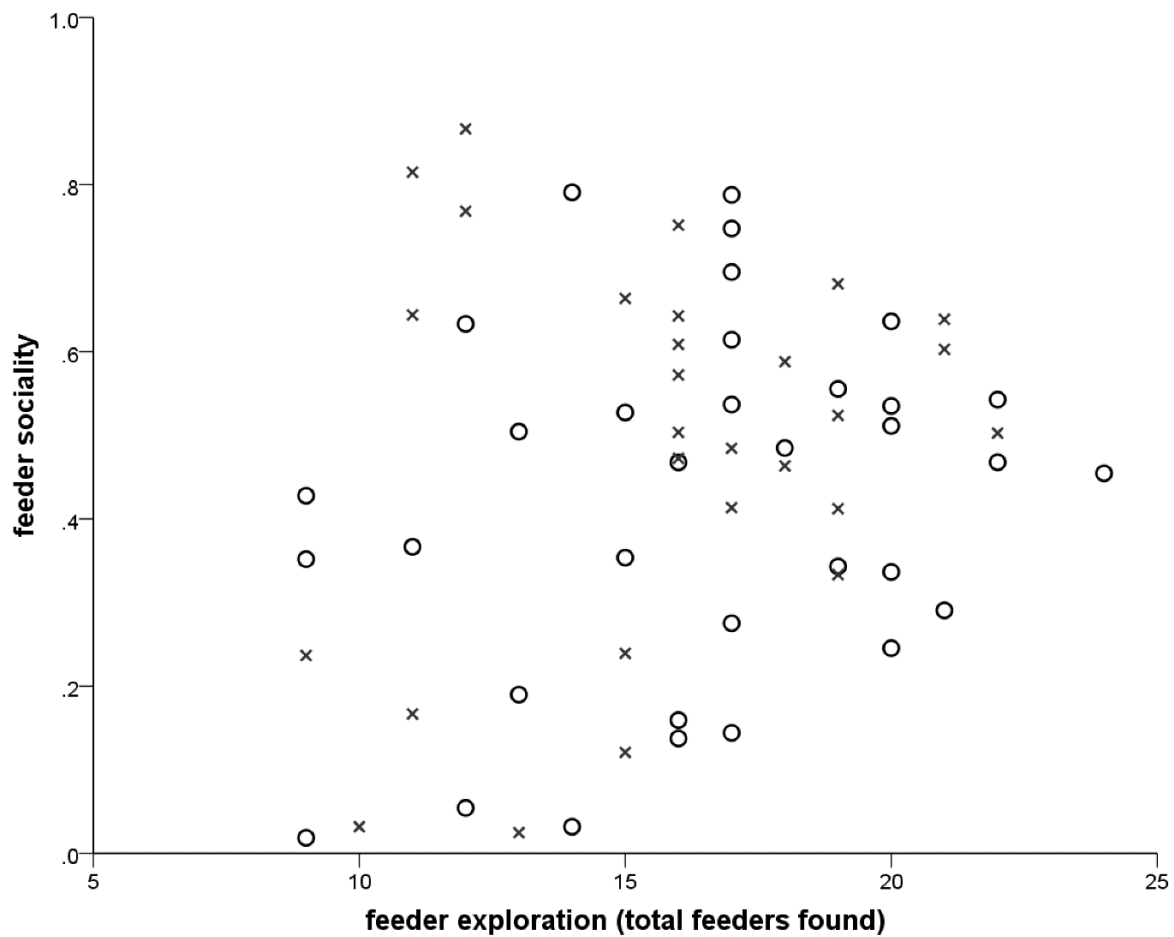
Figure 6.6: The correlation between *feeder exploration* and *feeder sociality*. A higher exploration score indicates a greater number of feeders found during the feeder experiment, while higher feeder sociality scores indicate a higher mean proportion of visits made to the most popular feeder (calculated from the same nine days for each individual, dependent on colony). Males are shown with open circles and females with crosses.
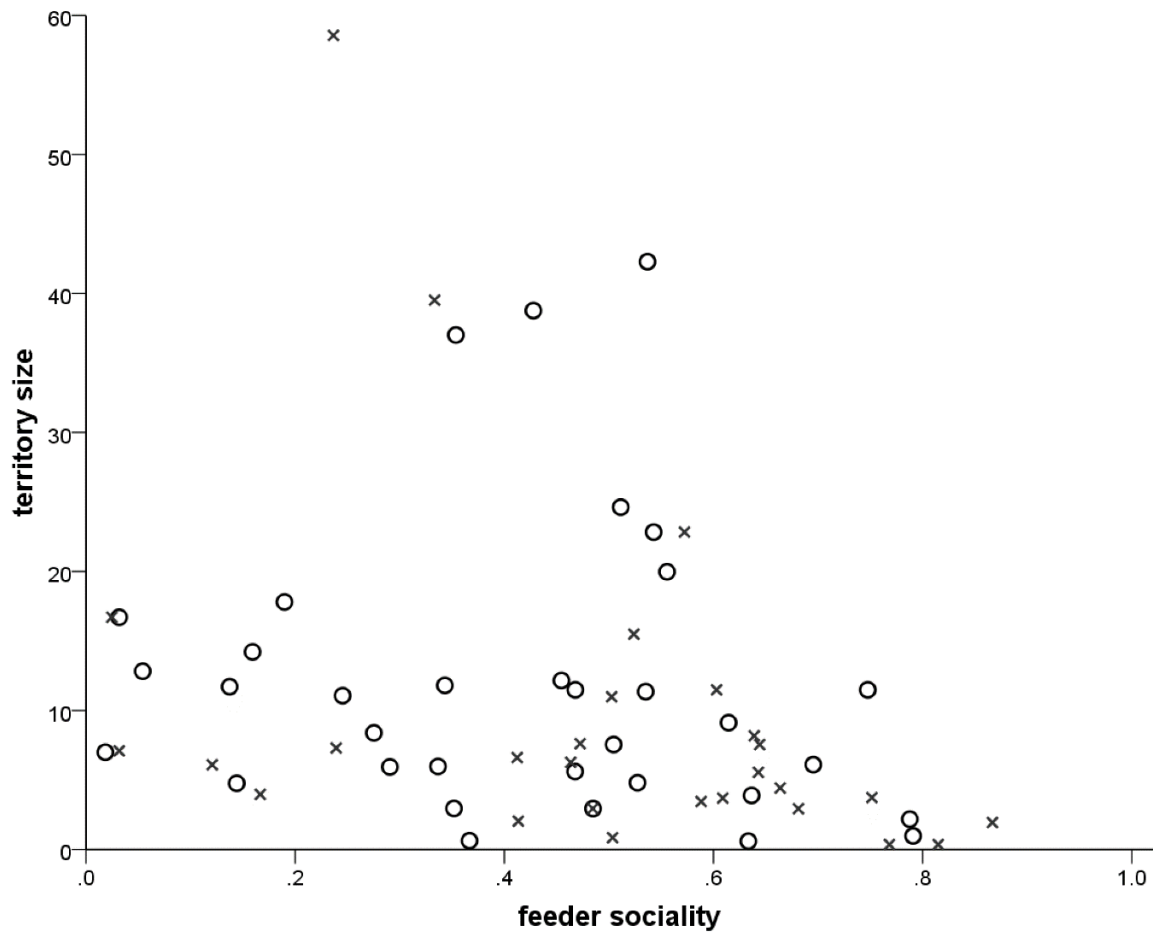
Figure 6.7: The correlation between *territory size* and *feeder sociality*. A higher *territory size* indicates a greater territory estimated from feeder use, while higher feeder sociality scores indicate a higher mean proportion of visits made to the most popular feeder (calculated from the same nine days for each individual, dependent on colony). Males are shown with open circles and females with crosses.

Table 6.4a: Summary of a Generalized Linear Model with negative binomial error structure examining variation in the exploration of a novel environment by zebra finches in relation to exploratory behavior at feeders around a colony, sex and colony identity.

Term	B	SE	DF	Wald Chi-Square	*P* value	Upper CI	Lower CI
(Intercept)	2.429	0.8674	1	9.630	0.002	0.729	4.129
Feeder exploration	-0.035	0.0491	1	0.498	0.481	-0.131	0.062
Colony (Saloon)	0.071	0.3454	1	0.043	0.836	-0.605	0.748
Sex (male)	-0.051	0.2861	1	0.032	0.858	-0.612	0.509

Table 6.4b: Summary of a Generalized Linear Model with negative binomial error structure examining variation in the exploration of a novel environment by zebra finches in relation to sociality behavior at feeders around a colony, sex and colony identity.

Term	B	SE	DF	Wald Chi-Square	*P* value	Upper CI	Lower CI
(Intercept)	0.692	0.4072	1	4.992	0.025	-0.106	1.490
Feeder sociality	2.193	0.6667	1	10.817	0.001	0.886	3.499
Colony (Saloon)	0.076	0.3205	1	0.056	0.813	-0.552	0.704
Sex (male)	0.119	0.2948	1	0.163	0.686	-0.459	0.697

Table 6.4c: Summary of a Generalized Linear Model with negative binomial error structure examining variation in the exploration of a novel environment by zebra finches in relation to the mean daily number of feeder visits at a colony, sex and colony identity.

Term	B	SE	DF	Wald Chi-Square	*P* value	Upper CI	Lower CI
(Intercept)	2.348	0.4867	1	29.394	<0.0001	1.394	3.302
Feeder visits	-0.073	0.0603	1	1.468	0.226	-0.191	0.045
Colony (Saloon)	0.107	0.3217	1	0.112	0.738	-0.523	0.738
Sex (male)	-0.030	0.2869	1	0.011	0.917	-0.592	0.532

Table 6.4d: Summary of a Generalized Linear Model with negative binomial error structure examining variation in the exploration of a novel environment by zebra finches in relation to territory size based on feeder use around a colony, colony identity and sex.

Term	B	SE	DF	Wald Chi-Square	*P* value	Upper CI	Lower CI
(Intercept)	1.930	0.3060	1	93.335	<0.0001	1.330	2.529
Territory size	-0.006	0.0144	1	0.201	0.654	-0.035	0.022
Colony (Saloon)	0.116	0.3403	1	0.116	0.734	-0.551	0.783
Sex (male)	-0.062	0.2856	1	0.047	0.828	-0.622	0.498

Table 6.8: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder exploration* and *colony* (Saloon, Sandstone) for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	4.856	1.794	1	15	10.803	0.005	1.031	8.681
Feeder exploration	-0.076	0.095	1	15	0.634	0.438	-0.278	0.127
Colony (Saloon)	1.368	0.774	1	15	3.122	0.098	-0.282	3.018

Table 6.9: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder sociality* and *colony* (Saloon, Sandstone) for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	4.235	0.648	1	15	54.628	<0.0001	2.854	5.617
Feeder sociality	-2.052	1.403	1	15	2.138	0.164	-5.043	0.939
Colony (Saloon)	1.719	0.721	1	15	5.682	0.031	0.182	3.255

Table 6.10: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder visits* and *colony* (Saloon, Sandstone) for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	4.215	1.516	1	15	11.095	0.005	0.985	7.446
Feeder visits	-0.084	0.163	1	15	0.266	0.614	-0.432	0.264
Colony (Saloon)	1.521	0.753	1	15	4.073	0.062	-0.085	3.127

Table 6.11: Summary of a General Linear Model examining variation in *brood size* in relation to *territory size* and *colony* (Saloon, Sandstone) for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	2.389	0.621	1	15	28.308	<0.0001	1.066	3.712
Territory size	0.102	0.049	1	15	4.399	0.053	-0.002	0.205
Colony (Saloon)	1.597	0.668	1	15	5.709	0.030	0.172	3.021

Table 6.5: Summary of a General Linear Model examining variation in *brood size* in relation to *novel environment exploration* and *colony* (Saloon, Sandstone) for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	3.836	0.333	1	45	293.641	<0.0001	3.164	4.507
Novel environment exploration	-0.059	0.028	1	45	4.391	0.042	-0.116	-0.002
Colony (Saloon)	1.000	0.433	1	45	5.349	0.025	0.129	1.872

Table 6.12: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder exploration* and *colony* (Saloon, Sandstone), for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	3.181	2.693	1	14	2.372	0.146	-2.596	8.958
Feeder exploration	0.001	0.157	1	14	0.000	0.994	-0.336	0.338
Colony (Saloon)	1.516	0.967	1	14	2.459	0.139	-0.558	3.589

Table 6.13: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder sociality* and *colony* (Saloon, Sandstone) for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	4.780	1.087	1	14	27.283	0.0001	2.449	7.111
Feeder sociality	-3.189	1.891	1	14	2.843	0.114	-7.245	0.867
Colony (Saloon)	1.683	0.864	1	14	3.799	0.072	-0.169	3.535

Table 6.14: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder visits* and *colony* (Saloon, Sandstone) for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	1.662	1.603	1	14	2.168	0.163	-1.777	5.100
Feeder visits	0.203	0.198	1	14	1.060	0.321	-0.220	0.627
Colony (Saloon)	1.413	0.912	1	14	2.398	0.144	-0.544	3.370

Table 6.15: Summary of a General Linear Model examining variation in *brood size* in relation to *territory size* and *colony* (Saloon, Sandstone) for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	2.106	0.834	1	14	22.469	0.0003	0.317	3.895
Territory size	0.136	0.078	1	14	3.024	0.104	-0.032	0.304
Colony (Saloon)	1.981	0.895	1	14	4.907	0.044	0.063	3.900

Table 6.16: Summary of a General Linear Model examining variation in *brood size* in relation to *novel environment exploration* and *colony* (Saloon, Sandstone) for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	3.318	0.413	1	41	144.566	<0.0001	2.484	4.151
Novel environment exploration	0.016	0.032	1	41	0.257	0.615	-0.048	0.080
Colony (Saloon)	1.150	0.540	1	41	4.532	0.039	0.059	2.240

Table 6.17: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *feeder exploration*, *brood size* and *colony* (Saloon, Sandstone), for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	10.464	1.285	1	13	64.605	<0.0001	7.687	13.241
Feeder exploration	-0.042	0.049	1	13	0.748	0.403	-0.147	0.063
Brood size	-0.093	0.169	1	13	0.305	0.590	-0.457	0.271
Colony (Saloon)	0.195	0.411	1	13	0.223	0.644	-0.694	1.083

Table 6.18: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *feeder sociality*, *brood size* and *colony* (Saloon, Sandstone), for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	9.878	0.686	1	13	162.237	<0.0001	8.396	11.360
Feeder sociality	-0.928	0.766	1	13	1.470	0.247	-2.583	0.726
Brood size	-0.060	0.155	1	13	0.152	0.703	-0.394	0.274
Colony (Saloon)	0.367	0.415	1	13	0.783	0.392	-0.529	1.262

Table 6.19: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *feeder visits*, *brood size* and *colony* (Saloon, Sandstone), for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	9.899	1.099	1	13	73.802	<0.0001	7.525	12.273
Feeder visits	-0.037	0.082	1	13	0.207	0.657	-0.213	0.139
Brood size	-0.061	0.167	1	13	0.135	0.719	-0.421	0.298
Colony (Saloon)	0.244	0.419	1	13	0.341	0.569	-0.660	1.149

Table 6.20: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *territory size*, *brood size* and *colony* (Saloon, Sandstone), for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	9.452	0.645	1	13	172.403	<0.0001	8.059	10.844
Territory size	0.012	0.030	1	13	0.152	0.703	-0.053	0.077
Brood size	-0.066	0.173	1	13	0.147	0.707	-0.440	0.308
Colony (Saloon)	1.597	0.668	1	13	0.404	0.536	0.172	3.021

Table 6.21: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *feeder exploration*, *brood size* and *colony* (Saloon, Sandstone), for males only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	9.627	0.604	1	34	215.496	<0.0001	8.399	10.856
Novel environment exploration	0.021	0.027	1	34	0.586	0.449	-0.035	0.076
Brood size	-0.139	0.146	1	34	0.911	0.347	-0.436	0.157
Colony (Saloon)	0.249	0.363	1	34	0.468	0.498	-0.490	0.987

Table 6.22: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *feeder exploration*, *brood size* and *colony* (Saloon, Sandstone), for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	11.202	1.966	1	9	35.259	0.0002	6.755	15.649
Feeder exploration	-0.045	0.075	1	9	0.370	0.558	-0.215	0.124
Colony (Saloon)	0.471	0.424	1	9	1.235	0.295	-0.488	1.430
Brood size	-0.319	0.289	1	9	1.223	0.297	-0.973	0.334

Table 6.23: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *feeder sociality*, *brood size* and *colony* (Saloon, Sandstone), for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	10.303	1.577	1	9	43.855	<0.0001	6.736	13.871
Feeder sociality	0.053	0.958	1	9	0.003	0.957	-2.113	2.220
Colony (Saloon)	0.518	0.439	1	9	1.395	0.268	-0.475	1.511
Brood size	-0.292	0.300	1	9	0.951	0.355	-0.971	0.386

Table 6.24: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *feeder visits*, *brood size* and *colony* (Saloon, Sandstone), for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	9.012	1.853	1	9	24.940	0.001	4.820	13.205
Feeder visits	0.109	0.106	1	9	1.052	0.332	-0.131	0.348
Colony (Saloon)	0.499	0.401	1	9	1.548	0.245	-0.408	1.406
Brood size	-0.194	0.294	1	9	0.436	0.525	-0.859	0.471

Table 6.25: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *territory size*, *brood size* and *colony* (Saloon, Sandstone), for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	10.327	1.406	1	9	56.044	<0.0001	7.146	13.508
Territory size	-0.005	0.043	1	9	0.011	0.919	-0.102	0.093
Colony (Saloon)	0.500	0.484	1	9	1.069	0.328	-0.594	1.595
Brood size	-0.283	0.318	1	9	0.792	0.397	-1.002	0.436

Table 6.26: Summary of a General Linear Model examining variation in *mean nestling mass* in relation to *feeder exploration*, *brood size* and *colony* (Saloon, Sandstone), for females only.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	9.327	0.668	1	32	171.265	<0.0001	7.967	10.688
Novel environment exploration	-0.011	0.017	1	32	0.434	0.515	-0.046	0.024
Colony (Saloon)	0.251	0.346	1	32	0.523	0.475	-0.455	0.956
Brood size	-0.063	0.155	1	32	0.162	0.690	-0.379	0.254

For the following analyses we included the rule that all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of 0 rather than removed from the analyses:

Table 6.27: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder exploration* and *colony* (Saloon, Sandstone) for males only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	-1.399	1.975	1	31	0.263	0.612	-5.427	2.630
Feeder exploration	0.191	0.110	1	31	3.053	0.091	-0.032	0.415
Colony (Saloon)	0.973	0.895	1	31	1.182	0.285	-0.852	2.798

Table 6.28: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder sociality* and *colony* (Saloon, Sandstone) for males only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	2.733	0.875	1	31	10.179	0.003	0.948	4.518
Feeder sociality	-2.036	1.927	1	31	1.116	0.299	-5.966	1.894
Colony (Saloon)	0.549	0.865	1	31	0.403	0.530	-1.215	2.312

Table 6.29: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder visits* and *colony* (Saloon, Sandstone) for males only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	-2.176	0.958	1	31	3.553	0.069	-4.129	-0.223
Feeder visits	0.551	0.118	1	31	21.908	<0.0001	0.311	0.791
Colony (Saloon)	1.098	0.673	1	31	2.663	0.113	-0.274	2.469

Table 6.30: Summary of a General Linear Model examining variation in *brood size* in relation to *territory size* and *colony* (Saloon, Sandstone) for males only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	2.100	0.689	1	31	13.342	0.001	0.695	3.505
Territory size	-0.011	0.038	1	31	0.086	0.772	-0.090	0.067
Colony (Saloon)	0.289	0.855	1	31	0.114	0.738	-1.455	2.033

Table 6.31: Summary of a General Linear Model examining variation in *brood size* in relation to *novel environment exploration* and *colony* (Saloon, Sandstone) for males only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	2.990	0.403	1	58	126.152	<0.0001	2.183	3.796
Novel environment exploration	-0.069	0.036	1	58	3.692	0.060	-0.140	0.003
Colony (Saloon)	1.326	0.535	1	58	6.138	0.016	0.255	2.397

Table 6.32: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder exploration* and *colony* (Saloon, Sandstone), for females only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	0.082	2.111	1	25	0.315	0.580	-4.267	4.431
Feeder exploration	0.099	0.127	1	25	0.614	0.441	-0.162	0.361
Colony (Saloon)	2.103	0.939	1	25	5.021	0.034	0.170	4.037

Table 6.33: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder sociality* and *colony* (Saloon, Sandstone) for females only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	2.623	1.033	1	25	10.815	0.003	0.494	4.751
Feeder sociality	-2.131	2.028	1	25	1.104	0.303	-6.308	2.045
Colony (Saloon)	2.324	0.973	1	25	5.704	0.025	0.320	4.328

Table 6.34: Summary of a General Linear Model examining variation in *brood size* in relation to *feeder visits* and *colony* (Saloon, Sandstone) for females only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	-0.740	1.145	1	25	0.012	0.915	-3.099	1.619
Feeder visits	0.361	0.155	1	25	5.441	0.028	0.042	0.680
Colony (Saloon)	1.732	0.856	1	25	4.092	0.054	-0.031	3.495

Table 6.35: Summary of a General Linear Model examining variation in *brood size* in relation to *territory size* and *colony* (Saloon, Sandstone) for females only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	1.839	0.699	1	25	24.857	<0.0001	0.399	3.279
Territory size	-0.013	0.037	1	25	0.115	0.737	-0.089	0.064
Colony (Saloon)	1.879	0.984	1	25	3.649	0.068	-0.147	3.905

Table 6.36: Summary of a General Linear Model examining variation in *brood size* in relation to *novel environment exploration* and *colony* (Saloon, Sandstone) for females only. In this analysis all individuals that completed the feeder experiment but were not recorded as breeding in the nest boxes be given a *brood size* score of '0'.

| Term	B	SE	DF1	DF2	F	*P* value	Upper CI	Lower CI
(Intercept)	2.353	0.418	1	52	78.374	<0.0001	1.514	3.192
Novel environment exploration	0.027	0.037	1	52	0.517	0.475	-0.048	0.101
Colony (Saloon)	1.628	0.595	1	52	7.483	0.009	0.434	2.822

Figure 6.8: Photograph showing the interior of the novel environment test apparatus. The door through which individuals entered the apparatus is shown in the top right.
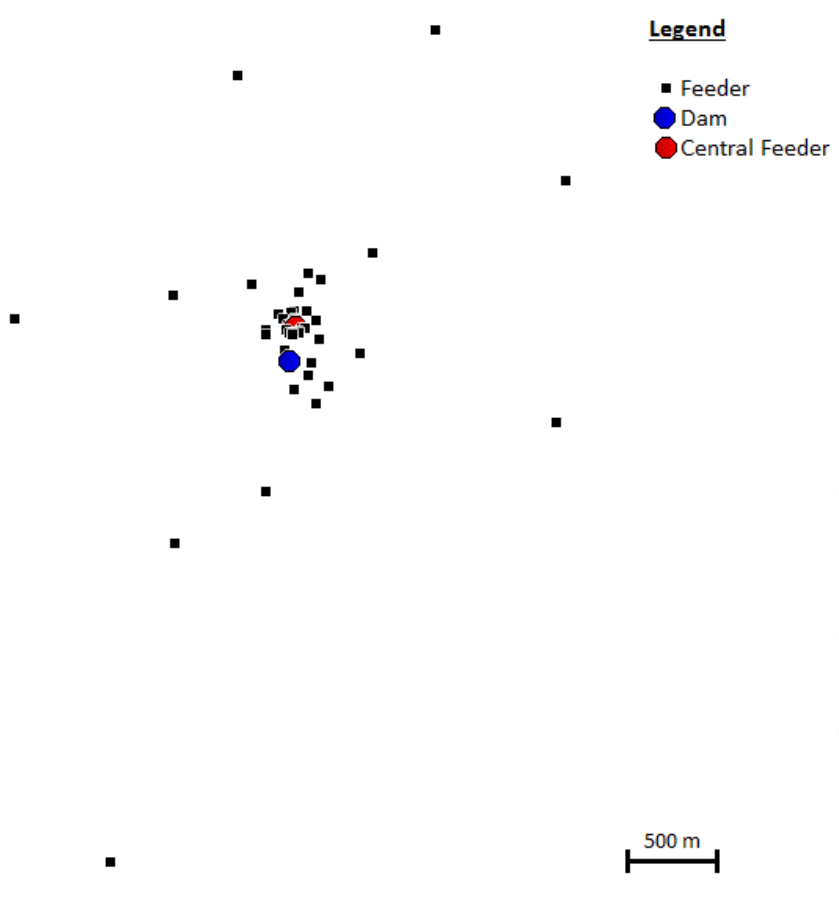
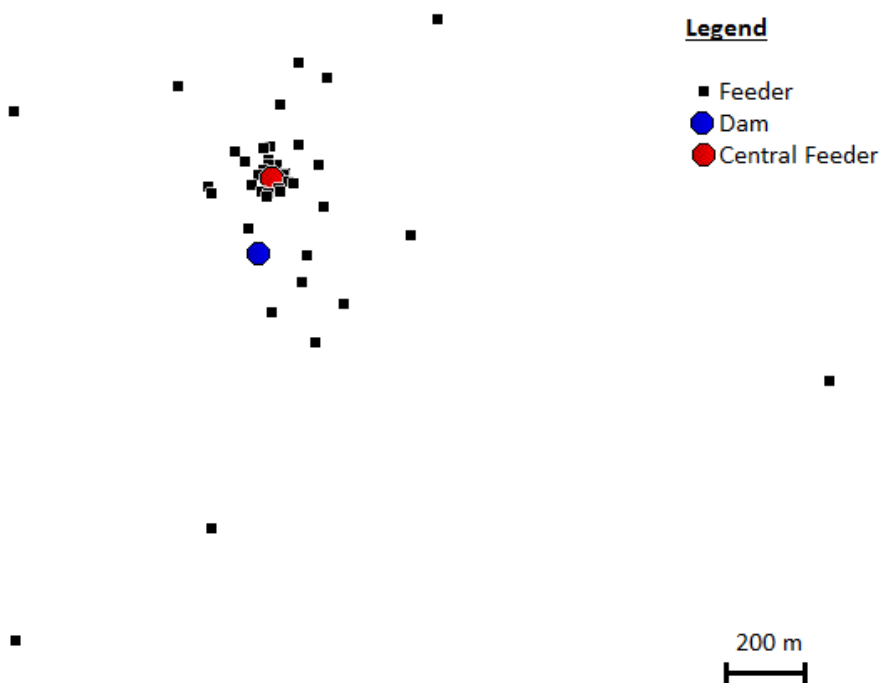**Figure 6.9:** A single feeder used in the feeder experiment.
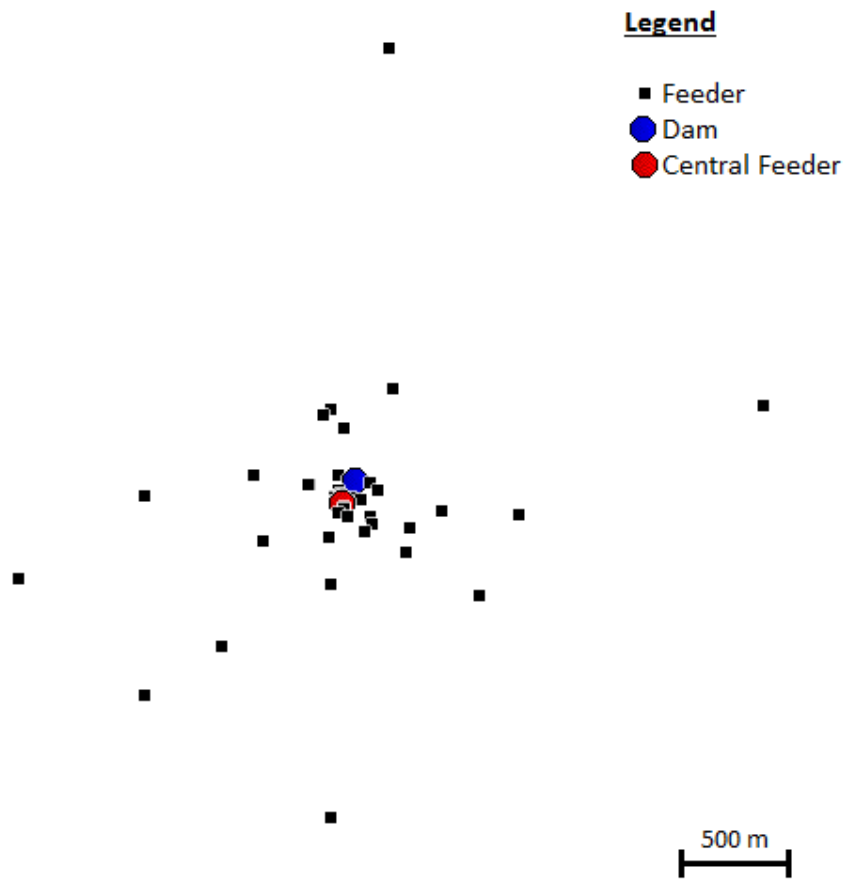
Figure 6.10: Map of the Saloon colony (a distant view including all feeders).
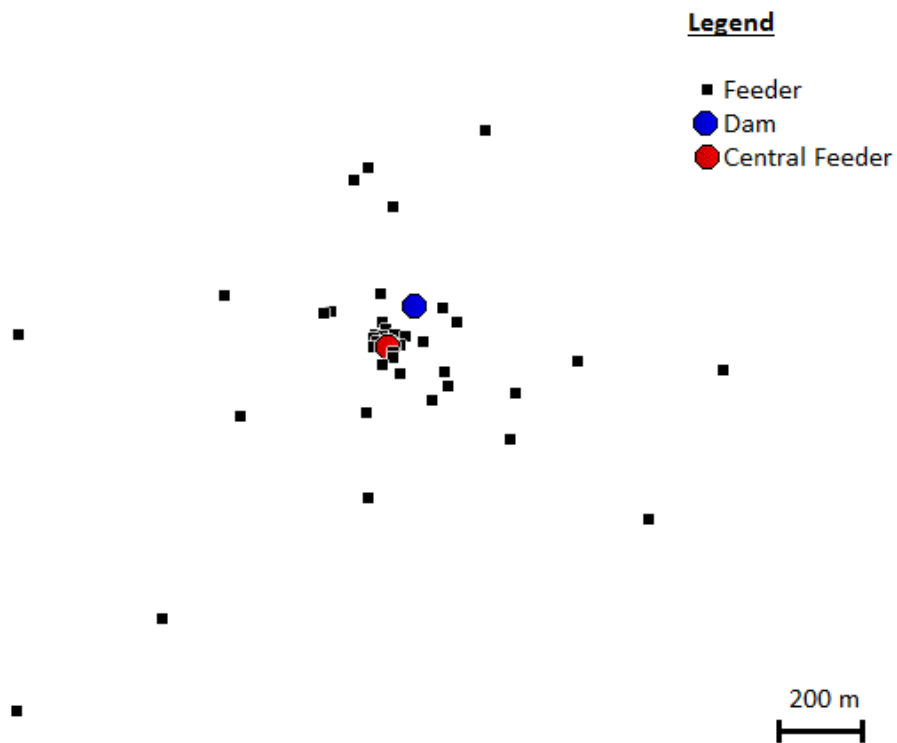
Figure 6.11: Map of the Saloon colony (a nearer view missing some of the more distant feeders).

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Figure 6.12: Map of the Sandstone colony (a distant view including all feeders).

Figure 6.13: Map of the Sandstone colony (a nearer view missing some of the more distant feeders).