Social Specialists? Personality variation, foraging strategy and group size in the chestnut-crowned babbler, *Pomatostomus ruficeps*.

Submitted by Matthew John Stanley Creasey, to the University of Exeter as a thesis for the degree of *Doctor of Philosophy* in Biological Sciences, April 2018.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

…………………………………………………………………………………

“The beauty of the universe consists not only of unity in variety, but also of variety in unity.”
Umberto Eco, The Name of the Rose

“Be yourself; everyone else is already taken.”
Attributed to Oscar Wilde

William: "I'm sure we can all pull together, sir."
Vetinari: "Oh, I do hope not. Pulling together is the aim of despotism and tyranny. Free men pull in all kinds of directions.”
Terry Pratchett, The Truth

ABSTRACT

Although group-living is widespread in animals, the degree of social complexity varies markedly within and among taxa. One important precondition for the evolution of higher forms of social complexity is increasing group size. However, this imposes a challenge: finding sufficient food for growing numbers of individuals. One hypothesis is that the (in)ability to avoid resource competition as group size increases, could partly explain variation in social complexity among vertebrates. Increasingly, evidence suggests that resource competition can be reduced *via* three forms of individual specialisation. These are foraging niche specialisation, specialisation to a role under division of labour (DoL), and as a mediator of these two, personality variation. Yet few studies have directly investigated the role of these specialisations in mediating the costs of increasing group size in social vertebrates. In this thesis, I first review the evidence to date that specialising to a foraging niche, and/or to a task under DoL, is (1) mediated *via* personality variation and (2) can be a means of reducing competition, generated by increasing group size, in social species (Chapter 2). Then, using the cooperative breeding chestnut-crowned babbler (*Pomatostomus ruficeps*) as my model system, I empirically test some of the hypotheses posed in this review, regarding foraging niche specialisation and associations with personality variation. In Chapter 3, I show that babblers do show personality variation in traits likely to facilitate niche segregation, and in Chapter 4 that variation among individuals within groups is sufficient to lead to intragroup niche specialisation. However, I find that the level of variation within groups is not associated with group size. Then in Chapter 5, I show that in a direct measure of foraging niche, there is only limited evidence for intragroup specialisation, and again that any specialisation is not associated with larger group sizes. I therefore find no evidence that niche specialisation is a means through which babblers can overcome the costs of increasing group size. I discuss the implications of these results for the rise of social complexity in this system, and social vertebrates generally.

ACKNOWLEDGEMENTS

This thesis represents the culmination of 5 years which have been some of the most enjoyable and challenging of my life, and would not have been possible without the following people.

First, my two supervisors, Andy and Sasha. Andy, from the outback to the office, working with you has always been an adventure. You have taught me so much, not least how to bring fun and a light heart into even the most challenging situations. Your guidance, support and advice, both academically and personally, have been invaluable and I am hugely grateful. Sasha, your incisive eye for the good and bad in my ideas and writings, combined with your positivity, have been a huge help throughout. Your door has always been open when I have needed to call on you. Thank you.

Next, Dre. I realised early on that I would never be able to live up to the extraordinary example you set. But, I did take inspiration from it. From those early days, you went from being a teacher, to a mentor, to a friend. You are all of these and more. From making sure I was out of bed early enough for work, to making sure I didn’t return to it before several beers had been consumed, you made field work an unforgettable experience. I feel lucky to have had the chance to work together and wish you every happiness.

For their help and friendship in the field, I would like to thank all the members of the babbler team I have worked with in Fowlers Gap. Caitlin, Elliot, Hannah, Marley, Niall, Sabs and Tom: not only would I not have been able to collect the data for this thesis without you, but I would not have had nearly so much fun in doing so. Thank you all.

I also owe enormous gratitude to all those who live and work at Fowlers full time and welcome us each year with such warmth. Vicky, I will never see another barbeque spread like the one you put on. Gary, Booz, Eddie and Keith, late nights round the camp fire will always stay with me. Field seasons would not have been possible without any of you, so thank you.

I would like to thank all those I have met in Falmouth and have made it feel like home. All those that I have surfed, walked, cycled and climbed with, and all the staff at the Centre for Ecology and Conservation, for making it such an exciting place to work.

My parents also deserve much of the blame, I mean credit, for getting me here. You both instilled in me a love of the natural world – from my earliest years all I dreamt of being was a field ecologist, but I would be no closer towards achieving that dream today were it not for your constant support, love and guidance. Dad, I am so sorry that you were not able to see me finish this degree, or to see what comes next, but you have been, and always will be, with me in everything I do. I hope to make you proud. Mum, from a passion for the truly wild (Morston in the driving rain and arctic wind is a love that perhaps only you and I fully understand), to drinking me under the table at Fowlers, we have shared so much. I am so lucky to have had your unwavering support and love. I can never thank you enough.

Lastly, Beth. Since we met you have been a friend, a companion, a motivator and inspiration, and perhaps above all a reassuring, supportive and fun-loving partner. You've been with me, and felt the brunt, during some of my most difficult experiences, and have been understanding, forgiving and supportive through it all. You have helped me to keep plodding and ploughing on, and to see sillion shine in the furrows we've followed. Let's see where the tracks lead us.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 1: General introduction.

Chapter 2: Personality variation and the rise of social complexity.

Chapter 3: Personality and syndromes in chestnut-crowned babblers: highlighting the difficulty with standardised approaches in a skittish, neophobic, social animal.

Chapter 4: Among - versus within-group variation in personality in chestnut-crowned babblers: implications for niche specialisation.

Chapter 5: Limited evidence of niche specialisation in a cooperative-breeding bird.

LIST OF FIGURES

Chapter 2: Personality variation and the rise of social complexity.

Chapter 3: Personality and syndromes in chestnut-crowned babblers: highlighting the difficulty with standardised approaches in a skittish, neophobic, social animal.

Chapter 4: Among - versus within-group variation in personality in chestnut-crowned babblers: implications for niche specialisation.

Chapter 5: Limited evidence of niche specialisation in a cooperative-breeding bird.

AUTHOR'S DECLARATION

The research in this thesis was supported by funding from the Natural Environment Research Council (NERC).

All chapters were written by MJSC, with comments and editing from Professor Andy Russell (all chapters) and Dr Sasha Dall (Chapters 2 and 3). Statistical analysis was also conducted by MJSC, with input from Professor Andy Russell (Chapters 3-5) and Dr Fumiaki Nomano (Chapters 3 and 4).

Data for this thesis were collected as part of a long-term study of a wild population of chestnut-crowned babblers (*Pomatostomus ruficeps*), at Fowlers Gap Arid Zone Research Station, led by Professor Andy Russell. Data for Chapters 3 and 4 were collected with the assistance of Dr Andrea Liebl, Elliot Capp, Hannah Fitzjohn, Tom Harris, Marley Henskens, Caitlin Higgott, Charlotte Martin-Taylor and Niall Stopford. Data for Chapter 5 were collected by Dr Lucy Browning and Professor Andy Russell.

With these exceptions, I declare that the work contained in this thesis is my own and has not been submitted for any other degree or award.

CHAPTER 1

General introduction.

1.1 INTRODUCTION

Group-living occurs throughout the animal kingdom. And yet, the degree of social complexity within groups varies markedly across taxa. In particular, while many social insects establish colonies of thousands, with complex divisions of labour and full eusociality (Anderson and Ratnieks, 1999; Bourke, 1999), social complexity among vertebrates is much more limited. In mammals, for example, division of labour is rare and eusociality has been documented in just two species: Damaraland mole rats, *Cryptomys darnarensis,* and naked mole rats, *Heterocephalus glaber* (Jarvis, 1981; Jarvis and Bennett, 1993). In birds, eusociality is not known to occur at all. The evidence suggests that for more complex forms of sociality to evolve, individuals must live in stable groups of increasing size, where interactions among the same individuals are frequent (Anderson and Ratnieks, 1999; Bourke, 1999; Freeberg, Dunbar and Ord, 2012; Ferguson-Gow *et al.*, 2014; Dunbar, 2018). In vertebrates, although many species form large aggregations (take, for example, the herds of ungulates seen on the African plains), in many cases, the fluid social structure of these groupings means that stable relationships among individuals, and therefore more complex forms of interaction and social structure, do not develop (Freeberg, Dunbar and Ord, 2012). For a definition of social complexity, and a clarification of the term's use within this thesis, see Table 1.1.

In vertebrate taxa, with the exception of primates, the most complex examples of sociality tend to be cooperative breeders. This reproductive system, in which breeders are assisted by non-breeding 'helpers' to raise their young, occurs in at least 3% of mammal species and 9% of birds (Komdeur *et al.*, 2017), but since Darwin (1859) has posed a major challenge to our understanding of evolutionary processes: how could selection favour individuals directing care towards young that are not their own? A solution to this challenge has finally been reached through a synthesis of work spanning six decades, which suggests that cooperative breeding is associated with unpredictable and challenging environments, where cooperation increases the chances of reproducing successfully under ecological constraints (Jetz and Rubenstein, 2011; Cornwallis *et al.*, 2017; Griesser *et al.*, 2017; Shen *et al.*, 2017). In such circumstances, non-breeders accrue fitness by delaying dispersal from the natal territory to act as helpers for, and increasing the reproductive success of their close relatives (Covas & Griesser, 2007; Emlen, 1982; Hamilton, 1964a, 1964b; Hatchwell & Komdeur, 2000; Komdeur et al., 2017). Importantly with regard to the evolution of more complex sociality, in many cooperative vertebrates, reproductive success increases with carer number (Jennions and Macdonald, 1994; Magrath, 2001), generating selection on increasing group size, while delayed dispersal results in prolonged relationships among individuals. Indeed, it has been suggested that kin-selected cooperative breeding could be a critical precursor to the evolution of full eusociality (Hughes *et al.*, 2008).

However, even among cooperative vertebrates there is significant variation in both group size and social complexity (which as I have discussed, are likely to be linked (Bourke, 1999; Ferguson-Gow *et al.*, 2014; Dunbar, 2018)). Among birds, for example, at the more complex end of the range, Southern pied babblers (*Turdoides bicolor*) form stable, kin-structured social groups of up to 15 individuals. Within these groups there is a strict social hierarchy, established (often through fierce fighting) prior to breeding (Raihani *et al.*, 2010; Ridley, 2016). Once this hierarchy is in place, reproduction by subordinates is rare (Nelson-Flower *et al.*, 2011). This species exhibits complex forms of social interaction and cooperation, often mediated *via* a large repertoire of vocalisations (which in itself can be a strong indicator of social complexity (Freeberg, Dunbar and Ord, 2012)). For example, in addition to an array of alarm calls made by the group (Ridley, 2016), sentinels will also frequently take exposed positions, from which they give specific alarm calls to alert other group members when a threat is seen (Ridley, Nelson-Flower and Thompson, 2013). Adults will also make ‘recruitment calls’, which direct inexperienced foragers to food-patches (Radford and Ridley, 2006) and experimental evidence even suggests that adults actively teach young, by giving specific vocalisations which indicate food (Raihani and Ridley, 2008). Cooperative behaviours amongst adults are highly coordinated, such that carers synchronously provision the young: a behaviour which increases reproductive success, likely because fewer nest-visits makes it harder for predators to locate the nest site (Raihani *et al.*, 2010). Finally, this species shows a form of division of labour, whereby some individuals stay at the nest area to provision and defend the young, while others conduct border defence of the territory (Ridley, 2016). In contrast, long-tailed tits (*Aegithalos caudatus*) exhibit a form of cooperative breeding where social complexity is relatively limited. In this species, although during the winter, kin do aggregate into groups of 6 – 30 individuals (Gaston, 1973; Hatchwell, Anderson, Ross, Fowlie, & Blackwell, 2001), at the start of the breeding season groups disband and all birds attempt to breed as pairs (Hatchwell, Russell, Fowlie, & Ross, 1999). Cooperation is facultative and individuals only become helpers should they fail to reproduce successfully themselves (MacColl and Hatchwell, 2002). This means that pairs may remain without helpers, and group sizes do not exceed 5 (Maccoll and Hatchwell, 2003). At cooperative nests, there is no evidence that the group as a whole coordinate provisioning visits to the nest, as evidenced by the higher overall number of visits at nests with helpers (Maccoll and Hatchwell, 2003), which may explain the very high nest-predation rates (Bebbington & Hatchwell, 2016; Hatchwell et al., 1999). The vocal repertoire of this species is limited, with 5 main calls (Sharp and Hatchwell, 2005). Finally, there is no evidence for more complex forms of cooperation and sociality, such as sentinel behaviour, teaching or division of labour in long-tailed tits.

In both the examples above, as in many other cooperative vertebrates, in addition to the general benefits of larger group sizes, such as increased competitive ability against other con-specific groups (Janson & van Schaik, 1988; Wrangham, 1980) and reduced predation risk (Wrona and Jamieson Dixon, 1991), reproductive success over the long-term increases with helper-number (Hatchwell et al., 2004; Jennions & Macdonald, 1994; Magrath, 2001; Ridley, 2016). Thus, in cooperative breeders, there is expected to be particularly strong selection on increasing group size. However, a fundamental challenge posed by increasing group size is finding food for increasing numbers of individuals (Korb and Heinze, 2016). Thus, variation in the ability to overcome this challenge may, in part at least, explain observed variation in group size, and therefore social complexity among cooperative vertebrates. And increasingly, evidence suggests that three forms of individual specialisation may play an important, but so far underexplored role in enabling groups of increasing size to optimise resource acquisition. These are (1) specialising to a task under division of labour (DoL), (2) specialising to a foraging niche and (3) personality variation (the latter as a possible mediator of the previous two) (see definitions in Table 1.1).

Table 1.1. Definitions of social complexity, division of labour, personality variation and intra-group niche specialisation.

Term	**Definition**
Social complexity	Social complexity may refer to either the interactions among individuals within social groups, or the social structures of such groups. In this thesis, because of the focus on cooperative breeding (where individuals adopt different reproductive roles within a group), I am particularly concerned with the conditions which can lead to complex social structures, for example the emergence of division of labour and caste differentiation.
Division of labour	When different tasks, for example foraging and offspring care, are consistently undertaken by different group members (Ratnieks and Anderson, 1999).
Personality variation	Consistent differences in behaviour, among individuals, across time and/or context (Dall, Houston and McNamara, 2004).
Intra-group niche specialisation	When individuals within social groups consistently use different foraging niches (e.g. target different food types, utilise different foraging techniques or forage in different areas).

1.2 GENERAL AIMS AND MODEL SYSTEM

In this thesis, I have 2 broad aims, and 3 sub-aims:

1. To review the current evidence that specialising to a task under DoL, and/or to a foraging niche is (1) mediated *via* personality variation and (2) can be a means of reducing competition, generated by increasing group size, in social species.
2. To test empirically some of the hypotheses and predictions which are presented by this review.
    i. To establish general patterns of personality variation in my model system (see below).
    ii. To explore how personality variation is manifest within social groups, and the association with group size. This is because, increasingly, evidence suggests that personality variation may be an important mechanism through which niche specialisation amongst group-mates can be achieved. Moreover, niche specialisation is expected to be under stronger selection in larger groups, where resource competition is greater.
    iii. To investigate consistent individual differences, within social groups, in direct measures of foraging niche, and again explore the link between intragroup variation and group size. Thus, through sub-aims *ii* and *iii*, I assess whether my study species has the behavioural capacity for niche specialisation, whether this is apparent in practice and if there is an association with larger numbers of individuals.

To address these aims, as my model system I use a population of chestnut-crowned babblers (*Pomatostomus ruficeps*), a 50g cooperative passerine endemic to South Eastern Australia, which has been studied intensively for 14 years (Russell, 2016). During this time, over 90% of the population has been fitted with metal and coloured leg-rings, and a passive integrated transponder (PIT) tag, with a unique alpha-numeric code, allowing each bird to be individually identified. Further, the methodologies required for catching birds and observing key behaviours related to foraging niche have been previously established. This includes an automated nest-camera system, which allows the identification of both the bird, and prey item, that provisioning adults deliver to nestlings (see Browning, Young, *et al.*, 2012; Young *et al.*, 2013 for details).

Next, this species presents an excellent opportunity to investigate the emergence of foraging niche specialisation in response to resource competition within social groups. Babblers breed in groups which vary in size from 2 – 15 individuals (Browning, Patrick, *et al.*, 2012). On average, larger groups achieve higher reproductive success (Browning, Patrick, *et al.*, 2012), favouring increasing group size. However, larger groups are not able to inhabit a larger range during the breeding season, due to constraints on the distance adults can travel from dependent young, and so deplete resources faster than smaller groups (Sorato, Griffith and Russell, 2016). Moreover, the availability of resources is key in determining reproductive success and offspring mortality is most commonly due to starvation (Browning, Young, *et al.*, 2012; Russell, 2016). For these reasons, there is also expected to be strong selection on mechanisms to optimise resource acquisition within a given area (for example, niche specialisation (Svanbäck and Bolnick, 2007)). Importantly in this regard, babbler territories contain a variety of foraging habitats, some which are open and stony, and others which have more cover from predators (Portelli *et al.*, 2009). Groups also forage on a range of prey types, which require the use of different foraging strategies (Browning, Young, *et al.*, 2012). Thus, in principle, this species has the opportunity, capacity and incentive to optimise resource acquisition *via* niche specialisation, in ways which previous research suggests are likely to be mediated *via* personality variation (Toscano *et al.*, 2016). Together, these elements allow me to test a range of important questions regarding the role of individual specialisation in reducing competition generated by increasing group size in a cooperative bird, and thus in the role such specialisation may play in facilitating the rise of social complexity in vertebrates.

1.3 THESIS STRUCTURE

Other than the General Introduction and Conclusion, this thesis comprises four main chapters. Chapter 2 is a review chapter. This begins by discussing the evidence so far for personality variation as a driver of foraging niche specialisation, and also of division of labour, and how together, these forms of specialisation may be important means of optimising resource acquisition in social species. In the second part of this chapter, I discuss possible constraints to the emergence of niche specialisation in particular, and the potential implications for a subsequent rise in social complexity. Then in Chapter 3, I investigate how my study species responds to standard personality assays and identify general patterns of personality variation. This is key, because it has previously been noted that the same assay can assess different traits in different species (Carter *et al.*, 2013), and understanding how personality variation might influence niche differentiation in this species relies on accurately interpreting behavioural variation under such standardised tests. In Chapter 4, I investigate personality variation within social groups, testing the prediction that if foraging niche specialisation is mediated by consistent behavioural differences, individuals within groups will differ significantly in personality traits related to foraging niche, and these differences will increase with group size. Then, in the final data chapter (Chapter 5), I test directly for consistent differences in the prey-types individuals within breeding groups deliver to dependent young (i.e. a measure of intragroup niche specialisation) and again investigate whether such differences are more apparent in larger groups. The thesis ends with a section in which I discuss several points raised by my findings, including the implications for the role of individual specialisations in explaining variation in group size, and levels of social complexity, across social vertebrates.

CHAPTER 2

Personality variation and the rise of social complexity.

2.1 ABSTRACT

For higher forms of social complexity to evolve, group sizes of sufficient size must be reached. Yet, for group size to increase, ways must be found of finding enough food for increasing numbers of individuals. When range-size is constrained, growing evidence suggests that two forms of individual specialisation, foraging niche specialisation and specialising to a task under division of labour (DoL), could enable groups to obtain resources more efficiently from a given area. However, we still lack a complete understanding of how these forms of specialisation emerge. One potentially important, but so far underexplored factor, is that in both forms of specialisation, personality variation may play a significant mediating role. In this chapter, I review the evidence so far that personality variation can affect niche specialisation. Then, I take three examples of social species where niche specialisation has been shown and discuss in detail how personality variation could mediate individual differences in foraging niche in each case. Next, turning to DoL, addressing social insects, non-human vertebrates and humans in turn, I discuss the potential role of personality variation in mediating DoL. Then to conclude, given that niche specialisation is likely to be the precursor to DoL, as it will enable groups to increase in size such that the latter can develop, I propose 3 factors which could inhibit niche specialisation, and so constrain any subsequent rise in social complexity.

2.2 INTRODUCTION

Evidence suggests that the evolution of advanced forms of social complexity, such as caste differentiation and division of labour, requires sufficiently large group sizes to be reached (Bourke, 1999; Ferguson-Gow *et al.*, 2014; Dunbar, 2018). Selection on increasing group size can occur for various reasons, including increasing costs to dispersal and independent breeding coupled with the indirect benefits of helping kin (as in some cooperative breeders (Magrath, 2001)), predator avoidance (Wrona and Jamieson Dixon, 1991) and enhanced competitive ability against other conspecific groups (Wrangham, 1980; Janson and van Schaik, 1988). But whatever the selective pressure on increasing group size, evolutionary responses will require the basic challenge of finding enough food for increasing numbers of individuals to be overcome.

Broadly, there are two ways in which larger groups might be able to obtain more resources. One possibility is that they can increase their foraging range (Goulson and Osborne, 2009; Duca and Marini, 2014). However, in many species this is not viable, for reasons including high population density and/or strong territoriality (Gaston, 1978; Hixon, 1980; Koenig *et al.*, 1992). In this case, the alternative is to maximise the efficiency with which resources are obtained from a given area. One way in which this can be achieved is when individuals that have located a food source are able to effectively communicate this information to other group members. Yet although examples of this are seen both in social insects (e.g. the waggle dance in honey bees (Riley *et al.*, 2005) and the laying of pheromone trails in some species of ant (Denny, Wright and Grief, 2001)), and in vertebrates (e.g. the pied babblers' (*Turdoides bicolor*) use of recruitment calls (Radford and Ridley, 2006) and the laying of odour trails in naked mole rats, *Heterocephalus glaber* (Judd and Sherman, 1996)), such strategies are far from ubiquitous, even among social insects, while in vertebrates, they appear to be very unusual.

Another way in which resources may be obtained more efficiently from a given area is through two forms of individual specialisation. These are (1) foraging niche specialisation and (2) division of labour (which can be seen as a form of social niche specialisation (Bergmüller and Taborsky, 2010)). The concept of foraging niche specialisation is best explained in terms of niche width (Roughgarden, 1972). Total niche width (TNW) represents the complete range of resources utilised by a group, while individual niche width (INW) represents the portion of the TNW utilised by each group member. Under resource pressure, groups may be able to reduce competition by adding new prey-types to their diet (increasing TNW), but individuals can also specialise to utilise a narrower range of resources (decreasing INW). Such niche specialisation reduces niche overlap (Roughgarden, 1972; Svanbäck and Bolnick, 2007), and can also increase the efficiency with which individuals obtain resources. For example, when phenotypic variation in the group means that some individuals are better able to utilise particular food-types, diet-phenotype correlations can develop. Svanbäck and Bolnick (2007) have shown how this can occur in practice. They found that experimentally increasing group size, and thus reducing prey availability, in controlled populations of three-spined sticklebacks (*Gasterosteus aculeatus*), resulted in (1) new prey types being added to the overall diet of the population (increased TNW), (2) increased dietary variation among individuals, due to individuals with different phenotypes adding different new prey types (narrow INW) and (3) an increased correlation between phenotype and the use of particular prey-types (i.e. a stronger diet-phenotype correlation).

Division of labour (DoL) meanwhile is thought to have been an important factor in the rise of the most complex examples of sociality, namely social insects and humans (Ferguson-Gow *et al.*, 2014; Nakahashi and Feldman, 2014). Under DoL, individuals within a group specialise to perform different cooperative tasks (e.g. foraging and offspring care) (Ratnieks and Anderson, 1999). Specialising in this way can be an effective means of acquiring resources more efficiently, thus facilitating increasing group size, for at least two reasons. Firstly, it has commonly been found that foragers increase their efficiency with time spent performing this task, either through trial-and-error learning or by improving their search-image (Pietrewicz and Kamil, 1979; Rissing, 1981a; Schmid-Hempel and Schmid-Hempel, 1984; Tebbich *et al.*, 2001). Secondly, by not having to perform the tasks which are being carried out by other workers, foragers are free to develop morphological adaptations which might impede their performance in other roles, but which increase their performance as foragers. This has been shown in the eusocial bee *Tetragonisca angustula,* where foragers have significantly larger heads than soldiers. The authors suggest that such large heads may be beneficial to foragers because it allows them to acquire and process the information required to find food effectively, whereas, such large heads appear to be unnecessary and therefore potentially costly, in other worker castes (Grüter *et al.*, 2012).

However, despite evidence that both these forms of specialisation can be important in increasing group size, and thus in the development of more complex forms of sociality, we still lack a complete understanding of how they might emerge. Recent evidence suggests personality variation may play a significant role. Personality variation is defined as consistent differences in behaviour, among individuals, across time and/or context (Dall, Houston and McNamara, 2004) – in other words, personality variation represents behavioural specialisation (Dall *et al.*, 2012). It is generally studied by repeatedly observing individuals, under standardised conditions and assessing the relative behavioural variation among, *versus* within individuals, in 5 key behavioural axes. The 5 trait-axes are (1) boldness-shyness ("an individual's reaction to any risky situation"); (2) exploration-avoidance ("an individual's reaction to a new situation"); (3) activity "the general level of activity of an individual", (4) aggressiveness "an individual's agonistic reaction towards conspecifics") and (5) sociability "an individual's reaction to the presence or absence of conspecifics (excluding aggressive behaviour))" (Réale *et al.*, 2007).

2.3 PERSONALITY VARIATION AND NICHE SPECIALISATION

In a recent review, Toscano *et al.* (2016) proposed five pathways through which personality variation can affect foraging niche specialisation. These five pathways are outlined in Figure 2.1, taken from their paper. The first pathway they discuss is *via* variation in activity levels. Here, the activity level of the forager influences the type of food they target and can manifest in two alternative foraging strategies – 'sit-and-wait' (a relatively inactive forager) versus 'active searching' (a relatively active forager). Toscano *et al.* (2016) cite two main studies which have both shown that activity level in standardised assays predicts the type of prey an individual will target. In both cases, it was found that relatively active individuals tended to consume less active prey, while inactive individuals tended to consume more active prey (Pruitt, Stachowicz and Sih, 2012; Sweeney *et al.*, 2013). The second way in which it is proposed that personality variation can drive foraging niche specialisation is through differential responses to a 'landscape of fear'. Here, variation in boldness influences the areas that individuals will forage in - bolder individuals in habitats with greater risk, and shyer individuals in less risky environments (Toscano *et al.*, 2016). Griffen, Toscano and Gatto (2012) have shown an empirical example of this. They found that in the mud-crab (*Panopeus herbstii*), bolder individuals were more likely to be found in subtidal areas, where predation risk is higher, while shyer crabs were more likely to inhabit intertidal areas, where they are less exposed to predators. The third hypothesis proposed by Toscano *et al.* (2016) is that foraging niche can be determined by social factors, such as dominance hierarchies and propensity to forage independently or with others, both of which can be influenced by personality variation (Fox *et al.*, 2009; Kurvers *et al.*, 2010; David, Auclair and Cézilly, 2011; Favati, Leimar and

Løvlie, 2014). For example, Kurvers *et al.* (2010) found that shy barnacle geese (*Branta leucopsis*) were more likely to join other individuals at a food source, and in sheep (*Ovis aries*), shy individuals were less likely to split into smaller sub-groups when foraging (Michelena *et al.*, 2009). Meanwhile, it has been shown that more dominant individuals, which may be more active, exploratory, and bolder (David, Auclair and Cézilly, 2011; Favati, Leimar and Løvlie, 2014), can be more likely to forage in patches of higher quality (Holbrook and Schmitt, 1992). In a fourth hypothesis, Toscano *et al.* (2016) suggest that spatial factors such as migratory or dispersal tendency and home range size can be key drivers of variation in foraging. Such macro-scale ecological considerations have less relevance regarding variation in foraging niche within social groups. However, I do recognise the key role that spatial factors on a smaller scale may play. For example, in great tits (*Parus major*), it has been shown that when a known food source is no longer available, more active individuals will travel greater distances to new foraging locations (van Overveld and Matthysen, 2010). This could be relevant is determining the spatial distribution of individuals from a group, within a territory. The final way in which Toscano *et al.* (2016) suggest that personality variation may affect foraging niche specialisation is through physiological variation among individuals. Here, it is proposed that differences in physiological traits such as metabolic rate, which can co-vary with personality type (Careau *et al.*, 2008; Biro and Stamps, 2010), may result in differences in foraging. This hypothesis is particularly based on what is termed the ‘increased intake model’, whereby behaviours which are energetically expensive, such as aggression, boldness and activity (Biro and Stamps, 2008; Réale *et al.*, 2010), require a higher metabolic rate, and thus increased foraging activity to support this (Biro and Stamps, 2010; Careau and Garland, 2012).

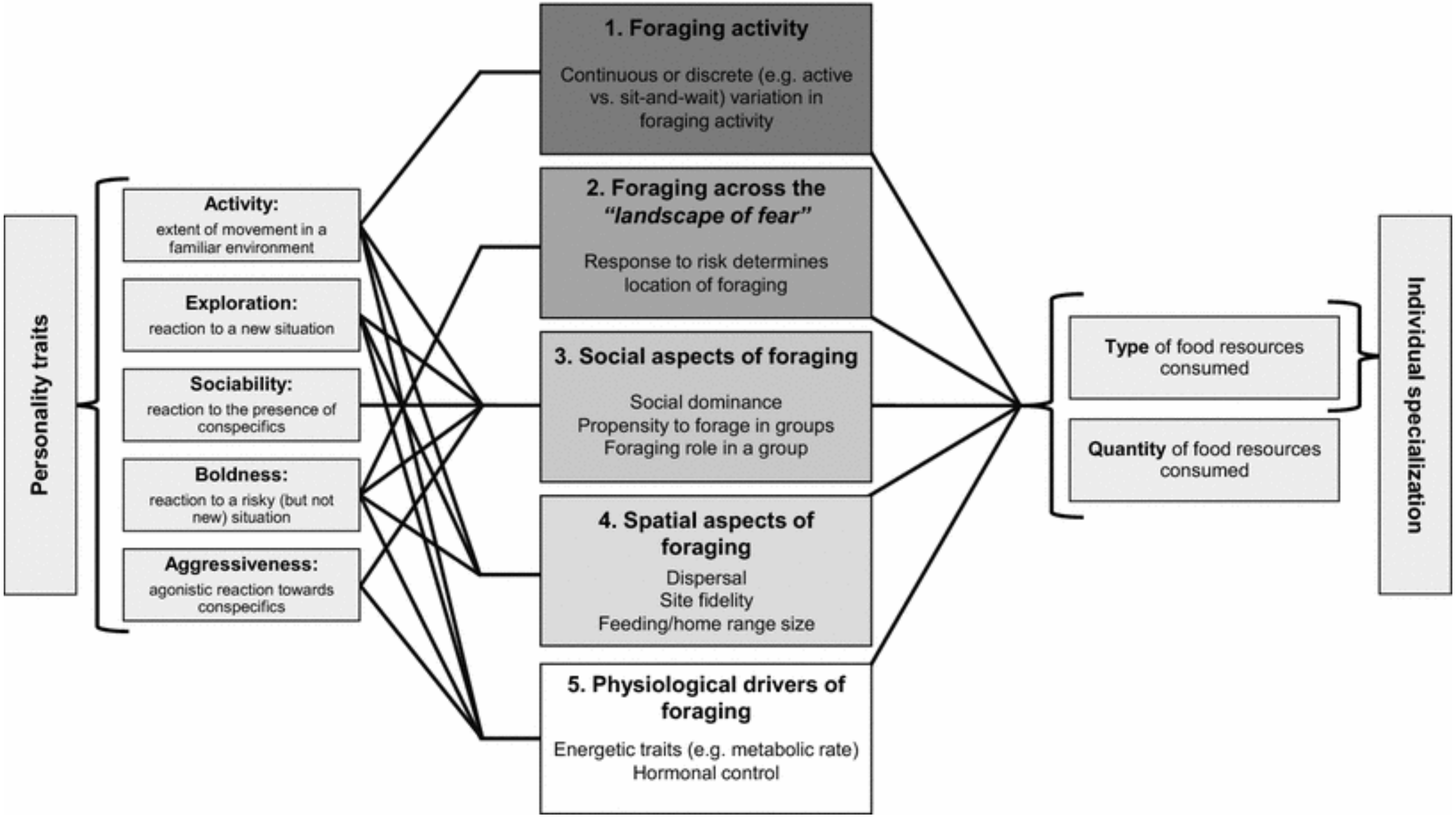


Figure 2.1. A diagram, taken from Toscano *et al.* (2016), showing how the authors suggest variation in the 5 personality trait-axes (defined by Réale *et al.*, 2007) could result in niche differentiation, *via* the 5 pathways they propose.

2.4 LINKING SOCIALITY, NICHE SPECIALISATION AND PERSONALITY VARIATION

In this section, I give three examples where individuals within social groups have been shown to have different foraging preferences. For each example, with reference to the personality literature, I discuss how personality variation could affect such niche specialisation and suggest how the particular example would fit within the framework outlined by Toscano *et al.* (2016). A summary of the how, in each case, niche specialisation manifests, how it could be mediated and the role of personality variation, is given in Table 2.1.

Domestic sheep: social foragers but not cooperative

Domestic sheep are highly gregarious, have a strong flocking instinct and forage together in groups (Sibbald and Hooper, 2004). However, smaller sub-groups are frequently seen to separate from the main flock when foraging. Earlier, I outlined work which showed that shy sheep were less likely to split into these sub-groups (Michelena *et al.*, 2009): findings which make sense, as with sheep, as in other species, smaller groups are likely to be more at risk from predators (Shackleton and Shafak, 1984; Wrona and Jamieson Dixon, 1991). Given that different patches can ultimately support different number of individuals, this tendency is likely to influence individuals' foraging niches, with larger groups in areas with more forage available. In addition to variation in boldness, another personality trait identified in a range of species (Cote *et al.*, 2010a), which may influence propensity to forage in larger or smaller groups, is sociability. This refers to individual reactions to the presence or absence of conspecifics (Réale *et al.*, 2007) and can manifest in variation in propensity to remain close to conspecifics (Cote *et al.*, 2010b). Thus, in sheep, variation in boldness and/or sociability could result in individuals consistently utilising different foraging habitats: shy, sociable sheep will be expected to consistently forage in areas with less risk and sufficient forage for larger groups.

In support of this, it has been shown that sheep that were more likely to stay with the flock also spent less time foraging in longer grass (Sibbald and Hooper, 2004), a habitat with potentially greater risk due to reduced ability to spot threats. Moreover, sheep that were more willing to forage away from the flock also had a higher bite rate when foraging in longer grass (Sibbald and Hooper, 2004), indicating that they spent less time on vigilance (which may indicate boldness). Thus, foraging specialisation in sheep is predicted to occur based on the 'landscape of fear' hypothesis outlined by Toscano *et al.* (2016).

European badgers (Meles meles): solitary foragers living in stable social groups

In the European badger, groups of up to twelve individuals occupy and defend strictly defined territories (Kruuk, 1978). In this species, individuals from the same group have been found to occupy distinct foraging niches (Robertson *et al.*, 2014), and niche specialisation is partly associated with resource competition generated by the availability of farmland - a key foraging habitat: groups occupying territories which contain a lower proportion of farmland also express a higher degree of dietary specialisation (Robertson *et al.*, 2014). Further, group size is also an important factor. Group size may in part be affected by the quality of a group's foraging range (Kruuk, 1978). Nevertheless, in larger groups, individuals that are more specialised relative to their group-mates maintain a higher body condition, suggesting that specialising is an effective way of overcoming resource competition due to increasing group size (Robertson *et al.*, 2015). Despite foraging independently, the foraging ranges of individual badgers from the same group have been found to overlap to a large degree (Kruuk, 1978). Thus, it is unlikely that niche differentiation is achieved by individuals foraging in different areas of the territory. Rather, evidence from isotopic analysis indicates that individuals specialise to forage on particular prey, or in certain habitat types (Robertson *et al.*, 2014). It has been shown that different prey types, such as earthworms and insect larvae, require different foraging strategies (Kruuk, 1978; Pigozzi, 1989). Moreover, although prey sources can be unevenly distributed within a territory (Kruuk, 1978), individuals can remember the location of foraging patches, using physical reference points such as fences, trees and bushes (Mellgren and Ropert, 1986). Thus it seems that learning both foraging techniques and patch locations may be key to niche specialisation in this species. And research suggests that both these routes to niche specialisation can be mediated by personality variation.

Firstly, a number of studies have shown that spatial learning may be influenced by personality variation. For example, in brook trout (*Salvelinus fontinalis*), bolder individuals were less able to use stable landmark cues to locate food sources (White *et al.*, 2017). This may be because although bold individuals can explore their environment more quickly (Verbeek, Drent and Wiepkema, 1994), they also may do so superficially (Sih and Del Giudice, 2012), and so do not acquire key information required for learning. In support of this, it was found that in black-capped chickadees (*Poecile atricapillus*), although fast and slow exploring individuals did not differ in the number of trials it took to learn a task, slow-exploring individuals did perform better in a subsequent test phase (Guillette *et al.*, 2015). This finding seems to indicate that although fast and slow explorers can both acquire and use information in the short-term, only the latter are able to retain and apply this information over longer periods. Together, the studies outlined above show how differences in spatial learning ability can be mediated by personality variation, and so could affect niche specialisation in badgers. This would fall under the spatial drivers hypothesis proposed by Toscano *et al.* (2016). Specifically, it would be predicted that tendency to forage on particular patches will be associated with variation in boldness and exploration.

Similarly, the evidence outlined above, suggesting that fast and slow explorers gather information differently, is also relevant to using alternative strategies for locating food within a given patch, and so could explain how niche specialisation based on utilising different foraging strategies could manifest in badgers. In some cases, in choosing between alternative foraging niches, individuals face a speed-accuracy trade-off, where in one niche, a high cost of errors favours a slow but accurate strategy, while in another where the cost of errors is lower, a faster but less accurate strategy is optimal (Chittka *et al.*, 2003; Burns, 2005; Burns and Dyer, 2008). Consistent differences in speed *versus* accuracy have been observed in various species, for example bumblebees, *Bombus terrestris* (Chittka *et al.*, 2003) and zebrafish, *Danio rerio* (Wang *et al.*, 2015). In both these examples, in a colour discrimination task associated with a food reward, some individuals consistently made fast but inaccurate choices, while others were consistently slower, but more accurate. Based on the research outlined above, regarding exploration speed and observational learning, shy, slow explorers would be predicted to perform more efficiently in foraging strategies which require careful observation, such as when prey are cryptic. Meanwhile bolder, fast explorers should perform better in foraging strategies where foraging is optimised by gathering food items quickly but indiscriminately. This is supported by research in great tits, which found that when introduced to novel, aposematic prey, shy, slow explorers were more wary at first encounter, and remembered their bad experience better, such that they were more cautious in a subsequent memory test (Exnerová *et al.*, 2010). Thus, we have a 2nd pathway through which niche specialisation in badgers might be mediated *via* personality variation. Broadly, this would fall under the 'foraging activity' hypothesis proposed by Toscano *et al.* (2016).

Cooperatively breeding mongooses: communal foragers and cooperative breeders

In two species of cooperatively breeding mongoose, meerkats (*Suricata suricatta*) and banded mongooses (*Mungos mungo*), although groups as a whole exploit a wide variety of prey-types (Rood, 1975; Doolan and Macdonald, 1996), within groups there is evidence of specialisation (Brotherton *et al.*, 2001; Sheppard *et al.*, 2018). In meerkats, this is primarily driven by the fact that small and young individuals cannot dig sufficiently deep to capture scorpions and geckos, leading larger individuals to specialise on such prey. Meanwhile, in banded mongooses, there is evidence that specialisation is driven by group size, such that niche specialisation increases in larger groups (Sheppard *et al.*, 2018). In both species, individual foraging niche has been shown to be affected, at least in part, *via* social transmission, and foraging strategies are likely learnt during ontogeny (Thornton and Malapert, 2009; Sheppard *et al.*, 2018). This learning is necessary because some prey-types can be difficult to process, and/or potentially dangerous and therefore require the acquisition of particular handling skills. For example, in meerkats, scorpions can be an important food source, but young pups are initially wary of even dead scorpions. Nevertheless, they are more likely to sample them, and later add them to their diet, if they've observed an adult eating them. Furthermore, they are increasingly likely to be given live scorpions by carers as they age (Thornton and Clutton-Brock, 2011). These factors indicate that young are taught how to handle these potentially dangerous prey effectively (Thornton and McAuliffe, 2006).

So, how might niche specialisation be mediated *via* personality variation in these species? Firstly, it would be predicted that if different prey types are associated with different levels of risk, these should be used differentially by individuals, based on their boldness. However, if foraging niche is socially transmitted, how will this interact with personality variation? In fact, research suggests that personality traits can also be 'socially transmitted', in that the personality traits of carers during ontogeny can determine the personality traits of offspring. For example, in a cross-fostering experiment in zebra finches (*Taeniopygia guttata*), the personality type of offspring was predicted by their foster parents, rather than their genetic parents (Schuett *et al.*, 2013). Thus, tendency to target more or less risky prey, could be influenced by variation in boldness, transmitted between care-givers and young.

Nevertheless, individuals also differ in their propensity to use personal and social learning. In this case, social transmission may be offset against personal learning, in determining foraging niche. For example, in meerkats, it was found that some individuals learned foraging techniques without observing others, and these techniques subsequently spread to others *via* social transmission (Thornton and Malapert, 2009). Thus, alternative foraging techniques persisted in the group, rather than group-level norms in foraging behaviour emerging (Thornton and Malapert, 2009; Thornton and Clutton-Brock, 2011). This maintenance of variation, combined with prey-preferences based on risk outlined above, is likely to generate niche specialisation. Moreover, tendency to use social or personal information can also be influenced by personality variation. For example, in wild chacma baboons (*Papio ursinus*), bolder individuals were more likely to improve in solving a foraging task after watching a demonstrator, i.e. were more likely to use social information (Carter *et al.*, 2014). Thus in the case of cooperative mongooses, how niche specialisation manifests could be determined *via* complex interactions between social transmission (of food preferences, and personality traits) and variation in propensity to use social or personal learning. Specifically, if, as in chacma baboons, bold individuals are social learners, then these individuals might acquire their foraging niche through social transmission, and also tackle risky prey like scorpions, while shy individuals might be more likely to favour personally learnt foraging strategies and target less risky prey-types. Finally, to apply the hypotheses of Toscano *et al.* (2016) to this intricate web, personality variation could drive niche specialisation in cooperative mongooses *via* two pathways: social drivers, and variation in foraging activity, but also *via* different responses to relative risk posed by different prey-types. This last does not fit neatly under any of the hypotheses presented by Toscano *et al.* (2016), but should not be underestimated in certain contexts.

Table 2.1. Examples of niche specialisation in social species and the way intragroup differences in foraging niche could be mediated by personality variation.

Species	How does niche specialisation manifest?	How is niche specialisation mediated?	The potential role of personality variation	References
Domestic sheep (*Ovis aries*)	Individuals forage in patches of different quality and/or size	Propensity to forage in larger or smaller groups	Variation in boldness and/or sociability influences group size preference	Cote *et al.* (2010a) Cote *et al.* (2010b) Michelena *et al.* (2009) Sibbald and Hooper (2004)
European badger (*Meles meles*)	Individuals specialise on different prey-types / foraging habitats	Possibly influenced by ability to re-locate specific foraging patches and/or employ certain foraging strategies	Variation in boldness and exploration can influence spatial learning ability and performance in different foraging strategies	Guillette *et al.* (2015) Robertson *et al.* (2014) Sih and Del Giudice (2012) White *et al.* (2017)
Cooperatively breeding mongooses (meerkats, *Suricata suricatta* & banded mongooses, *Mungos mungo*)	Individuals specialise on different food-types	Foraging preferences are inherited *via* social transmission, during interactions with a particular care-giver Individuals also add new food types to their diet *via* personal learning.	Propensity to use personal versus social learning can be influenced by variation in personality traits such as boldness	Carter *et al.* (2014) Sheppard et al. (2018) Thornton and Malapert (2009)

2.5 PERSONALITY VARIATION AND DIVISION OF LABOUR

Division of labour in social insects

Personality variation might not only help to explain how group size increases can be achieved *via* niche specialisation, but also how the division of labour can develop, once groups reach sufficient size. Division of labour refers to cases where different tasks, for example (e.g. foraging and brood care), are shared among group members (Ratnieks and Anderson, 1999). With a few notable exceptions, including mole rats and humans (O'Riain and Jarvis, 1997; Nakahashi and Feldman, 2014), vertebrates generally show little firm evidence for division of labour (but see below). It is perhaps unsurprising therefore, that the majority of the studies I am aware of to have addressed the link between personality variation and division of labour have been conducted in invertebrates. Firstly, in ants it has been found that personality type can influence which tasks an individual performs. For example, in *Leptothorax acervorum*, individuals differed consistently in the time they spent foraging. Furthermore, foraging time was negatively correlated with ovary-size, which in turn was positively correlated with exploration and activity levels. Meanwhile, Pamminger *et al.* (2014) investigated the role of personality variation in mediating differentiation between workers performing tasks inside and outside the nest, in *Myrmica rubra*. They found that outside-foragers were significantly more active, exploratory and aggressive than inside-workers, and suggest that these behavioural differences, along with significantly higher attraction to light seen in outside-workers, could be an important mechanism in generating division of labour in this species. Similarly, research in social spiders has also found that individuals performing different tasks can express different personality traits. In *Anelosimus studiosus,* females fall into two discrete behavioural phenotypes, 'aggressive' and 'docile'. Wright, Holbrook and Pruitt (2014) have shown not only that docile females participate more in parental care, while aggressive females spend more time engaged in colony defence, web building and hunting, but also that these two behavioural phenotypes are more effective in carrying out their ‘preferred’ tasks.

In the outside *versus* inside-worker example of DoL given above, where foragers are more active, exploratory and aggressive (Pamminger *et al.*, 2014), these trends align with predictions based on the personality and social insect literatures. For example, in order to locate food, foragers must actively search their environment (Gordon, 1995), and so cover greater distances, relative to their nest-mates. Further, although outside foragers can be at much greater risk from predators (Schmid-Hempel and Schmid-Hempel, 1984; Heinze and Schrempf, 2008), research has suggested that more aggressive ants are better able to repel predators (Rissing, 1981b).

In addition to splitting workers to perform inside and outside tasks, another way of dividing the labour force is to split outside workers into foragers and soldiers (i.e. individuals specialised to defend their nest-mates from predators and competitor conspecifics (Tian and Zhou, 2014)). Although it has not yet been shown empirically, I suggest it is likely that this form of DoL could also be mediated *via* personality variation. Firstly, although in some cases, soldiers possess morphological adaptations which enable them to effectively defend the colony (Grüter *et al.*, 2012), there must be something which actively encourages these individuals to respond more defensively against threats, relative to their nest-mates. I would therefore predict that soldiers will be more aggressive than other workers, including foragers. This prediction holds irrespective of whether soldiers in a particular species possess morphological specialisations, given that as I have already noted, aggressiveness in itself can be an effective way for social insects to discourage predators (Rissing, 1981b). It would be particularly interesting to test the prediction regarding relative aggression between foragers and soldiers, both of which work outside the nest and face significant threats (Schmid-Hempel and Schmid-Hempel, 1984; Heinze and Schrempf, 2008). Although Pamminger *et al.* (2014) found that in *Myrmica rubra*, foragers were more aggressive than their nest-mates, this species does not have a soldier caste, and so foragers must defend themselves against threats. In species which do have soldiers therefore, it would perhaps be predicted that foragers would express intermediate levels of aggression, between soldiers and inside workers. Moreover, in addition to aggression, if soldiers are to effectively defend the active, exploratory foragers, workers performing these tasks must stay together. I would therefore predict both these castes to be score highly in both these traits, relative to inside workers.

Division of labour in non-human vertebrates

Although, as I have said, the best known examples of DoL come from social insects, instances have also been identified in vertebrates and it seems likely that personality variation could be an important mediator in these also. For example, in noisy miners (*Manorina melanocephala*), the cichlid fish *Neolamprologus pulcher* and naked mole rats (*Heterocephalus glaber*), all of which are cooperative breeders, a division of labour in group-defence has been observed (O'Riain and Jarvis, 1997; Arnold, Owens and Goldizen, 2005; Le Vin *et al.*, 2011). In the case of the miners, individuals contribute disproportionately to one of two tasks: mobbing of predators, or provisioning young (Arnold, Owens and Goldizen, 2005). Here, I would predict that, based on the evidence I have outlined for earlier examples, 'mobbers' should be more aggressive, while 'provisioners' should express higher levels of activity and exploration.

Meanwhile, in *Neolamprologus pulcher*, helpers consistently perform one of two cooperative tasks: territory defence or territory maintenance. What is more, this is a rare example where researchers have directly explored the link between division is labour and personality variation in a vertebrate. Here it was found that bolder, more active and aggressive helpers were more likely to engage in territory defence, while shy individuals participated more in territory maintenance (Le Vin *et al.*, 2011). Moreover, contrary to the prediction that in cooperative breeders, contributions to cooperation will be based on relatedness, here it was found that these personality traits explained most of the variation in helping behaviour, even when relatedness was accounted for. This highlights how important personality variation can be in mediating division of labour.

In the third example I give, that of naked mole rats, DoL is rather more complex, as this species is one of only two vertebrates with full eusociality (Jarvis, 1981). Here, as in many social insects, there is both a reproductive division of labour, and a division amongst workers. Both these divisions are mediated *via* (1) variation in body-size and (2) personality variation. Firstly, reproduction is monopolised by a single breeding female and 1-3 breeding males (Reeve *et al.*, 1990). Reproductive individuals are both larger and more aggressive during intra-colony social interactions than all non-breeding workers (O'Riain and Jarvis, 1997; Clarke and Faulkes, 2001). This heightened aggression is likely to be a way of maintaining social order, inhibiting subordinate reproduction and/or inducing workers to perform cooperative tasks (Clarke and Faulkes, 2001). Secondly, reproductives rarely engage in colony defence (although in the rare case they do, high levels of aggression are exhibited). Instead, colony defence is conducted *via* a division of labour amongst non-breeding workers (O'Riain and Jarvis, 1997). Smaller workers, which are the least aggressive during social interactions, more frequently encounter intruders, due to their higher activity levels. However, rather than responding aggressively, they return to the nest chamber and recruit 'colony defenders' *via* alarm calling (O'Riain and Jarvis, 1997). These defenders are larger individuals, which express intermediate levels of social aggression (Clarke and Faulkes, 2001), then engage with the intruder (O'Riain and Jarvis, 1997). Thus, to summarise the role of personality variation in mediating division of labour in this species: (1) reproductives are more aggressive than workers; (2) small workers are more active than large workers, and show the lowest levels of aggression across contexts; (3) large workers show intermediate levels of aggression in both social and intruder contexts (O'Riain and Jarvis, 1997; Clarke and Faulkes, 2001).

Division of labour in humans

Humans express a more complex division of labour than any other species and this has long been seen as fundamental to the development of human society (Smith, 1776; Marx, 1867; Nakahashi and Feldman, 2014). Moreover, evidence suggests that personality variation may influence performance in different tasks, even in the most modern forms of DoL where individuals adopt different professional occupations, e.g. the police service or sales (Barrick and Mount, 1991). However, such forms of DoL are beyond the scope of this chapter, and I instead focus on one of the most common forms of division of labour seen in hunter-gatherer societies, where males hunt and females gather. In recent theoretical work, Nakahashi and Feldman (2014) explore how such a gender-based DoL could have evolved and suggest this could occur when (1) group size is large, (2) there are large differences between the sexes in ability to perform a task and/or (3) learning is required to perform a task effectively. So how might personality variation mediate this? One sex-difference seen in various human societies, which is relevant both to differential performance, and learning, is spatial learning ability. In a number of studies, women have been found to outperform men in an array of object location memory tasks (Silverman and Eals, 1992; Eals and Silverman, 1994; McBurney *et al.*, 1997), and these have led to the ‘gathering hypothesis’, which posits that these differences between men and women exist because women need such abilities in location memory to relocate valuable food sources when foraging. As I have already discussed, the ability to locate food sources based on landmark cues can be influenced by personality variation (White *et al.*, 2017). Specifically, shy individuals that explore their environment slowly, are predicted to express greater learning abilities (Sih and Del Giudice, 2012; Guillette *et al.*, 2015; White *et al.*, 2017). Thus, women might also be expected to be shyer than men. And this is indeed what has been generally found, in that women are commonly seen to be more risk-averse (reviewed by Eckel and Grossman, 2008). An important caveat to note here however, is that few studies have explored consistent differences among individuals, within and among sexes, and so it is not clear whether the observed variation represents differences in the mean level of behaviour between the sexes, or true personality variation. The literature on division of labour in humans, and the link to personality variation, spans the fields of economics, business, sociology, anthropology, archaeology, behavioural ecology and evolutionary biology. I would suggest that greater synthesis among these fields could reveal significant insights into the role of personality variation in increasing group size, the evolution of DoL and ultimately the rise of social complexity in humans.

2.6 CONSTRAINTS ON NICHE SPECIALISATION

While both niche specialisation and DoL can independently facilitate increasing group size, it is likely that the former will be the precursor, as it will allow groups to reach sufficient size for the latter to develop. Therefore, in this final section, I discuss 3 factors which could constrain niche specialisation and thus any subsequent rise in social complexity. Figure 2.2 gives a flow diagram showing when I predict niche specialisation will, and will not be able to develop.

1. Dietary restriction and/or a lack of viable alternative foraging niches

One obvious constraint on niche segregation among group-mates is when few foraging niche are available, and this clearly becomes more of an issue as group size increases. In the grey snapper (*Lutjanus griseus*), grey wolf (*Canis lupus*) and European badger, it has been shown that variation in diet among individuals decreases when the diversity of available prey is lower (Layman *et al.*, 2007; Darimont, Paquet and Reimchen, 2009; Robertson *et al.*, 2015). Meanwhile, the cooperative breeding Ethiopian wolf (*Canis simensis*), which exists in the harsh conditions of the Ethiopian highlands, is highly restricted in its diet, relying heavily on a few species of small mammal. For this reason prey preferences are in large part governed by which are available (Sillero-Zubiri and Gottelli, 1995) and so opportunities for niche segregation are severely limited. Moreover, in this species, the link has been made between resource competition and restricted group size: when food is abundant group sizes increase (Kruuk and Macdonald, 1985), but when food becomes scarce group size is reduced (Marino, 2003).

2. Unpredictable availability of particular food sources

When foraging resources are unpredictable, specialising can be a highly risky strategy. This is illustrated by a study which explored dietary breadth and foraging success in two closely related, sympatric raptor species; the pallid harrier (*Circus macrourus*) which specialises on hunting voles, and the Montagu's harrier (*Circus pygargus*), which is a generalist forager (Terraube *et al.*, 2011). This study found that when voles were abundant, pallid harriers achieved an intake-rate 40% higher than Montagu's. However, when voles were scarce, their intake rate was 50% lower than the generalist Montagu's. Thus, when resources are highly unpredictable, it would be expected that there will be selection against foraging specialisation.

3. Individuals don't forage independently, but hunt collectively for single prey items

In some cases, it is possible that the selective driver of group-living can itself preclude niche specialisation among group-mates. For example, in African wild dogs (*Lycaon pictus*), one of the things favouring group-living is the benefits of cooperative hunting, where groups of individuals target a single prey item. In this species, hunting success increases with the number of adults in the pack, and foraging efficiency (per capita food intake per km chased) is highest in modal adult group sizes (Creel and Marusha Creel, 1995). In this case, foraging specialisation and group-living are actively antagonistic.

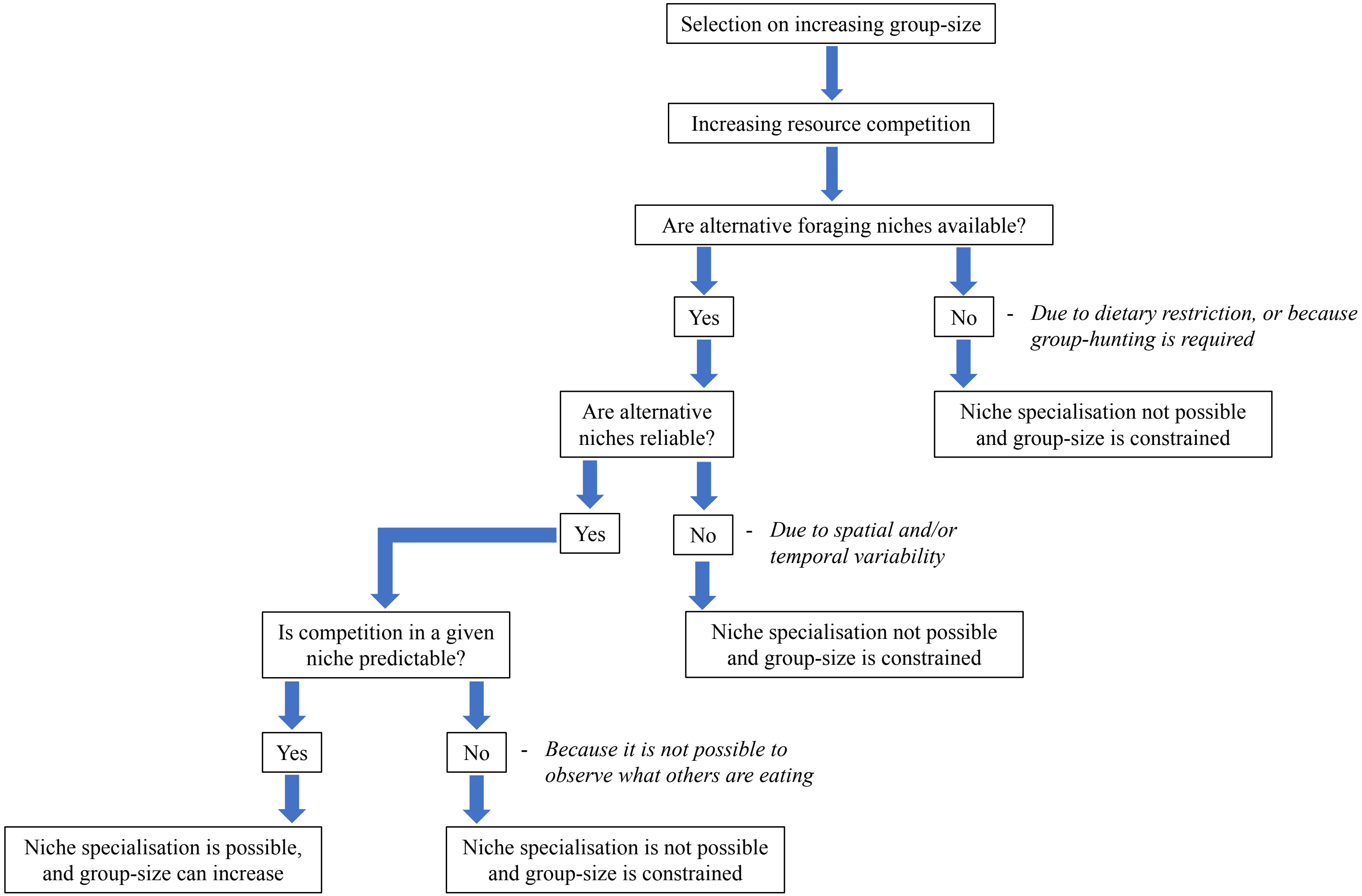


Figure 2.2. Flow diagram predicting when niche specialisation will, and will not develop and the consequences for group size.

2.7 CONCLUSIONS

Although personality variation is a field which has undergone rapid development in recent years, only now are we beginning to explore the diverse contexts in which this phenomenon could have a pivotal effect. In this review, I have suggested that one, as yet underexplored way in which personality variation could be important, is affecting niche specialisation and division of labour. Given the growing evidence that these two forms of specialisation can be important ways through which social species can reduce the costs of increasing group size, which is thought to be key to the rise of social complexity, I have highlighted the potentially key role that personality variation could play in the evolution of more complex social systems. In doing so, I have discussed studies which have explored this link so far, and found that particularly in the case of DoL, research is still only in the early stages. For this reason, I suggest that further work in this area could greatly increase our understanding of when complex forms of sociality do, and do not emerge. In particular, research which utilises the established personality literature to generate and test hypotheses for how consistent behavioural differences could affect niche specialisation and DoL in various species and contexts, is needed.

CHAPTER 3

Personality and syndromes in chestnut-crowned babblers: highlighting the difficulty with standardised approaches in a skittish, neophobic, social animal.

3.1 ABSTRACT

It is now clear that animals from diverse taxonomic groups show personality: consistent variation in behaviour across time and/or contexts, and that such variation can have marked evolutionary and ecological consequences. However, in our effort to standardise the methodology used to quantify personality variation, we might have overlooked the importance of species-specific socio-ecology in capturing and interpreting the behavioural responses to standardised assays. For example, it is becoming apparent that the same assay might be perceived differently by different species. Despite this, so far few studies have directly explored this issue, taking account of the socio-ecology of the model organism. Here, I conducted a range of common, standardised assays, in a social bird which is highly skittish and neophobic: the chestnut-crowned babbler (*Pomatostomus ruficeps*). I found significant, or near-significant repeatability in latency to enter a novel environment, the rate of movements made within the novel environment, response to a startle and propensity to go into tonic immobility, but not in responses towards a mirror. These results suggest that most of the assays conducted captured variation in behavioural responses. However, because most responses to different assays were positively, not negatively correlated, the assays failed to capture the full spectrum of expected personality traits. Specifically, latency to enter a novel environment, the rate of movements in this environment and response to a startle, were all positively correlated, suggesting that each captures a single personality trait, which may be called 'response to novel environments and/or potentially risky situations', broadly falling under the 'shyness' trait category. I discuss the implications of these findings for the study of personality variation in skittish, neophobic species and highlight the need to take the socio-ecology and general temperament of a given study species into account, when selecting/designing assays to assess different personality traits.

3.2 INTRODUCTION

Traditionally, individual differences in behaviour have been viewed as troublesome noise, blurring signal around the "golden mean" (Bennett, 1987). Standard practice was to deal with this variation by averaging behaviour across the sample to identify general patterns there-in. However, the realisation that these differences were not only consistent across time and/or context, but could also be a target for selection (Dall, Houston and McNamara, 2004; Biro and Stamps, 2008), led to a change in attitudes and the study of these differences, termed personality variation, is now a fast growing and dynamic field in behavioural ecology research. The result is a burgeoning theoretical and empirical literature, which has revealed several important aspects regarding personality variation. For example, research has shown that personality variation can be influential in a number of important ecological contexts, including: foraging (Toscano *et al.*, 2016); mating and reproductive success (Schuett, Tregenza and Dall, 2010; Schuett, Dall and Royle, 2011; Wright, Holbrook and Pruitt, 2014); and during predator-prey interactions (Sweeney *et al.*, 2013). It has also been shown that the expression of different personality traits can co-vary. Called behavioural syndromes, these trait associations may be a by-product of gene-linkage or pleiotropy (Dochtermann and Dingemanse, 2013), or may confer some adaptive advantage (Bell, 2007). One way in which covariation in traits has commonly been described is along a spectrum variously called the bold-shy continuum, proactive-reactive coping styles or a fast-slow behavioural axis (Coleman and Wilson, 1998; Koolhaas *et al.*, 1999; Réale *et al.*, 2010). In general, it is predicted that covariation in traits along this spectrum will mean that bolder individuals are relatively exploratory, active, aggressive and asocial (see Figure 3.1, adapted from Réale *et al.* (2010)). So, research has shown that investigations of personality variation can yield significant insights into patterns of phenotypic variation, with evolutionary and ecological implications.

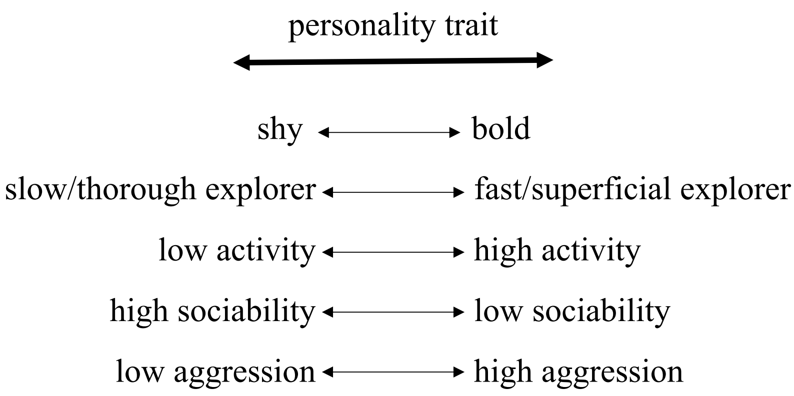


Figure 3.1. Covariation in the 5 personality trait categorises, along a fast-slow/bold-shy continuum (adapted from Réale *et al.* (2010)).

Personality variation has generally been studied by assessing variation in 5 key trait categories, which have been defined by Réale *et al.* (2007). These are shyness-boldness, exploration-avoidance, activity, sociability and aggressiveness (full definitions given in Table 3.1). Variation in these traits is assessed by conducting repeat, standardised assays which previous studies have shown to predict behaviour under natural conditions and then testing statistically for relative levels of variation across repeats, within and among individuals. So for example, in grey mouse lemurs (*Microcebus murinus*), individuals that are faster to approach a novel object (a common test of boldness) are also less averse to risk when foraging (Dammhahn and Almeling, 2012). Meanwhile, in common lizards (*Lacerta vivipara*), individuals that are attracted to the odour of conspecifics in standardised assays (i.e. show high sociability), are more likely to disperse if the density of lizards is low. Conversely, in high-density populations, individuals that show aversion to conspecifics in these assays are more likely to be dispersive (Cote and Clobert, 2007). These studies show that variation in behaviour during standardised assays can be a strong predictor of behaviour in ecologically relevant contexts. Details of how behavioural responses to various of the classic personality assays are traditionally interpreted are given in Table 3.2.

Table 3.1. The 5 personality trait categories, as defined by (Réale *et al.*, 2007).

Trait category	**Definition**
shyness-boldness	"An individual's reaction to any risky situation, but not new situations."
exploration-avoidance	"An individual's reaction to a new situation. This includes behaviour towards a new habitat, new food, or novel objects."
activity	"The general level of activity of an individual."
aggressiveness	"An individual's agonistic reaction towards conspecifics."
sociability	"An individual's reaction to the presence or absence of conspecifics (excluding aggressive behaviour)."

Table 3.2. Interpretations of the standardised personality assays used in this study, based on previous research.

Personality assay	Behavioural measure	Interpretation of the personality trait tested, based on a 'classic' interpretation	Reference
Tonic immobility (TI)	Propensity to go into TI	Higher propensity indicates relative **shyness** (towards a predator)	Edelaar *et al.* (2012)
Latency to emerge from a place of shelter	Emergence time	Faster emergence times indicate relative **boldness**	Brown, Jones and Braithwaite (2005) Cote *et al.* (2010) Beckmann and Biro (2013) Kerman *et al.*(2016) Perals *et al.* (2017)
Movement in a novel environment	Number of novel areas visited	More areas entered indicates higher **exploratory tendency**	Guillette *et al.* (2009)
	Total number of movements between different areas	More movements indicate higher relative **activity** levels	Quinn and Cresswell (2005) Le Vin *et al.* (2011)
	Number of flights made (in birds)	More flights indicate higher relative **activity** levels	Quinn and Cresswell (2005)
Startle test	Level of behavioural response to a startle stimulus	A higher-level response indicates relative **shyness**	Briffa, Rundle and Fryer (2008) Rudin and Briffa (2012)
Mirror test	Interactions with the mirror, such as displaying or making direct contact	More interactions indicate higher tendency to engage in **social behaviours, such as aggression**	Hirschenhauser *et al.* (2008) Schuett and Dall (2009)

However, more recently, various issues have been raised with this standardised methodological approach (see Biro, 2012; Beckmann and Biro, 2013; Carter *et al.*, 2013). One of these, which has been noted but has so far received less attention than others, is that the same assay may be perceived differently by different species (Carter *et al.*, 2013). For example, a classic test of boldness is to measure the time it takes for an individual to emerge from a place of shelter into an open arena. Shorter emergence times are typically taken to indicate relative willingness to be exposed to (predation) risk, i.e. boldness (Brown, Jones and Braithwaite, 2005; Cote *et al.*, 2010; Beckmann and Biro, 2013; Kerman *et al.*, 2016; Perals *et al.*, 2017). However, open habitats may represent high or low predation risk for different species (Blumstein and Daniel, 2003; Whittingham *et al.*, 2004), so in some cases, faster emergence times may in fact indicate aversion to risk. Moreover, a related issue is that species may respond differently to artificial testing paradigms *per se*, depending on their socio-ecology and general temperament. This might occur because, as O'Reilly and Wingfield (2001) have shown, even closely related species can show marked differences in their stress response at being captured from the wild, with implications for their behavioural response to the array of standardised assays used to assess personality variation. In such cases, assays designed to assess different traits may in fact test the same underlying trait: response to novel environments and/or potentially risky situations. These points suggest that interpreting behavioural responses to a given test based on previous research in other species can lead to behavioural variation being misunderstood and wrongly classified.

Although various studies have investigated the efficacy of different tests in different species (e.g. Burns, 2008; Dammhahn and Almeling, 2012; Kerman *et al.*, 2016), fewer have taken a predictive approach to testing whether or not behavioural responses to different assays are repeatable and correlated, based on the socio-ecology and temperament of the study species. Here I use a range of commonly used assays to investigate patterns of repeatability and trait correlations, under standardised conditions, in a wild population of chestnut-crowned babblers (*Pomatostomus ruficeps*). This population has been studied intensively for 14 years (Russell, 2016) and I used socio-ecological information gathered during this time to inform my *a priori* predictions. The chestnut-crowned babbler is a 50g, highly social bird that lives year-round in groups, in the semi-arid and arid region of south-eastern Australia (Russell, 2016). At our field site in the arid zone, the habitat in which they live is open, and is characterised by large areas of bare ground, interspersed with low shrubs and trees confined to isolated clumps or short linear stands (Portelli *et al.*, 2009; Sorato *et al.*, 2012). Babblers are not agile fliers, and so are highly responsive to potentially threatening situations, alarm calling and either immediately escaping for cover in a low bush, if possible, or flying to do so, when a threat is perceived. From personal observation, situations which babblers perceive as threatening include the presence of humans, the presence of novel objects in their environment and separation from their social group. I therefore hypothesised that being captured and placed in a novel environment, isolated from other birds, would represent a highly challenging situation to babblers generally. Nevertheless, based on previous research, there is also reason to believe that there would be variation among individuals in the level of response to these situations. For example, a number of studies, in various species, have shown that even in a context which is clearly threatening to all individuals, such as the presence of a predator, there is consistent variation among individuals in their response to this threat (e.g. Quinn and Cresswell, 2005; Edelaar *et al.*, 2012; Quinn *et al.*, 2012).

Based on these considerations, I made a set of predictions for patterns of repeatability and covariation among traits, tested using standard personality assays. First, I predicted that behaviours associated with risk and activity were more likely to be repeatable than those related to social interaction. For example, assays such as latency to emerge from shelter into a novel environment, patterns of movement in this environment (e.g. exploration and activity) and response to a startle, might be expected to show greater repeatability than assays of social behaviour. This is because in this skittish species, under the novel and potentially threatening conditions presented by standardised personality assays, birds might be less likely to engage in ‘normal’ responses to social stimuli. In addition, again taking the skittish, neophobic nature of this species into account, I predicted that short emergence times, and high scores in measures usually taken to indicate exploration and activity, would in fact all indicate relative ‘anxiousness’, generally a component of the ‘shyness’ trait category. These behaviours should therefore be positively correlated with each other, and also with other measures of shyness, or stress-responsiveness, such as response to a startle and propensity to go into tonic immobility.

3.3 METHODS

Field site

I conducted this study during the breeding seasons of 2013 and 2014, at the Fowlers Gap Arid Zone Research Station, New South Wales, Australia (141°43′E, 31°05′S). The field site is on the eastern edge of the Strzelecki desert. Annual rainfall is low, but variable (mean = ~215 mm). Temperatures range from <0 °C (min. winter night-time) to >45 °C (max. summer day-time). Full details of the study site are provided elsewhere (Portelli *et al.*, 2009; Sorato *et al.*, 2012; Russell, 2016), but briefly, vegetation covers about 70% of the habitat, primarily consisting of small chenopod bushes 20cm to 1m high, with scant arboreal growth typically 3-10m high, confined to short linear stands along drainage lines that descend from the Barrier ranges that run the length of the field site. All fieldwork was conducted with the approval of Macquarie University Animal Care and Ethics Committee (license no. 06/40A), the NSW National Parks and Wildlife Service, and the Australian Bat and Bird Banding Scheme.

Personality tests

To obtain repeated behavioural measures of individuals, I used mist nets to capture babbler groups on 2-3 occasions in each breeding season. Before assaying, birds were held in cloth bird-bags, with both time of capture and time of assay recorded. Overall, I conducted five different assays under standardised conditions. These were: the propensity to enter tonic immobility; the latency to emerge from shelter into a novel environment; as well as movement in the novel environment, response to a startle test and response to a mirror – all of which were conducted in the novel environment. For a subset of these assays, I recorded more than one behaviour, leading to nine behaviours being recorded overall. The assays conducted are usually used to capture the essence of five traits: boldness; exploration; activity and social behaviours (e.g. aggression). Tonic immobility was performed in 2014 on 109 individuals, all of which were assayed five times on capture and 22 of which were assayed five times on two separate occasions (time between captures for those 22 ranged from 6–71 days; mean = 43, ±20 SD)). All other assays were conducted in 2013 and 2014. Overall, I performed 217 latency, novel environment and startle tests on 159 individuals, with 30 birds repeatedly assayed within a year and 24 birds assayed in both years. The average interval between repeat assays within a year was 41 days (±19.7 SD), and for assays conducted across both years of the study, the average interval was 311 days (±27 SD). Finally, in 8 instances, mirror tests were not performed, leading to a total for this assay of 209 on 151 individuals, with 26 birds repeatedly assayed within a year and 24 birds across years.

In 2014 only, the first assay I conducted was to test for propensity to go into tonic immobility (TI). TI is an impermanent physical immobility which can be induced by physically restraining an individual when it is in a fearful state (Marx *et al.*, 2008). Previous studies have shown that in some species, lower propensity to go into TI can be an indicator of relative boldness towards a predator (Edelaar *et al.*, 2012). This test was conducted using a see-through plastic box (hereafter "TI box": length = 27cm, width = 18cm, height = 18cm). A small hole in the lid enabled the researcher to place and hold each bird in the box, and then recapture it without it escaping. To attempt to induce TI, birds were taken from their bird-bags and placed on their backs in the TI box. They were then held gently but firmly in this position, completely covered with one hand, for 10 secs. After this time the hand was slowly removed. I recorded TI as having been induced if the bird remained still for ≥10 s following removal of the hand. Each individual underwent 5 attempts to induce TI. After the assay, birds were returned to their bird-bags.

After this test (or as the first assays in 2013), the next two assays I conducted were latency to emerge from shelter into a novel environment (a common measure of boldness) and movement in the novel environment. In the second of these assays, I recorded three behavioural measures usually taken to indicate different personality traits: exploration and activity. For the novel environment, I used a standardised wooden box (hereafter "field-box": length = 119cm; width = 47cm; height = 60cm). This was painted white, with a grid of 12 equal squares drawn on the floor. The roof of the box comprised two large translucent Perspex panels, which were slid into place. Two wooden branches were placed in the box as perches, one at either end. A small holding-box was fitted to the outside (length = 19cm; width = 17cm; height = 17cm), from which a sliding door gave access into the field-box. This holding box acted as the 'place of shelter' from which individuals emerged into the novel environment. A weighted white cotton bird-bag was placed discretely at the central point along one wall of the field-box, from which a string extended to the roof; this was used in the startle test (see below). Finally, a GoPro Hero 3 video camera was positioned in an upper corner, to record the birds' behaviour during the assay.

For these two assays, birds were first taken from their bird-bag and placed in the holding-box. After one minute of acclimatisation, the door between the holding-box and field-box was removed. Birds were given one minute to enter the field-box of their own accord. If they had not done so when this minute elapsed, they were encouraged out by opening the back door of the holding-box (36% of assays). The time a bird took to emerge from the holding-box was recorded as a measure of shyness-boldness: faster emergence times are commonly taken to indicate relative boldness (Brown, Jones and Braithwaite, 2005; Cote *et al.*, 2010; Beckmann and Biro, 2013; Kerman *et al.*, 2016; Perals *et al.*, 2017). Birds were then given ~2 minutes in which to move around the field-box (mean = 118 secs, ± 20.7 SD). I designated 15 'zones' which the bird could visit during the novel environment test: each of the 12 floor-squares, both perches and the holding-box. I recorded the number of these zones a bird entered (hereafter "new zones entered", out of 15) as a measure of exploration (Guillette *et al.*, 2009), and both the total number of times a bird entered a different zone (hereafter "total zones entered"), and the number of flights made: these two measures have previously been used to indicate activity level (Quinn and Cresswell, 2005; Le Vin *et al.*, 2011).

Following the above tests, and also in the field-box, the next assay I conducted was a startle test. This was designed to give another measure of shyness-boldness: previous studies have interpreted a high magnitude response to a startle as an indication of relative shyness (Briffa, Rundle and Fryer, 2008; Rudin and Briffa, 2012). For this test, at the end of the exploration period, the bird-bag on the floor of the field-box was raised to the roof by pulling the attached string. The bag was then held in this position for 1 minute. I recorded the combined number of flights made in the first 5 s, and floor-squares crossed in the first five movements immediately after the bag had reached the top of the box, as an indication of the intensity of response to the startle.

The final assay I conducted was a mirror test, a method which has previously been used to assess social behaviours (e.g. aggression) (e.g. Svendsen and Armitage, 1973; Schuett, Dall and Royle, 2011; Elwood *et al.*, 2014). After allowing 1 minute for the birds' behaviour to return to normal after the startle test, a mirror was inserted at one end of the field-box, almost covering the end wall, meaning that test-subjects could clearly see their reflection from most parts of the field-box. Birds were then given ~1.5 min in which to respond to their mirror-image (mean = 97 secs, ± 10.7 SD). I coded behaviour according to an ethogram which had been predefined. This included behaviours which I would predict, *a priori,* to indicate either relative sociability or aggressiveness. Of these behaviours, I selected *post hoc* those which occurred with high enough frequency for statistical analysis. These were touching the mirror gently with the beak, pecking hard at the mirror, and displaying the head and chest close to the mirror.

Statistical analysis

I conducted all statistical analyses using R version 3.3.2 (R Core Team, 2016). To estimate repeatability of each behavioural response, I used the rptR package, version 0.9.1 (Nakagawa and Schielzeth, 2010), which also utilises the packages lme4 (Bates *et al.*, 2015) and pbapply. The rptR package calculates the intra-class correlation (Lessells and Boag, 1987), partitioning the total variance into among and within individual components; with repeatability estimates indicating the proportion of the variance accounted for by variation among individuals, relative to the total variance. Thus, repeatability estimates can be low either if there is low variation among individuals or high variation within individuals (Nakagawa and Schielzeth, 2010). Details of the analyses used to test for correlations among traits are provided in the relevant section below. In each repeatability analysis, parametric bootstrapping and permutations were both set to 1000 (Brust, Wuerz and Krüger, 2013; Rangassamy *et al.*, 2015) and confidence intervals were set at 95%. Both time of day and the time from group disturbance to assay were included as covariates in all analyses (except in the analysis of tonic immobility, see below) and significance testing was carried out using likelihood ratio tests.

Repeatability analyses

For TI, I conducted two repeatability analyses. The first assessed repeatability within a capture event (i.e. across the 5 induction attempts: n = 109 individuals). The second included only birds caught more than once, and assessed repeatability across repeated captures (n = 22 individuals). In my analyses, TI was set as a binary factor (success/failure to induce TI in each attempt), with 1 (TI induced) set as the binomial denominator. Repeatability was calculated using the generalised linear mixed models (GLMM) method with logit link (Nakagawa and Schielzeth, 2010). For the analysis estimating repeatability of TI over repeat captures, contrary to all other analyses (see below), time of day was not included as a covariate, as the model could not converge when I did so. This is likely due to the small number of individuals that underwent repeat assays (n = 22).

The remaining four assays (eight behaviours) were analysed using three repeatability analyses each (24 analyses). First, to gain an overall measure of repeatability for each of the 8 behaviours, I performed 8 repeatability analyses (one for each behaviour) using all of the data irrespective of whether or not an individual had a repeat assay taken (see above for sample sizes). This data set included 217 assays of 159 individuals. In these broad analyses, individuals assayed once contribute information to the among-individual variance component and thus improve the reliability of the model, despite these individuals not being repeatedly assayed. I then performed two subsequent sets of eight analyses, including individuals for which I had repeat assays within a year (one set of eight, n = 30 individuals, 2 assays per individual) and those for which I had repeat assays between years (the other set of eight, n = 24 individuals, 2 assays per individual). The rationale here is that repeatability estimates might be expected to change as a function of the time between each assay (Dingemanse *et al.*, 2002, 2012; Quinn *et al.*, 2009). For the within-year and between-year repeatability analyses, if a bird had been assayed more than twice in the respective time-period, I selected the first two assays conducted. In all models, individual identity was included as a random factor.

For latency to leave the holding-box, because individuals either tended to exit the box immediately, or required encouragement after 1 min, this variable was converted to a binary score: those exiting in <10 s were given a 0 and those exiting after this time a 1. Repeatability was then calculated using the GLMM method with a logit link function. For the number of new zones entered, the total number of zones entered and number of flights during the ~2 min observation period, I first determined the rate at which each occurred to control for the variable observation time. I then normalised the distribution of the former using square-root transformation, and used the linear mixed effects model (LMM) method for determining repeatability (Nakagawa and Schielzeth, 2010). The latter two could not be normalised; so for these (total zones entered and rate of flights), I generated a binomial score of low and high based around the median values in each case; and used the appropriate GLMM method for estimating repeatability of each (see above for latency). For the magnitude of response to the startle, I used the combined number of flights in the first five seconds and floor-squares crossed in the first five movements, following the startle, as my metric (hereafter "startle-response"). Doing this generated a Poisson distribution of count data that were analysed using the GLMM method with Poisson errors and log link function. In this model, I also controlled for overdispersion by adding an observation-level random effect to the model (Nakagawa and Schielzeth, 2010), as recommended in Harrison (2014). Finally, for behaviour in the mirror test, I converted each behaviour (touching the mirror gently with the beak, pecking hard at the mirror, and displaying the head and chest close to the mirror) to a binary variable, with individuals that performed the behaviour given a 1, and those that did not given a 0. I then used the GLMM method with logit link to calculate repeatability, with a binary error distribution.

Correlations among behavioural measures

To test whether my behavioural measures represented the traits they would ‘classically’ be predicted to, or the traits I predicted they would represent based on the socio-ecology of the study species (see Introduction), I ran three analyses using the full data set (including all assays conducted in both years). I excluded the results of the mirror test since they were not repeatable (see Results). I first tested for correlations among my continuous repeatable variables (i.e. rate of new zones entered, rate of total zones entered, rate of flights and startle-response). For this I ran Spearman’s rank correlations, since not all could be normalised (see above), using the “rcorr” function in the Hmisc package. Here I used the data set including all repeats for all individuals (217 assays, of 159 individuals), meaning that some birds are in the analysis multiple times (range= 1-4). I acknowledge that there is therefore an issue with pseudoreplication (i.e. the assumption that all my data points are independent is not met). This may affect the outcomes of the analyses, which ideally should only include a single measure per individual. Then, I used generalised linear models (GLMs) to test the association between the above variables, and also with TI and latency to leave the holding-box (a categorical variable). Here, I fitted latency to leave the holding box (0 or 1) to a binomial error distribution with logit link function. Finally to test for associations between TI and my continuous repeatable measures, I used a data-set including all TI assays conducted, converting TI to a numerical variable: the number of successful inductions at each capture (0–5) and again used Spearman’s rank correlations. It should be noted that in the repeatability analyses, TI was a binary variable, and as I discuss below was found to be significantly repeatable within a capture. It was based on this (i.e. that the propensity to go into TI is stable within a capture), that I used the total number of successful inductions to test for a correlation between this, and other behavioural responses.

If my behavioural measures support 'classic expectations', leaving the holding-box quickly would be interpreted as boldness (Brown, Jones and Braithwaite, 2005; Cote *et al.*, 2010; Kerman *et al.*, 2016; Perals *et al.*, 2017), while the rate of new zones entered would be taken as a measure of exploration (Guillette *et al.*, 2009), and both the total rate of zones entered and the rate of flights made would both be taken as measures of activity (Quinn and Cresswell, 2005; Le Vin *et al.*, 2011). These behaviours would all be predicted to be positively correlated along a fast-slow behavioural axis (Réale *et al.*, 2010). Further, the propensity to go into TI and startle-response, both of which have been taken as indicators of relative shyness (Briffa, Rundle and Fryer, 2008; Edelaar *et al.*, 2012; Rudin and Briffa, 2012), should be positively correlated with each-other, but negatively correlated with the boldness, exploration and activity measures detailed above (Réale *et al.*, 2010). However, if as I predict based on the socio-ecology and temperament of the study species, individuals all show high levels of neophobia to the testing paradigms detailed above, and thus variation in behavioural responses represents inter-individual variation in response to novel environments and/or potentially risky situations, all my behavioural measures would be predicted to be correlated. That is to say, individuals that escape quickly from the holding-box should show a high rate of movements around the novel environment, a large response to the startle and show a high propensity to go into TI.

3.4 RESULTS

Repeatability of behavioural traits

I found considerable variation in individual responses to the five assays. For example, while 43% of individuals never entered TI, 22% did so on all five attempts, and 57% did so at least once. Similarly, in the latency test, 64% of birds left the holding-box of their own accord, often within a few seconds, while 36% required prompting after a minute. Further, the number of new zones (out of 15) that a bird entered varied from 1-15 (mean = 7), the total number of times a different zone was entered varied from 1-177 zones entered (mean = 25) and 0-81 flights were undertaken (mean = 5). Individuals also varied in their response to the startle, with some not showing any reaction at all, and others having a composite movement/flight score of 15 (mean = 4). Finally, although I have reason to believe the vast majority of individuals (if not all) would have seen their own reflection, 55% did not show any of the three responses which occurred which sufficient frequency for analysis for analysis, while of those that did, 45% displayed their head and chest close to the mirror, 36% touch the mirror gently with their beak and 31% pecked hard at the mirror.

As predicted, most of the behaviours associated with risk and activity were significantly repeatable in the overall analysis (R values ranged from 0.20 – 0.31), but none of the social behaviours (measured in the mirror test) were (R values ranged from 0 – 0.019) (Tables 3.3 and 3.4). For example, I found significant repeatability in an individual's latency to leave the holding box without prompting (R = 0.21, p = 0.022), as well as in the total zones entered (R = 0.20, p = 0.041) and rate of flights undertaken (R = 0.30, p = 0.026), while there was also a non-significant trend for repeatable variation in the rate of new zones entered (R = 0.15, p = 0.097). Finally, responses to the startle test were also significantly repeatable ((R = 0.31, p = 0.013). By contrast, I found no evidence to suggest that individuals were repeatable in their response to the mirror (displaying the head and chest close to the mirror: R = 0.018, p = 0.41; touching the mirror gently with the beak: R = 0, p = 0.5; pecking hard at the mirror: R = 0.019, p = 0.41).

A further important point of note here is that for a number of the behaviours measured which, based on p-values, were significantly repeatable, the confidence intervals (CIs) around the R estimates actually range to zero at the lower end (see tables 3.4 - 3.6) and so we cannot completely reject the null-hypothesis that these behaviours show no repeatability (Nakagawa & Cuthill, 2007). As Nakagawa & Cuthill (2007) discuss, this can often be an issue when working with low sample sizes, as is the case here and is commonly so in personality studies. This highlights the importance of both reporting CIs (which based on a perusal of the personality literature is not standard practise), and of using CIs as a guide to minimum adequate sample sizes required to allow robust conclusions to be reached. For example, if during data collection data are analysed and a significant p-value suggests a non-zero effect, but CIs cross zero, this indicates that more data should be gathered to allow the null-hypothesis to be rejected with confidence. Both of these will be addressed in future studies.

Table 3.3. Summary of results from the overall, within-year and between-year repeatability analyses. The overall analysis included 217 assays of 159 individuals, while the within and between-year analyses included 2 assays of 30 and 24 individuals respectively. Personality traits in column 1 are those which each behaviour is predicted to represent, based on a 'classic' interpretation. In all models (except TI across repeat captures, where time of day was not included, due to non-convergence), individual ID, time of day and time from 1st disturbance to assay were included as explanatory variables. For the response terms latency to leave holding-box, TI, rate of total zones entered, rate of flights and all social behaviours, the GLMM method of calculating repeatability was used, with a binary error structure. For the response term startle-response, the GLMM method was used, with Poisson errors. Overdispersion was controlled for by adding an observation-level random effect. For rate of new zones entered, the LMM was used, with Gaussian errors. All repeatabilities were calculated using the link-scale.

Trait category	**Behavioural measure**	**Overall repeatability**	**Within-year repeatability**	**Between-year repeatability**
shyness-boldness	latency to leave holding-box	R = 0.21 p = 0.022*	R = 0.48 p = 0.018*	R = 0.35 p = 0.075
	startle-response	R = 0.31 p = 0.013*	R = 0.31 p = 0.068	R = 0.14 p = 0.29
	tonic immobility (within 1st capture)	N/A	R = 0.47 p = <0.001***	N/A
	tonic immobility (across repeat captures)	N/A	R = 0.061 p = 0.055	N/A
exploration	new zones entered	R = 0.15 p = 0.097	R = 0 p = 0.5	R = 0.23 p = 0.13
activity	total zones entered	R = 0.20 p = 0.041*	R = 0.26 p = 0.078	R = 0.28 p = 0.087
	flights	R = 0.30 p = 0.026*	R = 0.032 p = 0.45	R = 0.36 p = 0.065
social behaviours	soft-peck to mirror	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5
	hard-peck to mirror	R = 0.019 p = 0.41	R = 0.041 p = 0.40	R = 0.13 p = 0.26
	display head and chest close to mirror	R = 0.018 p = 0.41	R = 0.023 p = 0.44	R = 0.051 p = 0.38

Table 3.4. Summary of results from the overall repeatability analyses (n = 217 assays of 159 individuals). Personality traits in column 1 are those which each behaviour is predicted to represent, based on a 'classic' interpretation. Model structures and methods as detailed in legend to Table 3.3.

Trait category	Behavioural measure	R	SE	CI	P
shyness-boldness	latency to leave holding-box	0.21	0.083	0, 0.276	0.022*
	startle-response	0.31	0.121	0.021, 0.504	0.013*
exploration	new zones entered	0.15	0.115	0, 0.41	0.097
activity	total zones entered	0.20	0.122	0, 0.466	0.041*
	flights	0.30	0.143	0, 0.569	0.026*
social behaviours	soft-peck to mirror	0	0.034	0, 0.115	0.50
	hard-peck to mirror	0.019	0.046	0, 0.151	0.412
	display head and chest close to mirror	0.018	0.035	0, 0.121	0.41

Unsurprisingly, because of the reduced sample sizes, fewer of the behaviours were significantly repeatable in the within-year analyses, while none were so in the between-year repeatability analyses, which normally would be presumed to be because of the increased time between assays (Tables 3.5 and 3.6). In the within-year analyses, within-capture TI (R = 0.47, p = <0.001) and latency to leave the holding box (R = 0.48, p = 0.02) were highly repeatable; with R estimates at the higher end of those found in other personality studies (Bell, Hankison and Laskowski, 2009). Further, I also found near-significant repeatability in across-capture TI (R = 0.061, p = 0.055), the total rate of zones entered (R = 0.26, p = 0.078) and the startle-response (R = 0.31, p = 0.068). However, I did not find evidence that the rate of new zones entered (R = 0, p = 0.5), the rate of flights undertaken (R = 0.032, p = 0.45), or any of the behaviours in the mirror test (displaying the head and chest close to the mirror: R = 0.023, p = 0.44; touching the mirror gently with the beak: R = 0, p = 0.5; pecking hard at the mirror: R =

0.041, p = 0.40), were repeatable in the within-year analyses. Similarly, I found little evidence to suggest that behaviours were repeatable between years (range of R values = 0 – 0.36; range in p values = 0.5 – 0.065), although there were trends for repeatability in latency to leave the holding box (R = 0.35, p = 0.075) and the two measures of ‘activity’ (total zones entered (R = 0.28, p = 0.087) and rate of flights (R = 0.36, p = 0.065)).

Table 3.5. Summary of results from the within-year repeatability analyses (n = 30 individuals, 2 assays included per individual). Personality traits in column 1 are those which each behaviour is predicted to represent, based on a ‘classic’ interpretation. Model structures and statistical methods as detailed in legend to Table 3.3.

Trait category	**Behavioural measure**	**R**	**SE**	**CI**	**P**
shyness-boldness	latency to leave holding-box	0.48	0.252	0, 0.947	0.017*
	startle-response	0.31	0.156	0, 0.531	0.068
	tonic immobility (within 1st capture)	0.47	0.113	0.136, 0.568	<0.001***
	tonic immobility (across repeat captures)	0.061	0.046	0, 0.159	0.055
exploration	new zones entered	0	0.105	0, 0.361	0.50
activity	total zones entered	0.26	0.16	0, 0.591	0.078
	flights	0.032	0.112	0, 0.385	0.45
social behaviours	soft-peck to mirror	0	0.095	0, 0.341	0.50
	hard-peck to mirror	0.041	0.135	0, 0.44	0.40
	display head and chest close to mirror	0.023	0.096	0, 0.335	0.44

Table 3.6. Summary of results from the between-year repeatability analyses (n = 24 individuals, 2 assays included per individual). Personality traits in column 1 are those which each behaviour is predicted to represent, based on a 'classic' interpretation. Model structures and statistical methods as detailed in legend to Table 3.3.

Trait category	Behavioural measure	R	SE	CI	P
shyness-boldness	latency to leave holding-box	0.35	0.277	0, 0.997	0.075
	startle-response	0.14	0.152	0, 0.483	0.29
exploration	new zones entered	0.23	0.173	0, 0.614	0.133
activity	total zones entered	0.28	0.172	0, 0.564	0.087
	flights	0.357	0.216	0, 0.709	0.065
social behaviours	soft-peck to mirror	0	0.095	0, 0.341	0.50
	hard-peck to mirror	0.13	0.196	0, 0.788	0.26
	display head and chest close to mirror	0.051	0.129	0, 0.467	0.38

Although one should not conduct further analyses on analytical estimates, since there is no way of accommodating the error inherent in such estimates (Hadfield et al., 2010; Houslay and Wilson, 2017), I do so here simply to elucidate whether or not apparent differences in the significance of repeatability estimates across the combined, within-year and between-year analyses are due to difference in sample size or the interval between assays. Given that sample size is considerably greater in the combined analyses, if there is no significant difference in levels of repeatability across the three sets of analyses, this would suggest that variation in the significance of R values is most likely explained by sample-size. To this end, I fitted the R estimates from the 8 behaviours tested in both years, from the combined, within-year and between-year analyses, as a response term in a Kruskal-Wallis analysis, and the level of analysis as a three-level factor. I found no hint of a systematic difference in R estimates across the three levels (Kruskal-Wallis, $X^2(2) = 0.82$, $p = 0.66$), suggesting that variation in the significance of R is best explained by changes in sample-size rather than repeatability estimates. Indeed, there was almost no difference in the average R estimates across the three levels of the factor, despite fewer of the within and between-year repeatability analyses showing statistical significance, and the substantially different intervals between repeated assays across these levels (mean R +/- SD: combined (0.17 ± 0.19); within-year (0.14 ± 0.18); between-year (0.19 ± 0.13).

Correlations among repeatable traits

To reiterate, based on the usual interpretations of these behavioural tests, leaving the holding box quickly (indicating boldness) should be positively correlated with measures of exploration and activity, but these measures should be negatively correlated with the propensity to go into TI and the level of startle-response (indicators of shyness) (Drent, van Oers and van Noordwijk, 2002; Réale *et al.*, 2010). Meanwhile, according to my predictions based on the socio-ecology and temperament of the study species, all behaviours will represent the same underlying trait, response to novel environments and/or potentially risky situations, and so should all be positively correlated.

In line with both 'classic', and my predictions, in analyses conducted on the full data set (including all assays carried out in both years), I found highly significant, positive correlations between measures usually taken to indicate exploration and activity (range of r_s values = 0.62 – 0.92; all p values = <0.001; Table 3.7, Figs. 3.2a-c). Further, as predicted, I also found significant positive correlations between these measures and the latency to leave the holding box (binomial GLMs: range in z-values = -2.761 – -3.434; range in p = 0.0058 – <0.001; Table 3.8, Figs. 3.3a-c). However, in line with my predictions based on the socio-ecology and temperament of the species, and not those based on more traditional interpretations, I found that measures usually taken to indicate exploration and activity were also positively, rather than negatively correlated with the startle-response (0.18 – 0.36; range of p values = <0.001 –

0.0076; Table 3.7, Figs. 3.2d-f). Finally, in contradiction to both sets of predictions, I found no association between latency to leave holding-box and startle-response (binomial GLM: z-value = -1.354, p = 0.18; Table 3.8, Fig. 3.3d), or between TI and any other measure (TI and latency: binomial GLM: z-value = -0.303, 0.76; TI and continuous repeatable variables: range of r_s values = 0.08 – 0.10, range of p values = 0.27 – 0.39; Tables 3.8 and 3.9; Figs. 3.4a-d).

Table 3.7. Spearman's rank correlation matrix of repeatable, continuous behavioural measures.

	new zones entered	**total zones entered**	**flights**	**startle-response**
new zones entered	1	r_s = 0.92 p = <0.001	r_s = 0.62 p = <0.001	r_s = 0.36 p = <0.001
total zones entered		1	r_s = 0.71 p = <0.001	r_s = 0.35 p = <0.001
flights			1	r_s = 0.18 p = 0.0076
startle-response				1

Table 3.8. GLM correlations between latency and continuous repeatable behavioural measures

Trait category	**Behavioural measure**	**Estimate**	**Std.Error**	**z-value**	**p-value**
shyness-boldness	tonic immobility	-0.03299	0.10901	-0.303	0.76
	startle-response	-0.07035	0.05194	-1.354	0.18
exploration	new zones entered	-13.7875	4.2433	-3.249	0.0012
activity	total zones entered	-2.94115	0.85636	-3.434	<0.001
	flights	-10.2976	3.7299	-2.761	0.0058

Table 3.9. Spearman's rank correlations between TI and other repeatable behavioural measures.

	Behavioural measure			
	new zones entered	total zones entered	flights	startle-response
r_s	0.08	0.08	0.10	0.10
p-value	0.39	0.36	0.27	0.27

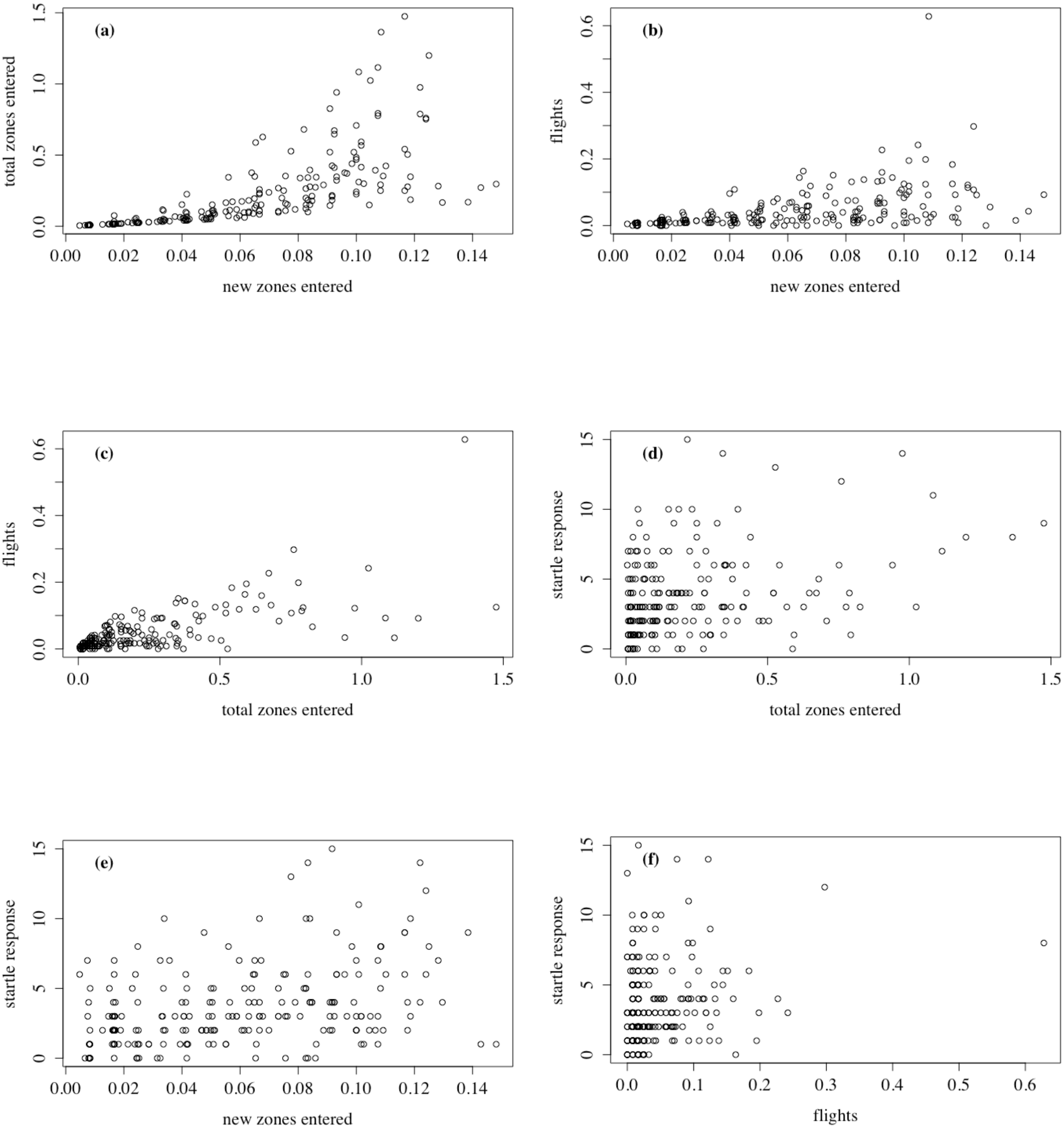


Figure 3.2. Correlations among continuous repeatable behaviours. (a) rate of total zones entered & rate of new zones entered, (b) rate of flights & rate of new zones entered, (c) rate of flights & rate of total zones entered, (d) startle-response & rate of total zones entered, (e) startle-response & rate of new zones entered and (f) startle-response & rate of flights.

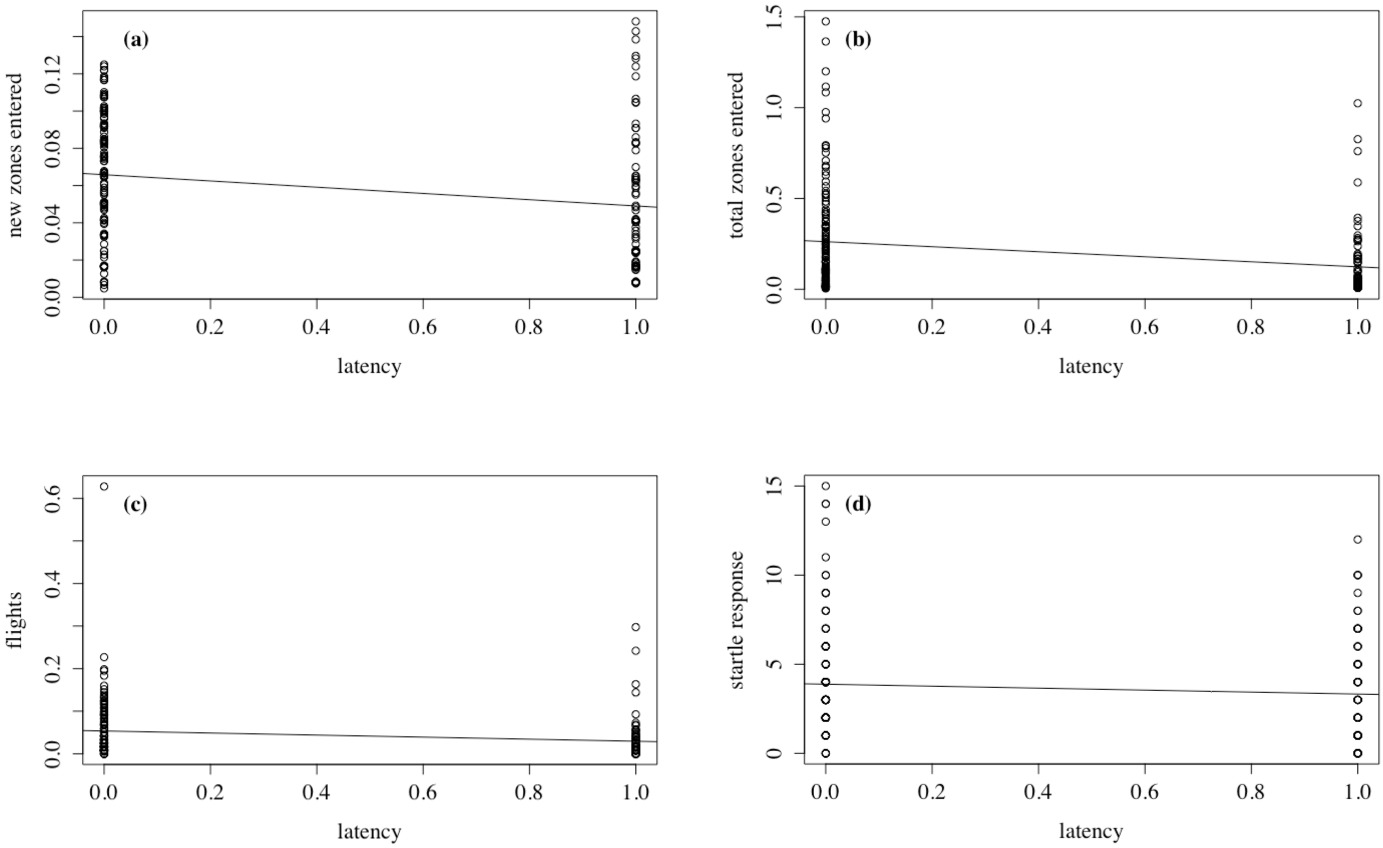


Figure 3.3. Correlations between latency to leave holding-box and continuous repeatable behaviours. (a) rate of new zones entered, (b) rate of total zones entered, (c) rate of flights and (d) startle-response.

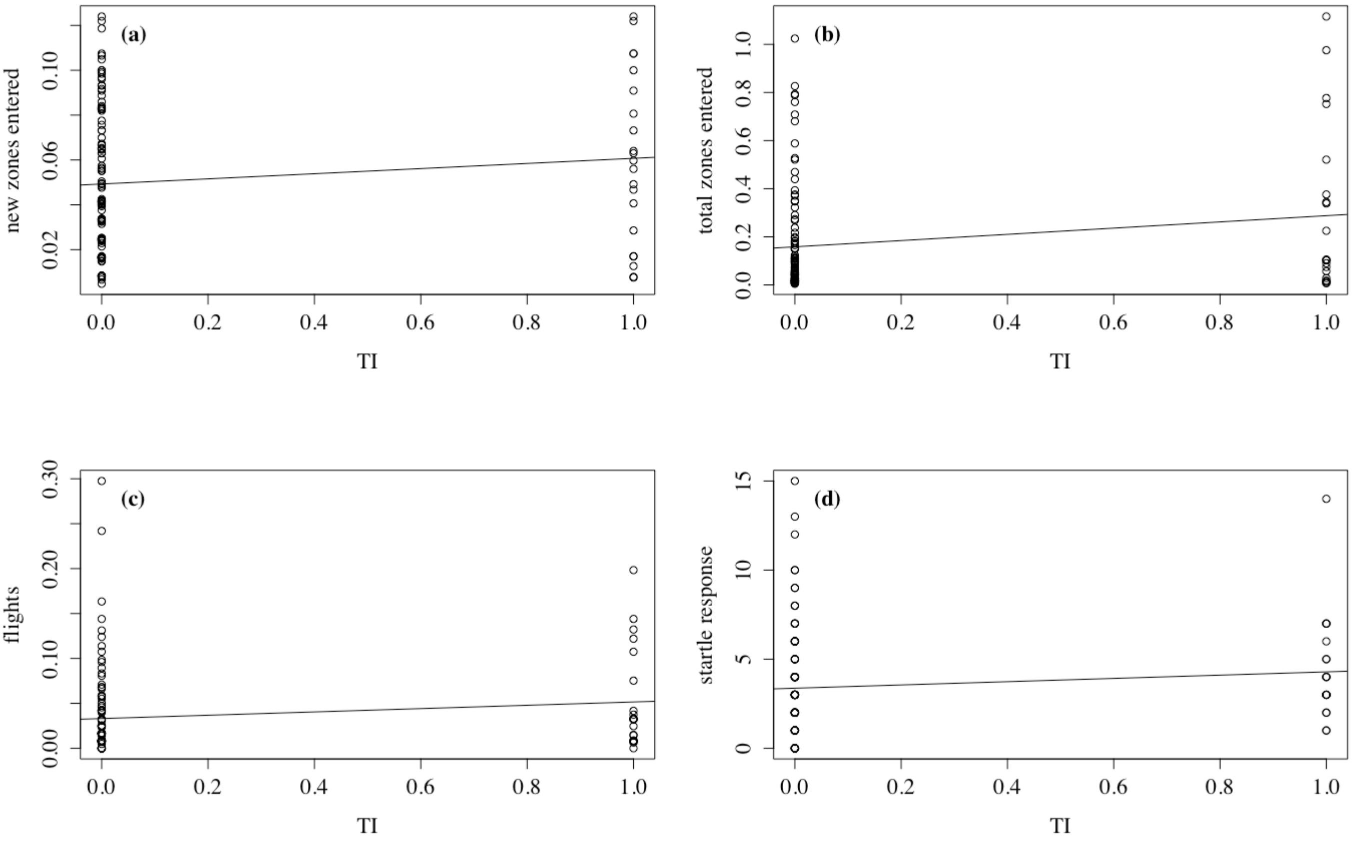


Figure 3.4. Correlations between TI and continuous repeatable behaviours. (a) rate of new zones entered, (b) rate of total zones entered, (c) rate of flights and (d) startle-response.

3.5 DISCUSSION

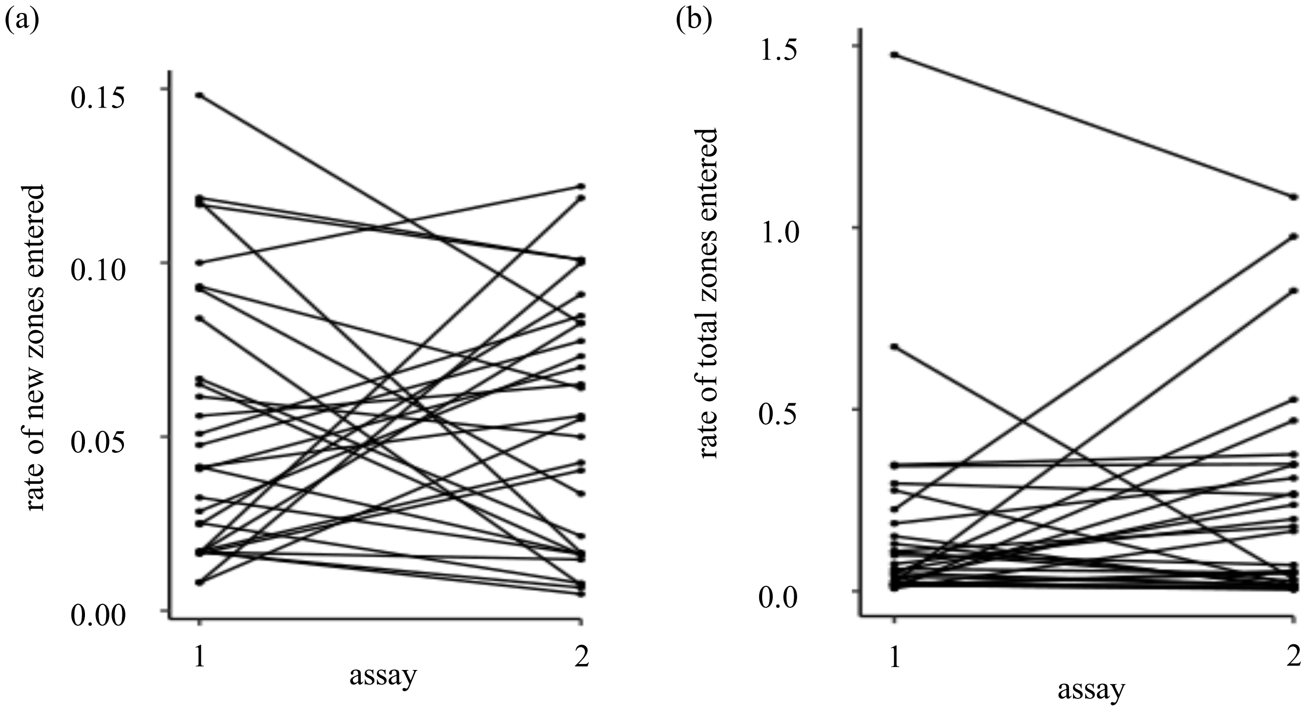
My results show that when data from both years of the study are combined, most (5 out of 8) of my behavioural measures were significantly, or near-significantly repeatable. Indeed, the only behaviours that showed no repeatability in these analyses were those in the mirror test. However, when the data were split into repeats conducted within and between years, fewer were found to be significantly repeatable, although this is likely to be largely due to the lower sample sizes in the within and between-year analyses. Interestingly associations among repeatable traits did not wholly conform to either 'classic' predictions, or those based on the socio-ecology and temperament of the study species. In general, the association analyses appear to lend greater support to my predictions, in that I found positive, not negative, associations between 'exploration/activity' behaviours and response to the startle test. However, I also unexpectedly found no association between latency to leave the holding box and the startle response, or between TI and any of my other measures. I discuss these results with reference to the implications for behavioural variation within my study system, and for the study of personality variation more broadly.

Before discussing my findings in detail, two general points regarding the methodology, which may have influenced these results, should be addressed. First, because each test ran concurrently, there is the possibility that there was a carry-over effect between assays, with the preceding test influencing behaviour in the subsequent, and also the correlations between behavioural responses. While this cannot be entirely dismissed, I did take steps to minimise, and/or test for, such effects. To assess whether movement in the novel environment was influenced by the latency test, I tested whether there was a correlation between the number of movements made in the 1st and last 5 second periods after emergence (i.e. immediately post-emergence, versus when the greatest time post-emergence had elapsed). If there was a correlation, this would suggest that movement in the novel environment was not significantly influenced by the latency test. I found a highly significant correlation (GLM: t-value = 14.14, p = < 0.001), and therefore I suggest it is highly unlikely that carry-over effects were important here. Immediately after the novel environment assay was the startle test. This meant that by definition birds always had a period of time to acclimatise to the novel environment before the startle test took place, while to reduce the chances of the startle test influencing behaviour in the subsequent mirror test, a minute was allowed to elapse after the startle, with no sound or movement within or outside the box. This was designed to allow birds' response to the startle to conclude, before the next test began. I acknowledge that despite these measures, it is possible that there may still be some carry-over effect between these tests. However, by always running the tests in the same order, I controlled for variation in the stimuli received, across individuals, and thus hopefully minimised the extent to which such effects will alter my results. The second point to address is that variation among individuals could be explained by differences in the age, sex and dominance rank among birds. Ideally I would have included these as covariates in the analysis to control for their effect. Unfortunately however, the data were not available to allow this. One point which may suggest a limited role for such effects, is that age, sex and carer status (dominant breeder *versus* helper) were found not to affect variation in provisioning behaviour in a subsequent chapter (see Chapter 5). Although in a different context, this suggests that behaviour may be relatively consistent across sexes, age classes and social ranks. However, because I cannot test this directly, such effects must remain a possibility to bear in mind, when considering my findings.

In the combined analysis, latency to leave the holding-box, rate of total zones entered, rate of new zones entered, rate of flights and startle-response were all significantly, or near-significantly repeatable. My overall repeatability estimates for these behaviours were between 0.15 and 0.31. These estimates are in excess of the mode of 0.11-0.19 found in other studies and, at least in some cases approach the average of 0.37 (Bell, Hankison and Laskowski 2009).

These comparisons suggest that the approach of assaying soon after capture and in a relatively small novel environment, was sufficient to generate repeatability estimates well within the normal range found for other studies, which more commonly have a longer habituation period in a larger enclosure.

As I show through the analysis comparing R values in the combined, within and between year analyses, the variation in the significance of repeatability across these is, in large part, likely explained by reduced samples sizes in the split analyses. This is an usual result, as Bell, Hankison and Laskowski (2009) have shown that on average, repeatability decreases with the interval between assays, and suggests that in this study system, the selective drivers of personality variation remain relatively stable across longer-than-average time periods. Nevertheless, I did also find evidence that interval length had some effect in this study. Overall, fewer behaviours showed any repeatability in the between-year analysis (3 out of 8 between years, where the interval between assays averaged 311 d), *versus* the within-year analysis (5 out of 10 (incl. TI) repeatable within a year, where the interval between assays averaged 41 d). However, I also found evidence for exceptions to this: the repeatability of the rate of flights undertaken, for example, was 0.032 in the within-year analysis and 0.36 in the between-year analysis. Moreover, overall, the average level of repeatability was actually slightly higher in the between, *versus* the within year analyses (mean R +/- SD: within-year (0.17 ± 0.19); between-year (0.19 ± 0.13). These findings might also hint that habituation effects are reducing within-year repeatability estimates (Hayes and Jenkins, 1997; Martin and Réale, 2008). Variation in rates of habituation has been found in a number of studies (e.g. van Oers, Klunder and Drent, 2005; Biro, 2012), and might be especially likely in highly social species such as chestnut-crowned babblers which have been suggested to be relatively ‘advanced’ cognitively (Ashton *et al.*, 2018). Formally testing for such habituation effects is only possible with larger sample sizes than those obtained here (Martin *et al.* 2011), but plots of individual responses to within-year repeat assays are suggestive; particularly for the rate of flights (Figs 3.5a-e; 3.6a-d; see accompanying legend for details). The take home points here are that: (1) when sample-size is maximised, behaviours in assays designed to test for boldness, exploration and activity are significantly repeatable; (2) estimates of repeatability are higher than the mode reported from other studies; and (3) although sample-size is likely the primary factor in explaining instances where R-estimates are lower, my estimates might also be influenced to varying degrees by habituation effects.



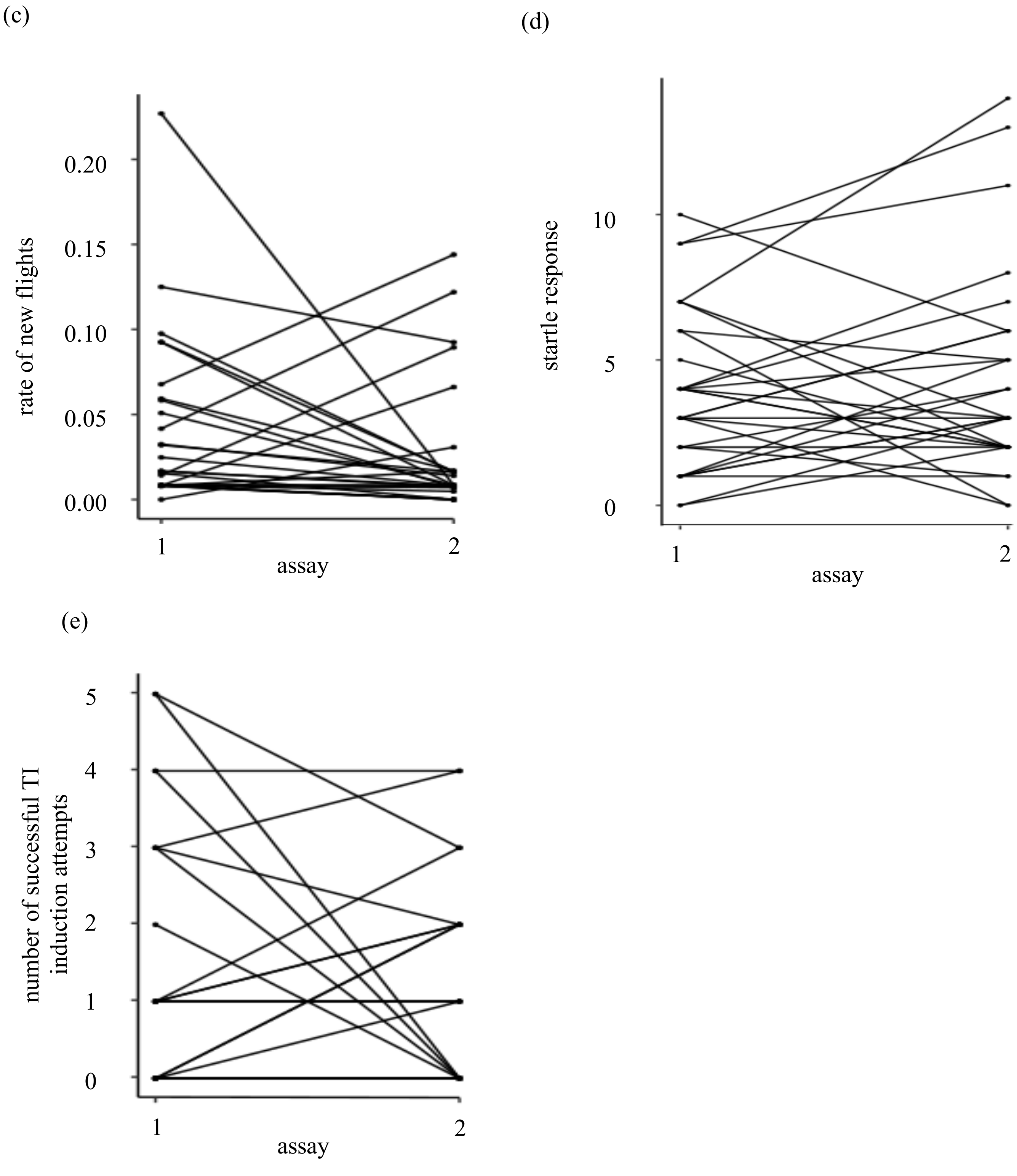


Figure 3.5. Reaction norm plots of change in behaviour between assays in the within-year analyses. (a) rate of new zones entered, (b) rate of total zones entered, (c) rate of flights, (d) startle-response and (e) number of successful attempts to induce TI. Horizontal slopes indicate a high degree of consistency between the 1st and 2nd assay. Angled slopes, from high to low, or *vice versa*, indicate that behaviour changed between assays. A combination of horizontal and angled sloped may suggest individual differences in the rate of habitation.

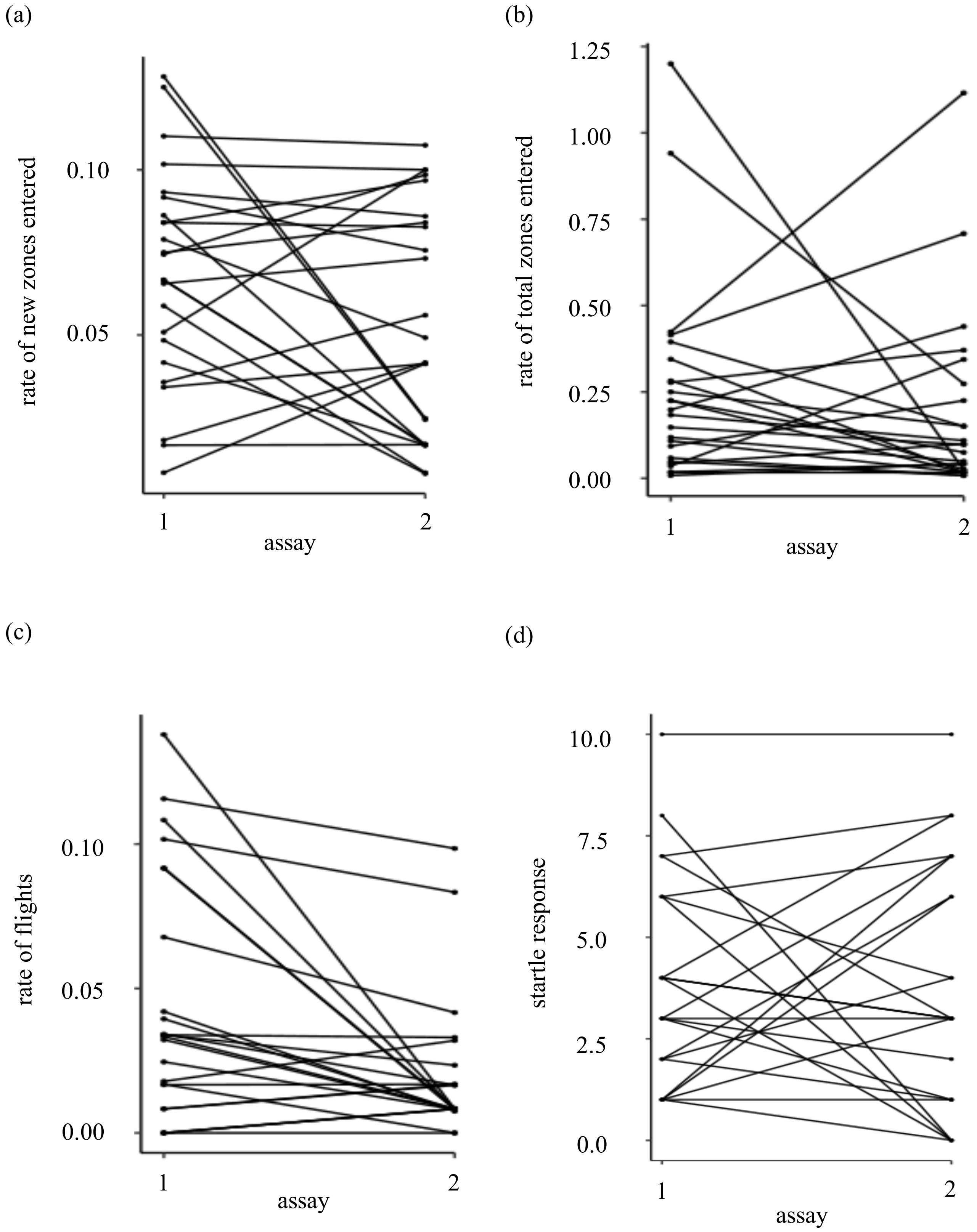


Figure 3.6. Reaction norm plots of change in behaviour between assays in the between-year analyses. (a) rate of new zones entered, (b) rate of total zones entered, (c) rate of flights and (d) startle-response.

In contrast, none of the behaviours recorded in the mirror test were repeatable in any of my analyses. One obvious explanation is that birds did not perceive their reflection as another babbler, and so the test did not illicit social behaviours. In this case, it would be expected that few, if any birds would show any social interaction with the mirror-image. This was not the case: in 45% of assays, birds directly approached and interacted with their reflection, showing at least one of the three responses I used for analysis, while in 36% of assays, birds made direct contact with their mirror-image by pecking at it. An alternative explanation is that expression of social behaviours is influenced by fluctuations in intrinsic state (e.g. nutritional status). For example, aggressive responses by brown trout (*Salmo trutta*) in a mirror test were found to be contingent on their being in low condition (Näslund and Johnsson 2016). If this were the case in babblers, we might expect time of day or time since capture to influence responsiveness to the mirror test, but no evidence for either was found. Further, we might also expect the similarity of responses between repeat assays to be higher when the interval between each was low (i.e. in the within, versus between-year analyses), since conditions are likely to have varied less, but again I found no evidence of this for behaviours in the mirror test, with R values being equal, or higher between years, in all cases. Finally, as predicted, we might expect a skittish, neophobic and highly social animal to be less likely to engage in meaningful complex social interactions under artificial testing conditions on lone individuals. Testing this hypothesis will require a different approach to the mirror test. Two ways of measuring sociability and aggression might be to conduct conspecific playbacks of affiliative versus antagonistic calls in an aviary setting, or to introduce a second familiar versus unfamiliar bird.

Based on previous studies, my findings could be interpreted as indicating that babblers differ consistently in boldness, exploration and activity. Whether or not this is the case can be clarified through analyses of the level and direction of association among behavioural responses to each assay (Drent, van Oers and van Noordwijk, 2002; Réale *et al.*, 2010).

‘Classically’, emerging quickly from a shelter into a novel environment, which has commonly been suggested to indicate boldness (Brown, Jones and Braithwaite, 2005; Cote *et al.*, 2010; Kerman *et al.*, 2016; Perals *et al.*, 2017; but see Beckmann and Biro, 2013), should be positively correlated with measures of movement in a novel environment, which have previously been taken to indicate exploration and activity (i.e. total number of zones and number of new zones an individual enters, and the number of flights it makes: Quinn and Cresswell, 2005; Guillette *et al.*, 2009; Le Vin *et al.*, 2011). Conversely, all these behaviours should be negatively correlated with measures thought to indicate shyness, i.e. propensity to go into TI and level of startle-response (Briffa, Rundle and Fryer, 2008; Edelaar *et al.*, 2012; Rudin and Briffa, 2012). Consistent with the above interpretation, I found that latency to leave the holding box, and subsequent measures of movement in a novel environment, were all positively associated (although, as acknowledged in the Methods section, pseudoreplication may have influenced these results). However, in opposition to this interpretation, I also found that movement behaviours were positively associated with response to a startle, while latency was un-associated. Further, TI was not associated with any other behaviour recorded. These latter results indicate that my results are unlikely to be explained simply by variation in boldness, exploration and activity.

There are at least three possible explanations for this pattern in the results. First, it is possible that testing so soon after capture, and conducting assays concurrently within a relatively short time period, caused behavioural responses, and so correlations among traits, to follow patterns different to those predicted by previous studies. The inference here is that behaviours may have following more ‘usual’ patterns, were the assays conducted once birds had recovered from the stress of capture, and or had been given a longer period between assays (thus avoiding potential carry-over effects (see methods, pg. 74)). It is indeed the case that other studies have often allowed a longer time between capture and assay, keeping subjects in captivity for this period, and that subjects may be exposed to single tests, rather than a battery, as in this study. As I discuss earlier, in this study, steps were taken to minimise the effect of running tests concurrently within a short period, and by standardising the order of tests, I ensured that all individuals were exposed to the same conditions. Another approach would be to randomise the order in which the tests were received among individuals, and control for test order in the statistical analysis. Although I do think the former option is valid, because it should limit the degree to which such carry-over effects will influence variation in behaviour among individuals (the subject of interest in this study), the latter option should be considered for future work. Next, to address the issue of conducting assays so soon after capture, it has been found in the past that although babblers can be held in captivity for a period of time post-capture, stress levels remain high (AF Russell, unpublished data) and so behaviour during the hours or days post-capture is still likely to be affected. What is more, as I discuss earlier, despite babblers showing a generally high level of response to capture and novel conditions, this does not preclude consistent variation among individuals in such responses still being apparent. And this is indeed what I found in this study. For these reasons, I do not feel that the decision to assay birds soon after capture impairs our ability to draw meaningful conclusions from the results.

Another possible explanation for the pattern of correlations among traits is that the assays did indeed capture variation in the range of traits they are designed to test (i.e. boldness, exploration, activity and response to stressors), but the predicted pattern of correlations among traits posited by Réale *et al.* (2010) does not hold for all species (i.e. for babblers). As Réale *et al.* (2010) review in their paper, the pattern of associations they outline has been found across a range of species, and can be affected because the expression of different traits is influenced by common underlying neuroendocrine pathways (e.g. the hypothalamic–pituitary–adrenal (HPA) axis), which are likely to be similar across species. For example, in mice, Koolhaas *et* *al*. (1999) showed that individuals artifically selected for high levels of aggression showed low reactivty in the HPA axis in stressful situations and were also fast, superficial explorers. Nevertheless, it should still not simply be assumed that the same patterns will be found in all species. Ideally therefore, multiple tests would be conducted which were designed to assess a single trait (i.e. test for convergent validity, see Carter *et al.*, 2013). If three out of four tests for boldness, for example, showed similar results, these three could all be taken as good indicators of the trait. Once this has been robustly ascertained, the correlations among traits can then be assesed with confidence. Unfortunately however, this was beyond the scope of this study. Therefore to conclude, the evidence so far suggests it is unlikely that babblers will express markely different trait-combinations to other species, but this is something which cannot be confirmed without further study.

Nevertheless, a remaining, and I suggest more likely explanation for at least one of the exceptions to usual interpretations of the tests conducted may lie in the socio-ecology and consequential temperament of chestnut-crowned babblers. Indeed, the skittish, neophobic and social characteristics of this species led us to predict that all (non-social) behaviours would capture a single underlying trait relating to 'response to novel environments and/or potentially risky situations' that positively co-vary along a single continuum. That babblers are adversely affected by the novel arena presented in the standardised trials is exemplified by comparison with a similar study conducted on the less skittish, less neophobic and less social zebra finch (*Taeniopygia guttata*), in the same novel environment field-box, at the same site (McCowan *et al.*, 2015). For example, while wild-caught zebra finches seldom moved across more than 10 zones (max = 55), in less than half the observation time (2 min *vs*. 5 min), babblers moved across an average of 25 zones (max = 177). Nevertheless, while this hypothesis can explain why exploration and activity levels can be positively associated with the startle response, it neither explains why latency to leave holding-box was not associated with the startle response, nor why TI was not associated with any behaviour. The latter is particularly surprising given that TI is expected to be a metric of shyness-boldness (Edelaar *et al.*, 2012), and so given the temperament of the species, I would expect it to be positively associated with the other traits recorded. It is unlikely that this lack of association with other traits can be explained by the reduced sample size of this assay, owing to it being conducted in a single year. One explanation is that because TI tests replicate a highly specific situation (i.e. response to attack (Marx *et al.*, 2008), and represent a markedly different context to being in a novel and potentially risky environment, but without a direct threat apparent, they might not be directly comparable to other assays conducted. Either way, this result further suggests that making assumptive interpretations on the meaning of particular behavioural responses in standardised assays can be challenging.

This study is not the first to find that caution should be exercised when using standardised personality assays to assess personality variation in different species. For example, Burns (2008), Dammhahn and Almeling (2012) and Kerman *et al.* (2016) all investigated the efficacy of different assays used to test boldness, in guppies (*Poecilia reticulata*), grey mouse lemurs (*Microcebus murinus*) and monk parakeets (*Myiopsitta monachus*) respectively. All three used a novel object assay, where willingness to approach is taken to indicate boldness. Burns (2008) and Dammhahn and Almeling (2012) both found that this was a robust measure, based on correlations with another test, willingness to be exposed to predation risk. However, in guppies there were problems with interpreting the response to this, and another test (latency to emerge from shelter), and so Burns (2008) concluded that these tests were not appropriate for this species. Similarly, Kerman *et al.* (2016) also found that latency to emerge from a shelter was not a reliable measure in monk parakeets, based on the lack of a correlation with the other two measures (novel object assay and willingness to be exposed to predation risk). This complex pattern of correlations, among responses to multiple assays used to assess the same underlying trait, shown by these studies, illustrates how difficult it can be to interpret the responses to a given test, even within a species, let alone among species. And these difficulties are only increased by the growing evidence showing that personality variation can be influenced by levels of stress (reviewed in Cockrem, 2007). Although much of the work on this has been done at the intra-specific level, rather than comparing the relative stress-responsiveness of different species, it highlights the importance of taking temperament, and particularly stress-responsiveness, into account when designing/selecting personality assays.

The findings in this chapter lend support to the growing body of literature which has highlighted challenges with the use of standardised assays in the study of personality variation. If, as my results suggest, the temperament of the study species has a major bearing on how it responds to artificial testing paradigms, then this brings into question comparisons of behavioural responses to the same test across species. On the one hand, having a relatively strict set of standard methods with which to test personality variation allows rare opportunities for sound meta-analytical and comparative techniques. On the other however, such attempts need to take extra care to consider not only the direction and strength of repeatability estimates, but also their meaning. As this study, and others, testify, this is not always straight-forward. I suggest that future study adhere to the classic approaches where possible, and relevant, but conduct additional system-specific assays to help clarify the interpretation.

CHAPTER 4

Among - versus within-group variation in personality in chestnut-crowned babblers: implications for niche specialisation.

4.1 ABSTRACT

A key constraint on stable group-living, and thus on the evolution of complex social systems, is the acquisition of sufficient resources for increasing numbers of individuals. When opportunities for range expansion are limited, one way this can be achieved is through individual specialisations, as this might be expected to increase the efficiency with which resources can be acquired within a given area. Recent research suggests that such specialisation can be manifest *via* personality variation, since particular personality traits are likely to be associated with exploitation of a particular foraging niche. Here, I evaluate personality variation within *versus* among groups of the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*), a species in which I have previously documented personality variation at the individual level. I predicted that if groups comprise individuals specialising in different foraging niches, then individuals within groups should be behaviourally dissimilar. Further, I also predicted that metrics of dissimilarity should increase with resource pressure and so group size. I found some support for the first of these predictions. Despite in fact finding significant behavioural similarity among individuals within groups, *versus* among groups, in most of the standard personality assays conducted, repeatability estimates were relatively modest (R = 0.14-0.16), suggesting that group members are still relatively dissimilar, and individual responses to a startle test were equivalent within and among groups. However, I found no evidence to suggest that metrics of behavioural dissimilarity increase with group size. Together, these results suggest that some degree of niche specialisation is possible, but not that any such specialisation mediates increases in group size.

4.2 INTRODUCTION

The emergence of cooperative care systems, and any subsequent rise in social complexity, requires in large part solving the issue of acquiring sufficient resources for increasing numbers of individuals in a group (Korb and Heinze, 2016). In cooperatively breeding vertebrates, one way in which the extra resources required to sustain larger groups can be obtained, is by increasing range size, as seen in the white-banded tanager, *Neothraupis fasciata* (Duca and Marini, 2014). However, strong territoriality and high population density, which are characteristics of many such systems (Gaston, 1978; Koenig *et al.*, 1992), mean that opportunities for group range expansion will often ultimately become limited (Hixon, 1980). In such cases, other means by which individuals in groups can secure sufficient resources, might be required.

In social insects, while larger colony sizes can be associated with increased foraging ranges (Goulson and Osborne, 2009), the large colony sizes seen in many species are commonly achieved by increasing the efficiency with which food is obtained from a given area. For example, foragers may employ strategies to efficiently communicate the location of food sources to other colony members, e.g. pheromone trails, used by some ant species (Denny, Wright and Grief, 2001) or the waggle dance in honey bees (Riley *et al.*, 2005). Although analogous mechanisms have been found in a few species of cooperative vertebrate, e.g. odour trails in naked mole rats, *Heterocephalus glaber* (Judd and Sherman, 1996) and recruitment calls in pied babblers, *Turdoides bicolor* (Radford and Ridley, 2006), these appear to be exceptions. An alternative possibility is that individuals may develop specialisations that enable them to utilise resources more efficiently, and/or reduce resource competition among group-mates. The classic example of this is morphological specialisations among castes in the social insects. For example, in some ant species, foragers possess morphological adaptations which enhance their ability to transport food (Traniello, 1989). Again however, although niche partitioning in social vertebrates can be associated with morphological differences, as in the case of green woodhoopoes, *Phoeniculus purpureus,* where sexes differ in bill length (Radford and Du Plessis, 2003), such examples appear to be rare. Perhaps a more general possibility is that groups can reduce foraging competition through behavioural specialisation of their constituent members. Although this might often be challenging to quantify, recent evidence suggests that it can be manifest *via* personality variation (Toscano *et al.*, 2016), but so far, tests of this possibility are lacking.

Defined as consistent among-individual differences in behaviour, across time and/or context (Dall, Houston and McNamara, 2004), personality variation is studied by assessing consistent variation in behavioural traits such as shyness-boldness, exploration-avoidance and activity (Réale *et al.*, 2007). This is generally done by conducting repeated, standardised tests aimed at quantifying consistent behavioural differences across time or context (Bell, Hankison and Laskowski, 2009). Mounting evidence in non-cooperative care systems suggests that expression of these, and related traits, can associate with foraging niche. For example, in great tits (*Parus major*), birds that are faster to explore a novel environment are also more likely to attack novel, aposematic prey (Exnerová *et al.*, 2010) and will travel further to find new foraging locations when a known food source is removed (van Overveld and Matthysen, 2010). Meanwhile in mud-crabs (*Panopeus herbstii*)*,* Griffen, Toscano and Gatto (2012) found that bold individuals were more likely to inhabit subtidal areas of the reef, where predation risk is higher, while shyer crabs were more likely to inhabit intertidal areas.

Further, specialisation to foraging niches has been shown to enhance foraging success in two ways. First, individuals can develop their ability to utilise a resource over time, for example by improving their ability to detect a cryptic food type, as seen in the blue jay, *Cyanocitta cristata* (Pietrewicz and Kamil, 1979), or by improving their foraging technique through trial-and-error learning, as in the woodpecker finch, *Cactospiza pallida* (Tebbich *et al.*, 2001).

Second, as has been shown in the California sea otter (*Enhydra lutris nereis*), specialisation can reduce competition over limited resources as the number of individuals in a given area increases (Ostfeld, 1982; Tinker, Bentall and Estes, 2008). Nevertheless, despite strong evidence for a link between personality variation and foraging niche (reviewed in Toscano *et al.*, 2016), as well as between niche specialisation and resource use optimisation with increasing population density, studies have yet to investigate whether patterns of personality variation within and across cooperative groups are consistent with evidence of niche specialisations.

Here, I investigate personality variation among individuals within and across groups, in a population of the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*), which has been studied intensively for over 10 years (Russell, 2016). This 50g passerine is sexually monomorphic and is not known to use a food-recruitment call (Crane, Savage and Russell, 2016). It breeds in kin-structured groups which vary in size from 2-15 individuals (Browning, Patrick, *et al.*, 2012). Philopatric recruits can gain indirect fitness by increasing the reproductive success of related breeders (Browning, Patrick, *et al.*, 2012), but larger groups can potentially suffer from resource depletion (Sorato, Griffith and Russell, 2016). Despite this, large groups tend not to forage over significantly greater ranges during breeding than small groups, presumably because of the increased travel costs to and from the nest (Sorato, Griffith and Russell, 2016). Babbler territories are highly heterogeneous, containing a range of variably open foraging habitats (bare ground, low bushes, trees) within just a few metres (Portelli *et al.*, 2009), and babblers forage on a wide variety of invertebrates and small vertebrates (Browning, Young, *et al.*, 2012) which are extracted using a range of foraging techniques (digging, turning over stones and wood, gleaning, wood-pecking). Finally, the threat of aerial predation is high, and babblers reduce their time foraging on the ground following the observation of a falcon or accipiter hawk (Sorato *et al.*, 2012), suggesting that ground foraging is more risky than other methods. Thus, babblers have the opportunity to, and would appear in principal to be capable of, adopting alternative foraging niches within groups, with any such specialisation likely manifest in personality traits (see above).

In a previous study, I showed that individuals in this system vary consistently in various measures which all indicate an individual's response to a novel and potentially threatening environment (i.e. a trait which is likely to be key in influencing foraging niche) (Chapter 3). Here, by examining the repeatability of behaviour at the group-level, and the relationship between group size and the behavioural similarity of individuals within breeding groups, I test the hypothesis that in this system, pressure on groups to optimise resource-use can be elucidated by variation in individuals' responses to novel and potentially threatening situations. I test two main predictions. First, individuals sharing resources (i.e. those in the same breeding unit) will show more behavioural dissimilarity than expected based on population levels of personality variation. This prediction is based on the assumption that foraging niche is manifest in measures of personality variation in standardised conditions and the expectation that those in the same group will be under strong pressure to forage in distinct niches. Second, larger groups will be comprised of individuals more dissimilar in personality 'type' than smaller groups. There are two reasons for this prediction: (1) larger groups are under greater resource-pressure, creating a greater need to optimise resource use; and (2) they will need to incorporate a greater variety of resources into their diet, and so diversify more in their behaviour, if they are to avoid competition.

4.3 METHODS

Field site and study system

This study was conducted at the Fowlers Gap Arid Zone Research Station, (141°43′E, 31°05′S), in the arid zone of far western New South Wales, Australia. The climate is characterised by low, but variable annual rainfall (mean = ~215 mm) and both high and low temperature extremes, ranging from <0 °C (min. winter night-time) to >45 °C (max. summer day-time). Full details of the habitat, climate, foraging and breeding ecology are provided elsewhere (Portelli *et al.*, 2009; Sorato *et al.*, 2012; Russell, 2016). Importantly, the habitat is characterised by open chenopod shrubland: ~30% of the landscape is bare ground often in association with stones and to a lesser extent dead wood. The rest is comprised of low saltbush (*Atriplex spp.*) and bluebush (*Maireana spp.*), 20cm to 1m high. In almost all territories, trees of 3-10m are largely confined to short linear stands along drainage lines, which babblers commonly foraging along and from. Babblers spend much of their time digging in the ground, or turning over small stones and bits of dead wood, but can also chase surface dwelling prey such as crickets and moths. They can also glean prey from the small bushes and trees, and also spend time chipping off bark and wood-pecking. Fieldwork methods were approved by Macquarie University's Animal Care and Ethics Committee (licence no. 06/40A), the NSW National Parks and Wildlife Service and the Australian Bat and Bird Banding Scheme. All birds were released without issue and known to survive to the end the breeding attempt, after which monitoring ceased.

Personality tests

During the breeding seasons of 2013 and 2014, babbler groups were captured using mist nets and held in cloth bird bags before assaying; the time from group disturbance to assay, as well as time of day, were included as covariates in all analyses. Most birds were assayed within an hour of capture. For each bird, I conducted a set of behavioural tests in a large field-box, designed to assess personality traits which are relevant to foraging niche. Full details of these tests are provided in Chapter 3. To summarise my methods briefly, each bird was first placed in a small holding-box, attached to the large field-box, and given 1 min to acclimatise. The dimensions of the field-box were: length = 119cm; width = 47cm; height = 60cm in size. The inside was painted white, and the roof comprised two large translucent Perspex panels. At the end of the acclimatisation period, a door leading to the field-box was opened and the time the bird took to emerge was taken as my first behavioural measure. Birds that did not emerge after 1 minute were encouraged out (36% of assays). Here followed a period of ~2 min (mean = 118 secs, ± 20.7 SD), during which the birds could explore the novel environment, the floor of which was divided into 12 equal squares, with a perch at either end. Each square and perch was designated a 'zone', as was the holding box, which they could re-enter. I recorded the number of zones (out of 15), the total number of times the bird moved to a different zone and the number of flights a bird made, during the ~2 min, as three further measures. Finally, at the end of this period, I pulled a string, attached to a bird bag which had been earlier placed in the field-box, making it rise to the top of the test area. This startled the bird and I recorded the number of floor-squares crossed in the first five movements and number of flights made in the first 5 s immediately after the startle, as two further behavioural measures of an individual's response to a novel and potentially threatening environment. All of the behaviours included in the current study showed significant, or near-significant repeatability values of 0.15 – 0.31 at the level of the individual (Chapter 3). So to summarise, overall I recorded 5 behavioural measures: latency to enter a novel environment from a place of safety, 3 measures of movement within the novel environment (number of new zones entered, total number of zones entered and number of flights) and response to a startle. In Chapter 3 I showed that based on the pattern of correlations among these measures, the most likely interpretation is that each of these behaviours indicates variation in a trait which I have called "response to a novel and potentially threatening environment". Briefly, a fast emergence time was correlated with a high number of movements in the novel environment and a high-magnitude response to the startle. I based the prediction that variation in these behaviours, and thus in response to a novel and potentially threatening environment, would be associated with variation in foraging niche, because as outlined in the section "Field site and study system" (see above), the babbler's habitat is characterised by a range of foraging niches which each present differing degrees of cover from predators. Thus, individuals that respond more to risk would be expected to forage in habitats with more cover, while those that show a lower response would be more likely to forage in habitats which present a higher level of predation risk.

Overall, I performed 217 assays, on 159 individuals, from 41 groups. However, I imposed several restrictions on this data set for the purposes of the present study. First, although repeat assays on individuals conducted between years were retained, any repeats within the same breeding season were discarded (n = 30 assays). This decision was based on the fact that repeat assays conducted in close succession were less likely to be independent, and I have previously found some evidence to suggest a role for habituation in assay outcomes (Chapter 3). I also excluded assays of juvenile birds, since they are unlikely to have developed a consistent foraging niche, and any groups where I assayed less than 50% of the breeding unit (combined 62 assays). Thus, the final data set included 125 assays, of 102 individuals from 32 groups, from which at least 60% of group members were assayed (mean = 92%; SD = 0.12; range = 60 – 100%).

Statistical analyses

I conducted all statistical analyses using R version 3.3.2 (R Core Team, 2016). To assess the level of similarity in personality type among individuals within breeding groups, I calculated repeatability at the group level using the rptR package, version 0.9.1 (Nakagawa and Schielzeth, 2010). Repeatability analyses in this package partition the total variance into within and among-individual (in this case group) components. R values indicate the proportion of total variance accounted for by variation among groups (Sakal and Rohlf, 1995; Nakagawa and

Schielzeth, 2010). A significant R value thus indicates that there is consistent repeatability within, and so notable variation among groups, in the behaviour tested. Conversely, because I know *a priori* that the behaviours tested are repeatable at the individual level (see Chapter 3), a non-significant R value indicates that groups are not comprised of individuals that are more similar in personality type than expected by chance. So, to clarify the implications of this with regard to my prediction as to the similarity of behaviour among individuals within social groups, if groups do indeed contain individuals that are dissimilar in personality type, then R values at the group level should be low. Accordingly, and to maintain consistency, henceforth I use the term '(dis)similarity', in place of the more common term 'repeatability', when referring to all analyses conducted using the rptR package. In each analysis, group name was included as a random effect. Confidence intervals were set at 95% and both permutations and parametric bootstrapping set to 1000 (Brust, Wuerz and Krüger, 2013; Rangassamy *et al.*, 2015). The proportion of the group assayed was included as a covariate in all statistical models. All p-values were calculated using the likelihood ratio test (Bolker *et al.*, 2009; Nakagawa and Schielzeth, 2010). Details of subsequent analyses on the associations between within-group behavioural similarity and group size are provided in the relevant section below.

Group-level (dis)similarity analyses

Overall, I performed five analyses, each pertaining to one of the personality metrics measured. Firstly, for latency to leave the holding box, as individuals tended to either leave immediately or require prompting after 1 min, I converted this variable to a binary factor and fitted a logit link function, with 1 (exit box immediately) set as the binomial denominator. I used the general linear mixed model (GLMM) method to calculate (dis)similarity, and a permutation test to estimate significance (Nakagawa and Schielzeth, 2010). Secondly, I calculated the (dis)similarity of the rate at which new zones were entered during the ~ 2min observation period. This was square-root-transformed and fitted to a Gaussian error distribution. The total number of zones entered divided by observation time and the number of flights (the latter of which could not be normalised) both gave a general indication of each individual's overall activity level. In the first case, the rate at which zones were crossed, following log transformation, was fitted to a Gaussian distribution, while in the latter, the number of flights was fitted to a Poisson error structure with log link function, and observation time was fitted as an additional covariate (O'Hara and Kotze 2010). The sum of the number of floor-squares crossed in the first five movements and the number of flights in the first five seconds following the 'startle' was my final measure. Again, these data were fitted to a Poisson error distribution with log link function. In both models with Poisson errors, I fitted an over-dispersion term where necessary as an additional random effect (Nakagawa and Schielzeth, 2010; Harrison 2014).

Group-level similarity and group size

I used variation in the size of breeding units to test whether or not increasing resource pressure, which has been shown to increase with group size in this system (Sorato, Griffith and Russell, 2016), influenced the level of intra-group similarity in each metric of personality variation. A common way of generating a metric of within 'group' similarity for non-binary data is to use the coefficient of variation (CV) (e.g. Schuett, Dall and Royle, 2011). However, reliable estimates of CV require the constituent data to be normally distributed. This is unlikely to be the case for most groups in the study, because group sizes were typically low (range = 2 – 8). An alternative is to use the range, but this is highly sensitive to outliers and might be expected to increase with sample size, and so group size, leading to a spurious correlation between group size and personality variation. To circumvent these problems, I used the mean dyadic difference in personality measures among individuals in each group as my measure of within-group variation. For pairs, this is tantamount to the use of a range, but for trios, for example, it is the average difference between individual A and B, A and C and B and C, and so on for larger group sizes. In this way, I remove any potential for group size to correlate with personality variation by chance alone, allowing us to test the real associations between group size and personality variation.

Finally, for the binary metric of latency to leave the holding box, I generated an ordinal scale of similarity from 0 (maximal similarity) to 0.5 (maximal dissimilarity). To do so, I first calculated the proportion of the group to score 1. A value of 0.5 indicates maximal dissimilarity because with an equal number of individuals within the group leaving the box immediately (scoring 1) versus being induced out (scoring 0), the average is 0.5. To ensure that maximal scores would equal 0.5, groups with an average score of <0.5 were given their score (e.g. 0.25 where in a group of four, three individuals scored 0 and one scored 1), while groups with average scores >0.5 had their score subtracted from 1 (e.g. 1-0.75, for a group of four, where three individuals scored 1 and one scored 0). In this way, when 3 of 4 individuals behaved in the same way, irrespective of whether they left immediately or were induced out, would have the same average similarity score.

I then ran Spearman's rank correlations of the similarity metric for each behaviour against group size.

4.4 RESULTS

Group-level (dis)similarity

I found significant consistency within groups for all personality measures, other than my measure of startle response (Table 4.1). Overall in the latency test, both behavioural responses; exiting the holding-box immediately and requiring prompting after 1 min, occurred in a significant number of assays (exited immediately = 62%, required prompting = 38%).

However, individuals from the same groups were significantly more likely to respond to this test in the same way as their group-mates, compared to others in the population (R = 0.16, p = 0.026). Across the sample, I also found considerable variation among individuals in metrics of overall activity level in the novel environment. While some remained in a single zone for the duration of the trial, others 'explored' all 15 zones (mean = 7 ± 4 SD) and were highly active, visiting zones repeatedly (mean number of times a different zone was entered = 25, median = 11, IQR = 3,31) and/or performing multiple short flights (mean = 5, median = 2, IQR = 1,6). Again, however, individuals from the same group tended to show greater similarity, not dissimilarity, in both the rate at which distinct zones were entered (R = 0.14, p = 0.023; Fig. 4.1a), the total rate at which any zone was entered (R = 0.15, p = 0.022, Fig. 4.1b) and the rate of flights (R = 0.14, p = 0.041, Fig. 4.1c). Finally, although responses to the startle were also variable (mean number of flights and squares crossed combined, immediately post-startle = 4 ± 3 SD), in this case, group members did not respond more similarly to each other on average (R = 0.069, p = 0.20; Fig. 4.1d). Together, these results suggest that there is a significant degree of similarity in the 'personalities' of individuals within, *versus* among groups, but that because significant R values ranged from 0.14-0.16, considerable within-group variation still exists. Further, the startle test results indicate that here, responses are as variable within, as among groups, suggesting that groups are primarily comprised of dissimilar individuals in this regard.

Table 4.1. (Dis)similarity at the group level: analysis used for latency, number of flights & startle response = GLMM. Analysis used for total rate of squares entered and rate of new squares entered = lmm. Likelihood ratio tests used to estimate significance. N = 125. All R estimates given use the link-scale. * indicates significant behavioural similarity among group-members.

Behavioural measure	**R**	**SE**	**CI**	**P**
latency to leave holding-box	0.16	0.10	0, 0.37	0.026*
rate of new squares entered	0.14	0.086	0, 0.32	0.023*
rate total of squares entered	0.15	0.08	0, 0.32	0.022*
number of flights	0.14	0.095	0, 0.32	0.041*
startle response	0.07	0.066	0, 0.22	0.204

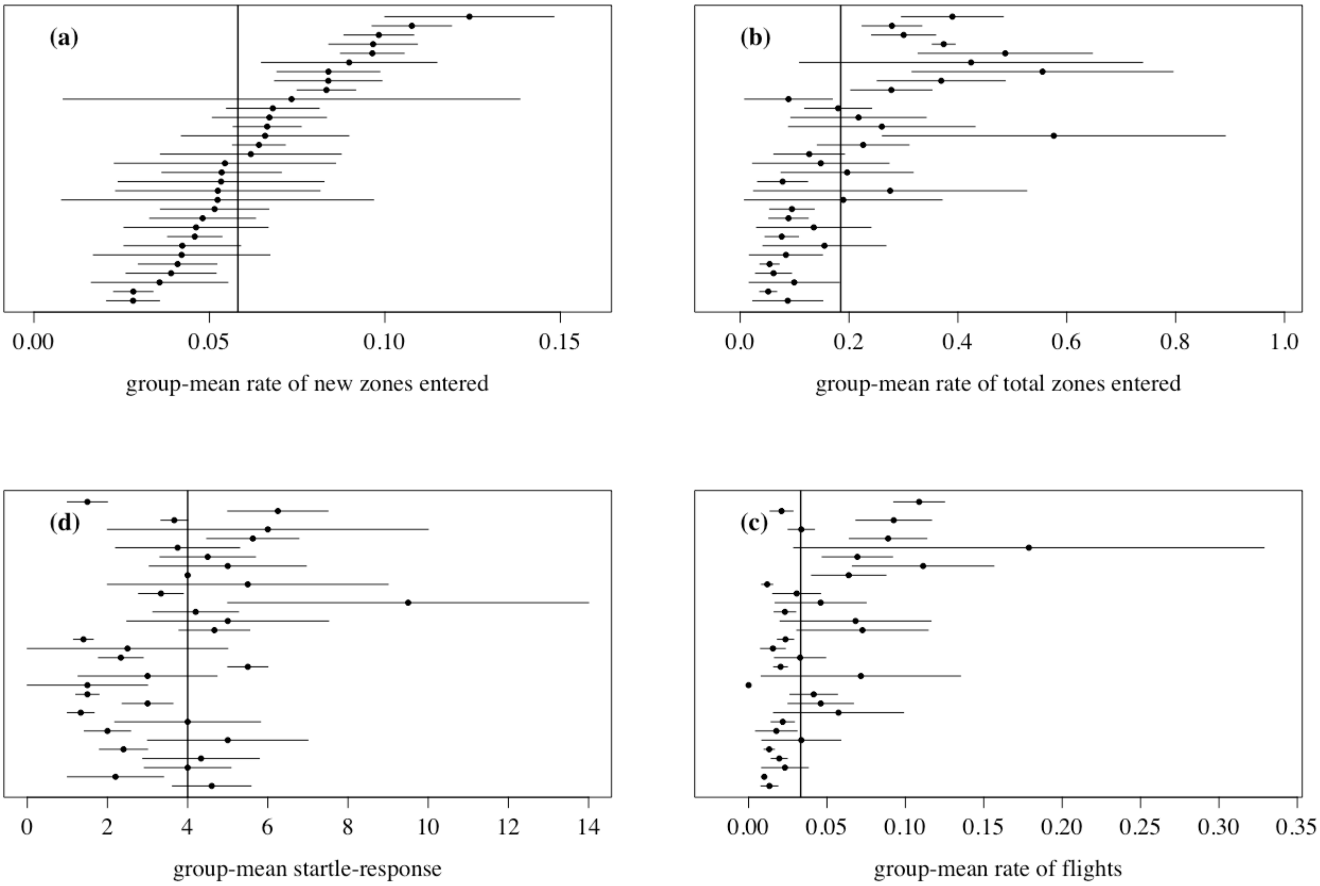


Figure 4.1 (a-d). Mean behavioural scores per group, for each behavioural measure (±SE). (a) group-mean rate of new zones entered; (b) group-mean rate of total zones entered; (c) group-mean rate of flights; (d) group-mean startle-response. Each point represents a different group. Vertical line = median score across groups. Groups ranked by score in rate of new squares entered. Variation in overlap in SE between panels indicates the extent to which groups differed in a given behaviour.

Groups size and group-level similarity in personality type

I found no evidence to support the prediction of my hypothesis that large groups comprised more behaviourally dissimilar individuals than small groups (Table 4.2; Fig. 4.2). For example, of the five correlations (4 traits) conducted between dyadic differences in behaviour and group size, only one was in the predicted positive direction and this was not significant (latency: r_s = 0.12, p = 0.5; Fig. 4.2a). Thus, 4 of the 5 correlations were in the opposite direction to that expected under a niche specialisation hypothesis, with r_s values varying from -0.07 (p = 0.7) for rate of total zones entered, to -0.32 (p = 0.08) for rate of new zones entered and startle response (Figs. 4.2b, c and e). Although these correlations were also non-significant, they suggest that, if anything, large groups comprise more behaviourally similar individuals than small groups.

Table 4.2. Spearman's rank correlations between the intra-group similarity metrics for each behavioural trait, and group size. Average dyadic differences were calculated as the average difference in the behavioural scores between group members (so for a group of 3, it is the average difference between individual A & B, A & C and B & C). I also provide coefficient of variation estimates (CV) for reference, as this is the method typically used for calculating intra-group variation. However, these are unlikely to be reliable, as CV requires data to be normally distributed, which was not the case here.

Behavioural measure	**Test**	**Spearman's correlation coefficient (r_s)**	**P**
latency to leave holding-box	similarity index	0.12	0.51
rate of new squares entered	average dyadic difference	-0.32	0.074
	CV	-0.20	0.26
rate total of squares entered	average dyadic difference	-0.07	0.69
	CV	0.11	0.57
rate of flights	average dyadic difference	-0.04	0.84
	CV	-0.18	0.32
startle response	average dyadic difference	-0.32	0.077
	CV	-0.11	0.55

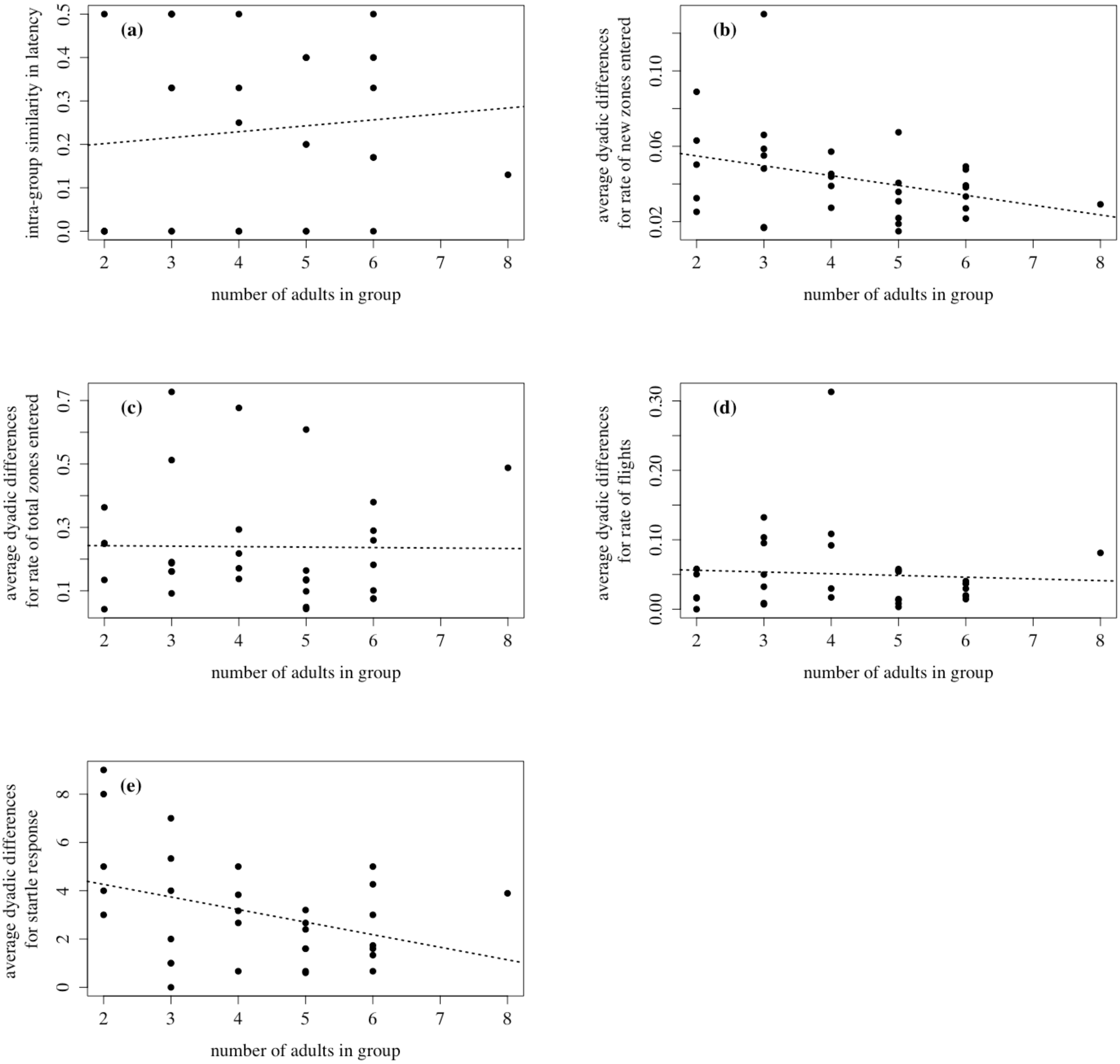


Figure 4.2(a-e). Associations between group size and group-level similarity metrics. Group size is on the X-axis, and similarity metric per/group (dyadic differences, for all but latency) is on the y-axis. Each point represents a different group. Dotted lines show the trend of the relationship for clarity, but do not infer causality. (a) intra-group similarity in latency to leave the holding-box; (b) intra-group dyadic difference in rate of new zones entered; (c) intra-group dyadic difference in rate of total zones entered; (d) intra-group dyadic difference in rate of flights; (e) intra-group dyadic difference in startle-response. None of these trends represent a significant relationship.

4.5 DISCUSSION

For any social-living species, one of the key challenges to overcome is acquiring sufficient resources under conditions of increased competition. However, in many cooperative systems, and particularly among vertebrates, the mechanisms through which this might be achieved remain unclear. In this study, I tested the hypothesis that personality variation previously observed at the individual level in a population of chestnut-crowned babblers, might facilitate optimisation of resource-use within groups. For example, if bolder individuals more commonly forage on the ground than shy individuals, because of a difference in predation risk (Sorato *et al.*, 2012), this will effectively result in niche specialisation and reduced foraging competition. I tested two predictions of this hypothesis: (1) individuals sharing resources (i.e. breeding groups) will be dissimilar in personality type; and (2) larger groups will comprise individuals that are more dissimilar in personality type than smaller groups. I found some support for the former hypothesis only. First, although four of the behaviours measured showed significant similarity for individuals within groups than among groups, R estimates were relatively modest (R = 0.14-0.16), suggesting that even for these behaviours, considerable consistent within-group variation is likely. The interpretation of these results, and the implications for intra-group behavioural similarity, are discussed below. Second, for one of the tests (response to a startle), individual responses were as dissimilar for those within the same group as they were for those in different groups. Third, however, I found no evidence to suggest that larger groups were comprised of behaviourally more dissimilar individuals than small groups. That groups of babblers are comprised of individuals that are relatively dissimilar in their behaviours, and that these behaviours are highly repeatable at the individual level (Chapter 3), provides significant scope for niche specialisation and reduced foraging competition in this species. On the other hand, the lack of evidence for increased dissimilarity with increasing group size suggests that increases in group size are not associated with increasing niche specialisation, at least as manifest in personality variation.

One potentially obvious explanation for the significant behavioural similarity within, and variation among groups is relatedness. Personality variation has been shown to be, at least in part, heritable (reviewed in van Oers, De Jong and Noordwijk, 2005), and babblers generally live in kin-structured units (Rollins *et al.*, 2012). As a consequence, intra-group similarity in personality traits may simply be an artefact of higher relatedness among group members. While I cannot rule this possibility out, there are at least two reasons why I believe intragroup relatedness is unlikely to explain significant (dis)similarity within groups. First, I have shown previously that repeatability for the traits measured averages ~0.30 at the individual level (Chapter 3). Given that individuals are related to themselves by 1, but individuals in babbler groups are related to each other by ~0.25 on average (Russell, 2016), even with generous heritability estimates (e.g. 0.20 – 0.50: van Oers, De Jong and Noordwijk, 2005; Oers and Sinn, 2013)), the genetic component of behavioural similarity in babbler groups would be expected to be undetectable (estimated $R < 0.02 – 0.04$). Second, in babblers, genetic relatedness is very low in small groups, with pairs being unrelated and trios being related by an average of ~0.1 (Russell, 2016). Despite this, there was little evidence that pairs and trios had particularly high dissimilarity compared with larger groups; in all comparisons at least some pairs and trios showed remarkable similarity in personality score despite their non-existent or low relatedness (Fig. 4.2). Finally, and related, in no case did I find a significant negative correlation between group size and behavioural dissimilarity scores, which would be expected if genetic relatedness explained the similarity of behaviour within groups – since large groups are comprised of more relatives. Thus, the available evidence suggests that genetic relatedness will have limited utility in explaining the significant consistency of behavioural responses among individuals within groups.

Two other, related candidates, that might explain the aforementioned consistency are predation pressure and habitat structure. We have shown previously in babblers that predation pressure varies across groups and influences foraging behaviour (Sorato *et al.*, 2012) and risk varies with fine-scale variation in habitat structure (Sorato *et al.*, 2015); while research in other systems has found that predation pressure can influence personality variation. For example, in the three-spined stickleback, predation pressure has been shown to influence the expression of personality traits such as exploration, activity and aggression (Bell and Sih, 2007; Dingemanse *et al.*, 2007), while in the poeciliid fish *Brachyraphis episcopi*, individuals that have been exposed to different levels of predation pressure also differ consistently in their latency to enter a novel environment (Brown, Jones and Braithwaite, 2005). Given that both predation pressure and the degree of cover vary considerably in the field site (Portelli *et al.*, 2009; Sorato *et al.*, 2012), this leads to the possibility that groups vary in their personality as a function of predation risk and habitat structure. From previous studies, shyness, for example, would be predicted to be associated with habitats with more shelter (Griffen, Toscano and Gatto, 2012). Conversely, in the more open areas, where predation risk is higher, boldness might be selected (Griffen, Toscano and Gatto, 2012; DiRienzo *et al.*, 2015). Further work is required, but the argument that predation pressure in combination with habitat structure offers a likely explanation for my results would appear compelling.

On the one hand, the interaction between of predation pressure and habitat structure might constrain niche specialisation, but on the other, it is exactly the situation that might allow niche specialisation to arise through personality variation. This is because individuals that are less responsive to novel and potentially threatening environments might be expected to engage in more risky modes of foraging, such as digging in the ground, compared with less risk-prone individuals, which might be expected to forage in the relative safety of foliage (Bell and Sih, 2007; Dingemanse *et al.*, 2007; Griffen, Toscano and Gatto, 2012). Although I found significant within-group consistency in most behaviours, the R estimates were relatively modest (R = 0.14-0.16). Thus, even for these behaviours, considerable consistent within-group variation is likely, lending some support to the first of my predictions, that groups will comprise relatively dissimilar individuals. This interpretation may appear somewhat counterintuitive, given the finding of significant behavioural consistency within groups. It was reached by consideration of the way in which the statistical package used (rptR version 0.9.1: Nakagawa and Schielzeth (2010)) partitions variance and estimates significance. Variance is partitioned into the within and among group components, and R-values indicate the proportion of variance among groups. P-values meanwhile indicate whether R is significantly greater than 0 (Nakagawa and Schielzeth, 2010). Thus, low R values suggest that a high proportion of the total variance is within groups. In this case, p-values can still be <0.05 if the variance among groups is significantly greater than 0, based on the structure of the overall variance. The reasons why this might be the case are discussed above. The judgement that R values in this study were relatively low was based on a comparison with estimates from previous studies. Meta-analysis has shown that the average R value at the individual level is 0.37 (Bell, Hankison and Laskowski 2009) and so those obtained in this study (0.14-0.16) are notably lower than those commonly found. Moreover, a further point of note is that confidence intervals for all behaviours measured crossed zero (see Table 4.1), indicating that the null hypothesis of the model (that there is no similarity in behavioural measures) cannot be rejected. Despite my conclusion that it can robustly be inferred that there was a relatively high degree of variation in the behaviour of individuals within groups, I still recognise that the method used was not perhaps ideal. Early versions of the rptR package enabled R values to go below zero, which would indicate that there was actually higher variance within individuals (or groups) than among them (Nakagawa and Schielzeth, 2010). This would have been the ideal way of analysing the data, but unfortunately these early versions of the package are not compatible with modern operating systems. Nevertheless, due to the manner in which the package partitions the variance, I suggest this still provides an informative means of establishing the degree of behavioural variation within and among measures, and thus of addressing one of the key questions of this study: how much behavioural variation exists among individuals within groups? Further, in terms of the startle test, individuals within groups responded similarly variably within as among groups. That all of the behaviours tested relate broadly to how individuals deal with novel and/or threatening environments, and are significantly repeatable at the individual level (Chapter 3), I therefore suggest, leads to the potential for niche specialisation to occur in babblers.

Notwithstanding, that I found no evidence for positive correlations between behavioural variation and group size runs counter to predictions of the niche specialisation hypothesis. Under this hypothesis, I predicted that in order to overcome the known increased competition for resources associated with increased group size in this species (Sorato, Griffith and Russell, 2016), larger groups might comprise behaviourally less similar individuals than small groups. That I failed to find support for this prediction leads to the ostensible conclusion that any niche specialisation in this species is not a major factor in allowing group sizes to increase. However, there may be alternative explanations for my findings. One possibility, which could explain both the lack of a relationship between group size and the traits measured, and also that I found some evidence of similarity in the behaviours of individuals within groups, is that niche specialisation is indeed occurring, but that the behavioural traits I assessed are not good indicators of this. Previous research has shown that niche specialisation can be mediated *via* a range of personality traits, in addition to response to risk, including sociability and activity (Toscano *et al.*, 2016). In Chapter 3 I show that despite conducting assays which have commonly been used to test for consistent variation in activity levels in other species, the pattern of correlations between responses to these, and other assays, indicated that the assays used were not appropriate for assessing activity in babblers. I therefore cannot assess how individuals differ in this trait. Meanwhile, in Chapter 3 I also found that babblers did not show repeatability in social behaviours, as assessed through standard assays. Sociability is defined as “an individual’s reaction to the presence or absence to conspecifics (excluding aggressive behaviour)” (Réale *et al.*, 2007). A highly sociable individual would be expected to respond positively to the presence of conspecifics, and negatively to their absence. Two alternative explanations may explain the failure of tests to find repeatability in this trait. Firstly, given that babblers as a species show such a high degree of sociability and are highly anxious when separated from their social group, individuals may not in fact differ markedly in their social propensity. Alternatively, it is possible that again the tests may not have been effective at elucidating variation, perhaps because of the stressful conditions in which they were conducted (see Discussion to Chapter 3). Without further research, I cannot distinguish between these alternatives, so as with activity, I am also unable to assess to the degree to which individuals consistently differ in their sociability. For this reason, that either or both of these traits may be mediators of niche specialisation in this species, which was therefore not apparent through the tests I conducted, remains a possibility. Nevertheless, this would not negate the prediction that response to risky situations would still likely be an important factor mediating niche specialisation in this species.

Another possible explanation, particularly for the finding that there is no relationship between intra-group behavioural variation and group size, is that larger groups are finding ways other than niche specialisation of avoiding the costs of increased resource competition. However, two factors argue against this. Firstly, larger groups deplete resources faster, but cannot expand their foraging range, likely due to the costs of travel between foraging sites and dependent young (Sorato, Griffith and Russell, 2016). Secondly, starvation is the primary cause of nest failure in babblers (Browning, Young, *et al.*, 2012; Russell, 2016). Together, these factors indicate that despite increased competition over resources in larger groups, babblers do not possess adequate strategies for overcoming this.

Finally, it is possible that my prediction regarding group size was overly simplistic. Most obviously, the validity of this prediction rests on the perhaps unrealistic assumption that the number of distinct niches available is sufficient to permit a positive association between behavioural dissimilarity and group size. If, individuals in small groups already benefit from foraging in different niches, and few distinct foraging niches occur overall, then we would actually be more likely to detect a negative association between behavioural dissimilarity and group size. This is for the simple reason, the larger the group, the more individuals must adopt one of the limiting number of niches; inevitably leading to greater behavioural similarity. Given that most of the correlations between behavioural dissimilarity and group size were negative, lends some support to this possibility.

In conclusion, understanding selection on, and limits to, increasing group size is a major question in social evolution that lies at the heart of explaining transitions to complex societies (Bourke, 1999). A key, but often, neglected part of the puzzle will inevitably lie with the ability for increasing numbers of individuals to secure sufficient sustenance. One means of doing so is through niche specialisation, as this will allow individuals to reduce foraging competition. However, testing this hypothesis directly is challenging in most social species, since detailed observations of foraging method and diet for individuals are close to impossible, with the notable exception of a few habituated study systems. Here I have used a novel indirect approach, based on the well-documented association between personality and foraging mode. Through doing so, I found some support for the suggestion that group-living might be facilitated by niche specialisation in chestnut-crowned babblers, but little support that niche specialisation facilitates increasing group sizes. Further work is required to elucidate the validity of these current conclusions.

CHAPTER 5

Limited evidence of niche specialisation in a cooperative-breeding bird.

5.1 ABSTRACT

Larger group sizes are thought to be critical for the emergence of more complex forms of sociality. But an inevitable challenge posed by larger group size is finding enough food for all individuals. Classic optimal foraging theory suggests that groups can respond in two ways to resource pressure generated by increasing numbers of individuals: groups can either increase the range of resources they utilise (i.e. become more generalist), or group-members can specialise to use different food-types. However, despite empirical evidence that both these strategies can be effective in reducing resource competition, few studies have yet explored these as facilitators of increasing group size in social species. Here, using the chestnut-crowned babbler (*Pomatostomus ruficeps*), a highly social cooperative bird, as my model system, I tested two hypotheses. The first was that individuals would specialise, relative to their group mates, in the prey types they utilised, and that the degree of specialisation would be greater in larger groups. Next, I tested the hypothesis that larger groups would utilise a greater range of prey types. Although I did find some evidence of specialisation within groups, differences among individuals were very low. Furthermore, there was no evidence that the degree of specialisation was related to group size. I also found no evidence that groups differed in the diversity of prey types they utilised, or that generalist foraging was associated with larger group sizes. Thus, I find no evidence that either of these strategies facilitate increasing group size in babblers. I suggest a likely explanation is that the highly challenging and unpredictable environment in which this species lives precludes greater generalisation, and selects against specialisation. I discuss the implications of these results with regard to the evolution of social complexity in vertebrates.

5.2 INTRODUCTION

A general prerequisite to increasing social complexity is a prior increase in group size (Bourke, 1999; Ferguson-Gow *et al.*, 2014; Dunbar, 2018). However, for group size to increase, the basic challenge of finding enough food for the growing numbers of individuals must be overcome (Korb and Heinze, 2016). One way this appears to be partly achieved in some primates, social insects and cooperative birds, is through home-range expansion (Snaith and Chapman, 2007; Goulson and Osborne, 2009; Duca and Marini, 2014). However, the capacity for such range increases can be constrained, due to high population density (Wrangham, Gittleman and Chapman, 1993), strong territoriality (Bateman *et al.*, 2015) and/or the costs of travel (Chapman, 1990; Chapman, Wrangham and Chapman, 1995; Snaith and Chapman, 2007). In these circumstances, alternative solutions, whereby groups optimise resource acquisition within a given area, might be expected. One such solution is to modify foraging niche and prey preferences: by becoming more specialist or more generalist, individuals within groups might be able to reduce competition with group members and so facilitate increases in group size.

Adopting a specialist diet relative to group mates can reduce foraging competition, and so facilitate increases in group sizes, for two related reasons (note that here the term specialisation can be seen as synonymous with others such as niche differentiation or niche partitioning, and refers to situations where individuals consistently utilise a narrow, and different range of resources, compared to others in their social group). First, and obviously, specialising in this way leads by definition to reduced dietary overlap with other group members (Roughgarden, 1972; Svanbäck and Bolnick, 2007). Second, specialising can also lead to improved efficiency in a given foraging niche, through the learning of specific skills in detection and/or handling (Pietrewicz and Kamil, 1979; Tebbich *et al.*, 2001). The two studies to my knowledge testing the here-named ‘intragroup niche-specialisation’ hypothesis provide broad support. In both banded mongooses (*Mungos mungo*) and European badgers (*Meles meles*), individuals within the same social groups differ significantly in their dietary niche (Robertson *et al.*, 2014; Sheppard *et al.*, 2018). Further, in mongooses, dietary specialisation increases with group size (Sheppard *et al.*, 2018), while in badgers, in larger groups, individuals that showed a higher degree of specialisation maintained a higher body condition (Robertson *et al.*, 2015). Thus the scant evidence to date suggests that dietary specialisation can mediate reductions in resource competition, and facilitate increasing group size in social vertebrates.

On the other hand, classic optimal foraging theory predicts that another way groups can overcome resource competition, is by individuals adopting broad foraging niches and generalist diets (Emlen, 1966; Macarthur and Pianka, 1966). Here, competition over resources is not reduced by individuals utilising different food types, but by individuals using a small amount of a wider range of shared resources. Research in bumblebees (*Bombus terrestris*) has provided recent empirical support for this hypothesis: Fontaine, Collin and Dajoz (2008) found that foragers became more generalist under increased forager density. Although generalists are likely to be outperformed by specialists in the use of learned foraging techniques (Tinker, Mangel and Estes, 2009), and can suffer greater interference competition (Case and Gilpin, 1974; Morse, 1974), this 'generalist-niche' hypothesis also has a number of advantages over the specialist-niche hypothesis outlined above for facilitating increasing group size in social species. For example, it is possible that groups comprised of generalist foragers are able to be more cohesive than those comprised of specialists, since competition for access to specific resources will be less intense (Stevenson and Castellanos, 2000). Thus, groups of generalists rather than specialists might be expected in species where group foraging is an important selective reason for group-living, which will include prey species living diurnally in open environments (Kre, 1999), and predators foraging on patchy prey (Pöysä, 1992). Further, groups of generalists might be expected to be favoured over groups of specialists in temporally variable environments, wherein the type of food available changes within and among years (Overington, Dubois and Lefebvre, 2008; Terraube *et al.*, 2011). Despite this logic, very few studies have explicitly tested whether generalist diets can facilitate increasing group size.

The aim of this study is to investigate whether, in the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*), individual foraging ecology consistently varies along a specialist-generalist axis, and whether this variation is mediated predictably by foraging competition. First, I investigate whether or not individuals show specialisation in their diet (based on food delivered to nestlings), and whether specialisation is positively associated with increasing group size. Second, I then investigate whether or not larger groups deliver a greater diversity of prey items, which would suggest larger groups are more generalist in their prey preferences; either because of increasing numbers of specialists or because individuals become more generalist in larger groups.

The chestnut-crowned babbler is a 50g, highly social cooperative passerine, found in the semi-arid and arid zone of South Eastern Australia. This species forages on a variety of invertebrates and small vertebrates (see Methods) and breeds in groups which can range in size from 2 – 15 adults (Browning, Patrick, *et al.*, 2012). Larger groups achieve higher reproductive success on average (Browning, Patrick, *et al.*, 2012), largely through their increased ability to meet the energetic demands of growing offspring and reduce their probability of starvation (Browning, Young, *et al.*, 2012; Russell, 2016). However, on the other hand, larger groups also deplete resources faster which leads to an increased loss of condition among group members in large groups (Sorato, Griffith and Russell, 2016). This latter effect presumably arises because range expansion is constrained during the breeding season by the energetic and predation costs of flying to and from the dependent young over increasing distances in open, arid habitat. For these reasons, there is expected to be strong selection on mechanisms to optimise resource-use within a given area. Here, I use this study system to test my two hypotheses: that larger groups will either become more specialist, or more generalist, in their foraging, in response to resource competition. I compare these against the null hypothesis that neither of these occur. I discuss the implications of my findings in the context of increasing social complexity among cooperative vertebrates.

5.3 METHODS

Fieldwork was conducted during the 2007 and 2008 breeding seasons, at Fowlers Gap Arid Zone Research Station, New South Wales, Australia (141°43′E, 31°05′S). The fieldsite is characterised by the classic open chenopod shrubland of the Australian arid zone: short saltbush (*Atriplex spp.*) and bluebush (*Maireana spp.*) of 20 cm to 1m high, interspersed with open ground, predominates, while trees are sparse and typically confined to water courses and drainage lines. Further, rainfall is highly erratic both within and among years, occurring in any month of the year and varying by up to an order of magnitude among years (median = 215 mm annually). Further details of the field site and the ecology of the study species, are provided elsewhere (Portelli *et al.*, 2009; Russell *et al.*, 2010; Sorato *et al.*, 2012; Russell, 2016). Fieldwork was carried out under the authority of the NSW National Parks and Wildlife Service and the Australian Bird and Bat Banding Scheme, with the approval of Macquarie University's Animal Care and Ethics Committee (licence no. 06/40A).

My hypotheses were tested using 1954 nest-provisioning visits, by 91 individuals from 27 breeding groups for which prey items were identified. This substantial quantity of provisioning data was made possible by the use of an automated camera system (see Browning, Young, *et al.*, 2012; Young *et al.*, 2013 for details). Briefly, a passive integrated transponder (PIT) tag, with a unique alpha-numeric code, was inserted subcutaneously along the flank of each bird. Because babblers breed in large dome-shaped nests, we were able to fit a cooper coil antenna to the entrance of each nest and a pen camera to the back; giving a view of the interior. Both the antenna and camera were attached to an LID650 decoder (TROVAN ™ Ltd), which was placed at the base of the tree (described in Young *et al.*, 2013). Each time a bird entered the nest, the coil sent an electronic signal to the decoder, recording the PIT tag number of the individual, along with the date and time, and triggering the camera, which then recorded for 1 min.

From the video data, I established that 3 broad prey types accounted for >85% of all food delivered. These were lepidoptera larvae (moth caterpillars; 41%), Araneae (mainly wolf spiders, Lycosidae; 24%) and coleopteran larvae (21%). Adult insects (largely crickets, Orthoptera) accounted for a further 12%, and a final category, labelled 'other', which was largely comprised of centipedes (Chilopoda) and small vertebrates (Scincidae, Gekkonidae, Agamidae), accounted for the final 2% of prey items. These prey have fundamentally different ecologies, and so require distinct foraging methods to obtain. Caterpillars and adult insects are generally gleaned from the surface of the ground and vegetation, while spiders, coleopteran larvae and prey types in the category 'other' are dug from beneath the earth or rocks (Portelli *et al.*, 2009; AF Russell pers. obs). To summarise, overall I identified 5 prey different prey types, which are obtained using two distinct foraging strategies.

I then used these data to test for among-individual differences in prey preferences and a link between these and group size. In particular, I hypothesised that if large group sizes are facilitated by, or drive specialisation, that there should be significant, consistent intragroup differences in the prey that adults delivered to nestlings, and that these differences should be greater in larger, compared with smaller groups. Further, I hypothesise that, conversely, larger groups might be more generalist, either because they comprise greater numbers of specialists which drive up overall prey diversity, or because individuals in larger groups are themselves more generalist. In this case, we might expect greater diversity of prey delivered in larger groups. While I use prey delivered to offspring to test my hypotheses, rather than prey eaten by adults, the former is justified while the latter is impossible (see also Powell and Taylor, 2017). Most importantly, we know that ratios of prey types delivered to offspring approximates those most commonly found in the habitat, although spiders (which are smaller) are more commonly delivered to young nestlings whereas beetle larvae (which are larger) are more commonly delivered to older nestlings (Browning, Young, *et al.*, 2012). Moreover, the nestling period is the time of greatest resource depletion in babblers, because foraging range is restricted and food requirements increased (Sorato, Griffith and Russell, 2016). Consequently, it is precisely the time when specialist or generalist foraging ecologies should be manifest across groups of increasing size.

Statistical analyses

All statistical analyses were conducted using R version 3.3.2 (R Core Team, 2016). To test my first hypothesis, that individuals will specialise relative to their group mates in the prey types they utilise, I used the rptR package version 0.9.1 (Nakagawa and Schielzeth, 2010). This package is generally used to assess personality variation, and calculates the relative proportion of the total variance accounted for within and among individuals. Thus, by taking each nest visit per individual as a repeat measure, I was able to test whether individuals within groups were consistently different from each other in their usage of particular prey types. I first extracted data for groups where I had provisioning records for ≥50% of group members, and so a good indication of the diversity of prey types the group on average foraged for (19 groups). Then, for each of these groups, I tested 5 different ways in which individuals could specialise to use specific prey, relative to their group-mates: specialising on any of the three dominant prey types delivered (caterpillars, beetle larvae or spiders), or specialising on 2 combinations of these: beetle larvae + caterpillars and beetle larvae + spiders. The first of these combinations was chosen because it comprises two commonly used prey types which are visually similar (both larva), and previous research has shown that foraging performance, *via* enhanced prey detection, can improve by forming a search-image (Pietrewicz and Kamil, 1979). The second was chosen because it comprises the two most common prey types obtained *via* the 'digging' foraging strategy. Thus, if individuals specialise to collect dug or gleaned prey, they would be expected to differ consistently in their use of these prey types. To test for foraging specialisation in these 5 categories, I ran generalized linear mixed models (GLMMs) with a logit link function and a binary error distribution (Nakagawa and Schielzeth, 2010), with the prey type(s) in question as the binomial denominator. In each model, I checked for an effect of chick age, and also the age, sex and status (dominant male, dominant female or helper) of the provisioning adult. Where any of these terms effected the fit of the model, they were included as covariates. In all repeatability analyses, individual was included as the random effect, permutations and parametric bootstrapping were both set at 1000 (Brust, Wuerz and Krüger, 2013; Rangassamy *et al.*, 2015) and confidence intervals were set at 95%. Likelihood ratio tests were used to test significance (Bolker *et al.*, 2009). One potential issue with this approach (i.e. conducting multiple analyses on small sub-sets of the data (5 analyses conducted per group, 27 groups, total = 135 analyses)), is that this greatly increases the probability of type one errors (i.e. false positive results). One way of avoiding this in this study would have been to conduct a single analysis, with individual ID nested within group fitted as the random term. This would maximise the power of the analysis, reduce the chance of type one errors and still effectively assess the relative behavioural consistency of each individual relative to their group mates. Unfortunately however, although extensive attempts were made to use this method, it was discovered that it is not currently possible to nest individual within group in the rptR package. Nevertheless, it would be desirable to find ways of achieving this in future. Finally, to test whether specialisation was effected by group size, where I found significant or near-significant ($p = <0.1$) intragroup variation in the use of a given prey type, in more than 5 groups, I ran Mann-Whitney-U tests, comparing the sizes of groups where I did, and did not find significant variation.

To test my second hypothesis, that larger groups will utilise a greater diversity of prey, I designated 5 prey types: each of the three most commonly delivered (caterpillars, beetle larvae and spiders), adult insects and ‘other’. This is somewhat different to other studies which have used diversity indices, which have commonly classified diversity to the species level (although see Powell and Taylor, 2017). This was not possible here, because the camera system used did not provide images of sufficient resolution to classify prey delivered to a finer scale. However, it is known from previous work that the diversity and abundance of different prey species is relatively low in this habitat (Browning, Young et al. 2012), and so to collect sufficient food, the prey types as categorised are likely to represent a realistic range of the viable foraging sources available. Once the 5 prey types had been identified, for each of the 19 groups where I had provisioning data for ≥50% of group members, I calculated the diversity of these prey types, averaged across days, utilised by each group. I did this using both Shannon’s and Simpson’s diversity indices. I then used a Spearman’s rank correlation to test whether the diversity of prey types utilised, based on Shannon’s index, was correlated with group size. Here, I used Shannon’s only, because Simpson’s takes less account of prey types that are infrequently used (Morris *et al.*, 2014). Given that we are interested in when such rarely used prey types are added to a groups’ diet, as I predict that this will be more common in larger groups, I decided that Shannon’s index was better suited for my purposes. However, I did also test whether the two indices gave comparable results, and found they were highly correlated (Spearman’s rank correlation of diversity score per group from each index: $r_s = 0.51$, $p = 0.025$).

5.4 RESULTS

Hypothesis 1: Individual foraging specialisation within groups, and the effect of group size.

First, for each of the 5 different ways in which individuals might specialise relative to their group mates, in at least 58% of groups, I found no evidence for consistent variation among individuals in their use of certain prey types. Moreover, across these prey types, there was no variation among individuals in >80% of groups (Table 5.1). In only two types of prey specialisation did I find significant or near-significant ($p = <0.1$) inter-individual variation in enough groups (>5) to allow me to test for differences among those where there was, and was not this variation. These were specialisation on caterpillars and specialisation on beetle larvae + spiders, where I found significant or near-significant variation in 8 and 6 groups respectively. I found evidence of specialisation in the other 3 possible prey-specialisations (beetle larvae, spiders, and caterpillars & beetle larvae (types of larva), in 0, 2 and 3 groups respectively (Table 5.1).

For the two forms of specialisation for which I have evidence in >5 groups (specialisation on caterpillars and specialisation on beetle larvae + spiders), the degree of inter-individual variation within groups accounted for between 2.7–17% and 3.8–24% of the total variance respectively. Further, despite group size ranging from 2-11 individuals (mean = 5.2, ±2.3 SD), there was no difference in the sizes of groups that did and did not show these inter-individual differences in the use of the given prey type (specialisation on caterpillars: $U = 44$, $Z = 0.041$ $p= 0.97$; specialisation on beetle larvae + spiders: $U = 25$, $Z = 1.18$, $p = 0.24$, Figs. 5.1 & 5.2). There was also no difference between groups that did and did not show this inter-individual variation, in the proportion of the overall prey delivered that was accounted for by these two prey type(s), indicating that a lack of specialisation was not due to a lack of availability (proportion of caterpillars: $U = 37.5$, $Z = 0.50$, $p = 0.62$; proportion of beetle larvae

+ spiders: U = 18, Z = 1.80, p = 0.072). So to summarise, I find limited evidence for low levels of specialisation in a minority of groups, but no evidence that this is related to group size.

Hypothesis 2: Larger groups utilise a greater diversity of prey types

With regard to my 2nd hypothesis, I found no significant difference among groups in the diversity of prey types utilised (ANOVA: f = 0.545, p = 0.91). Moreover, there was no correlation between group size and the diversity of prey a group utilised ($r_s = 0.278$, p = 0.250) (Fig. 5.3).

Table 5.1. Results of repeatability analyses (GLMM), testing for consistent differences among individuals within groups, in five different forms of niche specialisation. All repeatabilities given are using the link-scale. Results stated are from best-fitting model. All p-values calculated using the likelihood ratio test. Significant results are in **bold**. * indicates the level of significance. Near-significant results are in italics. Bottom row indicates the number and percentage of groups in which a significant or near significant result was found, for a given form of specialisation.

group ID	**specialise on beetle larvae**	**specialise on caterpillars**	**specialise on spiders**	**specialise on beetle larvae and spiders (dug prey)**	**specialise on caterpillars & beetle larvae (types of larva)**
CEB_07	R = 0.046 p = 0.5	**R = 0.027** **p = 0.049***	R = 0 p = 0.5	**R = 0.038** **p = 0.022***	R = 0.004 p = 0.408
CEJ_08	R = 0 p = 0.5	*R = 0.078* *p = 0.076*	R = 0 p = 0.5	R = 0.031 p = 0.24	R = 0 p = 0.5
CEK_07	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5
CEL_07	R = 0 p = 0.5	*R = 0.044* *p = 0.088*	R = 0.24 p = 0.27	**R = 0.24** **p = 0.014***	R = 0 p = 0.5
CEQ_07	R = 0 p = 0.5	*R = 0.41* *p = 0.068*	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5

CET_07	R = 0 p = 0.5	R = 0 p = 0.5	R = 0.02 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5
EFG_07	R = 0 p = 0.49	R = 0 p = 0.5	R = 0.03 p = 0.14	R = 0.013 p = 0.28	R = 0 p = 0.5
EFP_08	R = 0.038 p = 0.5	*R = 0.08* *p = 0.078*	R = 0.038 p = 0.5	*R = 0.082* *p = 0.076*	R = 0.03 p = 0.239
HSB_07	R = 0.14 p = 0.5	**R = 0.15** **p = 0.0081****	**R = 0.13** **p = 0.017***	**R = 0.20** **p = 0.0025****	**R = 0.13** **p = 0.026***
HSF_07	R = 0 p = 0.5	R = 0.13 p = 0.11	R = 0 p = 0.5	R = 0.13 p = 0.16	R = 0 p = 0.5
NFP_07	R = 0.01 p = 0.33	R = 0.028 p = 0.15	R = 0.19 p = 0.5	R = 0.034 p = 0.12	R = 0.027 p = 0.5
OFQ_07	R = 0 p = 0.5	R = 0.013 p = 0.42	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5
OFR_07	R = 0.02 p = 0.37	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5	R = 0.11 p = 0.15
OFR_08	R = 0 p = 0.5	R = 0 p = 0.5	R = 0.012 p = 0.48	R = 0 p = 0.5	R = 0.26 p = 0.12
OFS_07	R = 0 p = 0.5	R = 0.068 p = 0.101	*R = 0.099* *p = 0.061*	*R = 0.07* *p = 0.096*	*R = 0.076* *p = 0.092*
OFS_08	R = 0 p = 0.5	**R = 0.083** **p = 0.019***	R = 0.11 p = 0.5	R = 0.031 p = 0.17	R = 0.03 p = 0.17
SFE_07	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5	R = 0.009 p = 0.43
SFL_07	R = 0 p = 0.5	**R = 0.17** **p = 0.0018****	R = 0.021 p = 0.30	*R = 0.061* *p = 0.095*	**R = 0.13** **p = 0.015***
SFX_07	R = 0.053 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5	R = 0 p = 0.5
# sig/near sig results	**0** (0%)	**8** (42%)	**2** (11%)	**6** (32%)	**3** (16%)

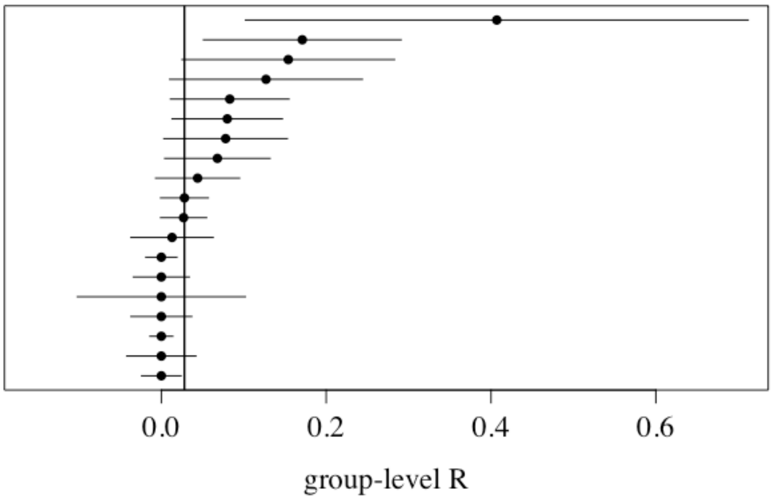


Figure 5.1. R scores indicating consistent differences among individuals in their use of caterpillars. Each point represents a different group. Vertical line = median score. Groups ranked by level of repeatability.

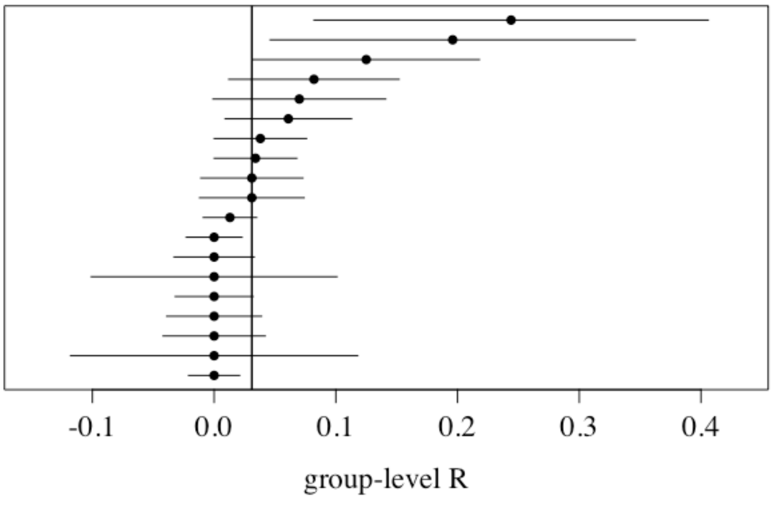


Figure 5.2. R scores indicating consistent differences among individuals in their use of beetle larvae + spiders. Each point represents a different group. Vertical line = median score. Groups ranked by level of repeatability.

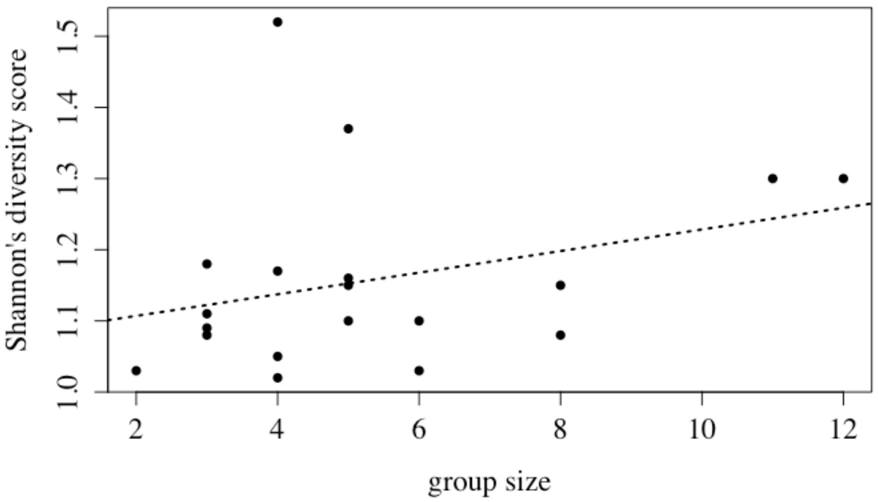


Figure 5.3. Correlation between group size and the diversity of prey types utilised (based on Shannon's index). The dotted line shows the trend of the relationship for clarity, but this relationship is not significant.

5.5 DISCUSSION

In this study, I have shown that in babblers, there is no evidence that larger groups utilise a greater range of food sources to overcome increased competition over resources (Fig. 5.3). I therefore do not find support for my hypothesis that in order to increase group size, larger groups will utilise a greater diversity of food-types. Furthermore, although I have found some evidence for niche specialisation, this was apparent in only a minority of groups (Table 5.1; Figs. 5.1 & 5.2) and was not correlated with larger group sizes. I therefore also find no clear evidence that niche specialisation is a viable means of overcoming the challenges of increasing group size in babblers.

One possible issue with this study is that my indicator of foraging niche, prey delivered to young in the nest, may not be a good proxy for what the adults are actually eating. For example, in green woodhoopoes (*Phoeniculus purpureus*), it was shown that breeding males selectively provisioned the incubating female with the largest prey items caught, perhaps because there is selection on breeding males to minimise the time the incubating female spends off the nest, as this increases the chances of the chicks hatching successfully (Radford, 2009). However, this study also found that helpers allo-fed different prey types in the same proportions as they ate them, suggesting that for most individuals provisioning prey can mirror foraging prey. In chestnut-crowned babblers, the prey provisioned to offspring by each individual is expected to reflect broadly the prey found. For example, we have found previously that spiders are not more likely to be delivered to young nestlings than expected based on their availability in the habitat (Browning, Young et al. 2012). Second, we have no evidence to suggest that babblers forage differently during breeding or non-breeding, and certainly not that babblers preferentially forage on large prey that are difficult for nestlings to handle, e.g. lizards. Finally, even if selective provisioning were occurring in babblers, consistent differences (or a lack thereof) among individuals in the prey they deliver to young would still be highly relevant with respect to optimising resource use. In fact, it would be another form of niche specialisation, and could be an important way of optimising resource use, at a time when pressure on resources is greatest. Another possible issue, which could explain why the evidence for foraging niche specialisation is so limited, is that the way in which prey items were classified was too coarse. In this study, prey were categorised into 5 broad groups (caterpillars, beetle larvae and spiders, adult insects and ‘other’), rather than to the species level, as is more common in analyses of prey diversity. The reason for this was two-fold: firstly, the resolution of images from the nest cameras did not allow more prey to be classified more finely, and secondly, all prey items within each of the categories are found in the same areas and gathered using the same foraging technique: all caterpillars and adult insects are gleaned from the surface of vegetation, while all beetle larvae and spiders are dug from beneath the earth or rocks (Portelli *et al.*, 2009). Thus, it is hard to conceive how and why foraging birds would reject palatable caterpillars of one species for example, and target only those of another. This seems particularly unlikely given that the abundance of single species is not expected to be sufficient to meet a babbler's energetic demands (Browning, Young et al. 2012). Nevertheless, if babblers were making such distinctions, it would indeed be possible for individuals to specialise at a finer level than the prey classifications used in this study. To test this possibility, it would be interesting to conduct prey-choice tests, offering alternative food types within each of the prey categories used here (for example, different species of caterpillar), under controlled conditions, to see whether individuals showed a consistent preference for a particular species. For now however, the possibility that the prey classifications missed finer-scale specialisation must be borne in mind, when considering the results. This is particularly relevant to section 3 of the Discussion below. A final potential issue to address is that I failed to find strong evidence for specialisation because the analyses were underpowered, as a result of conducting analyses on small sub-sets of data. The amount of data in each sub-analysis (i.e. the number of nest visitations per group member) was highly variable (range of nest visitations per bird = 1-99). This means that although in some analyses it is likely that power was sufficient, in others a lack of power may have been an important factor. One way to assess this would be to conduct a power analysis, which would enable me I identify when power was lacking, and so reduce the chance of type 2 errors (false negatives). An alternative, and I suggest more appropriate method would be to combine all data into a single analysis, with individual nested within group. This would increase power, reducing the chance of type two errors (a power analysis could still be used to confirm this), while also addressing the issue of conducting multiple analyses, and thus the chance of type one errors, as discussed in the Methods above. As outlined, this approach is not currently possible in the rptR package, but should be investigated further for future studies.

With these considerations in mind, and despite predictions based on classic optimal foraging theory, that competition generated by larger group sizes can be reduced by increasing the diversity of prey types utilised (Emlen, 1966; Macarthur and Pianka, 1966), I find no evidence to support my hypothesis that larger groups use a greater diversity of prey. I suggest a likely explanation is the temporally variable environment characteristic of the Australian outback. Because rainfall is so variable in extent and timing within and among years, and different food items are associated with each, babblers might be selected to be highly generalist irrespective of the size of group in which they currently live. Under this hypothesis, even small breeding units would already be using all available food sources; meaning that no new food-types are available to be added to the groups' diet as group size increases. This is supported by my finding that overall, there was no difference among groups is the diversity of prey utilised, irrespective of group size. I infer from this that babbler groups in general utilise the same, and likely the maximum possible, range of resources.

So given that larger groups do not appear to become more generalist, this might strengthen my alternative hypothesis, that larger groups reduce foraging competition *via* niche specialisation. However, although I did find some evidence for low levels of specialisation, this was only apparent in a minority of groups and was not associated with larger group sizes (Figs. 5.1 & 5.2). This indicates that groups are not specialising in response to higher levels of resource pressure generated by increasing group size and poses 3 important questions. Firstly, where I do find some evidence of specialisation, why is this not associated with larger group sizes? Secondly, how else can we explain why I find evidence for niche specialisation in some groups but not others? And finally, why is variation among individuals in groups with some evidence of niche specialisation not greater?

1) Why is niche specialisation not associated with larger group sizes?

From the video analysis, I have shown that babblers rely on 3 key food types (or a combination thereof), but the modal group size was 5 (mean = 5.2). This means that in most groups, it is not possible for all individuals to target different prey types, and for group sizes above average, there will inevitably be increasing overlap among individuals. Thus, I suggest that the capacity of larger groups to specialise is constrained by the same factor as that which constrains their capacity to become more generalist: a limited number of temporally-variable prey types are available, and these are already being fully exploited.

2) Why else might we find evidence for niche specialisation in some groups but not others?

Given that I find evidence for low levels of niche specialisation in some groups but not others (Table 5.1), but this cannot be explained by group size, the obvious question is, what else could explain this? One possibility, given I found that groups tended to specialise on only certain prey types (i.e. caterpillars and beetle larvae + spiders), is that these prey types are differentially available in different territories. However, this is unlikely, because I found no difference among groups in the overall proportion of prey delivered, that was accounted for by these two prey types. Another possibility is that differences can be explained by group composition. For example, perhaps different sexes or age-classes forage for different prey types and groups contain a different proportion of these individuals. Previous studies have shown that niche segregation by sex, seen in various species, is commonly mediated *via* sexual dimorphism and/or social dominance (Radford and Du Plessis, 2003; Chazarreta, Ojeda and Lammertink, 2012). However, babblers are sexually monomorphic. Moreover, as discussed, babbler prey typically requires two alternative foraging strategies: gleaning prey from the surface of the ground or vegetation and digging for prey under rocks or earth (Portelli *et al.*, 2009). When I categorise prey based on how they are obtained, I find no difference between the sexes in the prey types they target. Meanwhile, niche segregation might be based on age if foraging for a given food-type requires learning, and older individuals are therefore more successful in obtaining it (Marchetti and Price, 1989). However, here I find that differences between age-classes accounted for only 0.4% of the total variance among individuals, when prey types were categorised as above. Having accounted for group size, the availability of prey types on which individuals specialise and differences in group-composition, a final possibility is that some of the variation is explained by variation in personality differences within and among groups, but further work is required to test this hypothesis.

3) Why is variation among individuals, in groups with some niche specialisation, not greater?

Despite finding significant, consistent intragroup differences, in >5 groups, in the use of two different forage-types (caterpillars and beetle larvae + spiders), for both forage-types the degree of variation among individuals still only accounted for between 3–17% and 3–24% of the total variance respectively. This means that even in the groups that showed the highest levels of specialisation, individuals still overlapped to a large extent in the prey they utilised (Table 5.1). There could be various reasons for this. Firstly, it is possible that the prey classifications were too broad to capture specialisation, if this occurred at a finer level. However, as I discuss above, I do not feel this is likely. Secondly, because babblers forage in groups within the same general area, perhaps opportunities to utilise different resources are limited. To specialise, maybe you need to be an independent forager, as with the European badger (Kruuk, 1978)? However, Bolnick *et al.* (2002) highlight that niche specialisation can manifest *via* subtle differences in foraging niche, a point illustrated by both green woodhoopes and banded mongooses, which also forage in groups, in close proximity to each other, and yet still achieve niche specialisation (Radford and Du Plessis, 2003; Sheppard *et al.*, 2018). Babbler territories contain a high degree of fine-scale habitat heterogeneity, with trees and shrubs immediately adjacent to open rocky areas (Portelli *et al.*, 2009) and thus offer a range of alternative foraging niches within a small area. In green woodhoopes, niche specialisation is achieved by individuals foraging in different microhabitats which required different foraging strategies (Radford and Du Plessis, 2003), and this seems to be what we find in babblers. In the most frequent manifestation of specialisation, certain individuals either specialise on caterpillars, or on beetle larvae + spiders, and these two forage-types occur in different microhabitats and require distinct foraging strategies (the former are gleaned from the surface of the ground and vegetation, while the latter are generally dug from under rocks or earth (Portelli *et al.*, 2009)). This shows that foraging in groups does not, by itself, preclude niche specialisation in this species.

Instead, I suggest a more critical issue is that in such a challenging environment, no single resource is abundant or predictable enough by itself to sustain an individual. With regard to abundance, that babblers rely on a limited number of often scarce food-types, means that niche overlap is inevitable. Meanwhile, specialising on unpredictable resources is highly risky, as evidenced by work in two closely related, sympatric species of raptor: the Montagu's harrier (*Circus pygargus*), which is a generalist forager, and the pallid harrier (*Circus macrourus*) which is a vole specialist. Terraube *et al.* (2011) found that although the intake-rate of pallid harriers was 40% higher than Montagu's when voles were abundant, it was 50% lower when voles were scarce. In the areas inhabited by babblers, a key determinant of prey availability is rainfall. Previous work has shown that rainfall at different times brings out different types of prey (Sorato, Griffith and Russell, 2016). However, the timing of rainfall is highly unpredictable (Russell, 2016). Thus, it seems likely that in babblers, the capacity for niche specialisation in general, and particularly in larger groups, is constrained by the challenging and unpredictable nature of this environment.

The apparent constraints on niche specialisation, and therefore increasing group size, imposed by challenging and unpredictable environments, have important implications for the rise of social complexity in this species, and in avian taxa generally. Increasingly it is thought that there is an association between unpredictable environments and cooperative breeding in birds, which as I have discussed represents the most socially complex form of group-living in this class (Jetz & Rubenstein 2010; Griesser *et al.* 2017; Shen-Fen *et al.* 2017). And yet, my results suggest that these very conditions select against foraging specialisation, which is likely to inhibit increasing group size above a certain threshold. Moreover, other ways of increasing resource acquisition, such as increasing foraging range, are likely to be prohibited in cooperative breeders generally, due to the limited distance individuals can forage from dependent young (Sorato, Griffith and Russell, 2016). The implication is that the factors which select for basic forms of complex sociality in birds, and those which enable this complexity to increase, are antagonistic, and this may explain why birds do not show higher forms of social complexity. This idea is gaining increasing support. For example, Sheppard *et al.* (2018) suggest that the capacity to specialise in foraging niche may be a necessary precondition for group living. I therefore suggest that the link between (un)predictable environments, capacity for niche specialisation, group size and relative social complexity, merits further investigation across avian taxa.

CHAPTER 6

General conclusion.

6.1 Overview

In the main chapters of this thesis, I first conducted a review, in which I explored the role of individual specialisations in overcoming one of the principle challenges to increasing group size, and thus to the emergence of social complexity: finding enough food for increasing numbers of individuals (Chapter 2). Specifically, I discussed the possibility that when range-size is constrained, meaning that to obtain more food, groups must find ways to do so more efficiently within a given area, 3 forms of specialisation might be key in optimising resource acquisition. These are (1) foraging niche specialisation, (2) specialising to a particular role under division of labour (DoL) and (3) as a mediator of these two, personality variation (described by some as behavioural specialisation (Dall *et al.*, 2012)). I began Chapter 2 by reviewing the evidence so far, that niche specialisation in social species can be affected by personality variation. I then went on to give 3 examples where niche specialisation has been shown in social species, and discuss in detail how such specialisations could be mediated *via* personality variation. Next, I turned to DoL. I discussed examples in social insects, non-human vertebrates and humans in turn, focussing on the potential for personality variation to act as a mediator in each case. Where previous research has directly explored the link between DoL and personality variation, this was discussed. In the more common case where no research has yet directly explored such a link, I hypothesised how this link might manifest, using evidence from the personality literature. To conclude this chapter, given that niche specialisation is likely to precede DoL, as it will facilitate increases in group sizes such that DoL can develop, I suggested 3 factors which may constrain the emergence of niche specialisation, and thus any subsequent rise in social complexity. Overall, I found that although research into the link between personality variation and both niche specialisation and DoL is still in its early stages, there is good evidence to expect such a link to be widespread. I therefore suggest that personality may play an underappreciated role in increasing group size and so in the rise of social complexity. Moreover, I suggest that constraints on niche specialisation may, in part, explain instances where more complex forms of sociality have not developed.

Then, in Chapters 3-5, using the chestnut-crowned babbler (*Pomatostomus ruficeps*) as my model system, I set out to empirically test some of the hypotheses and predictions outlined in Chapter 2. In Chapter 3, I show that babblers have personality variation, but that standardised assays typically used to assess variation in a range of traits are not appropriate in this highly skittish, neophobic species. Instead, my experiments reveal that babblers show consistent differences in an underlying behavioural trait, 'response to novel environments and/or potentially risky situations', which nevertheless, as I go on to explore in more detail in Chapter 4, is expected to have a major bearing on individuals' use of different foraging niches, and thus, in principle at least, on the capacity of this species to respond *via* niche specialisation to resource competition generated by increasing group size.

Next, in Chapters 4 and 5, I investigate evidence for niche specialisation, and a link with personality variation and group size, in my model system. In Chapter 4, I test two key predictions of the hypothesis that personality variation among individuals within groups will present a viable means through which this species can overcome competition over resources as group size increases. These are that (1) individuals within groups should be relatively dissimilar in their personality 'types', and (2) dissimilarity should increase with group size (a metric of resource competition). I found some support of the first of these predictions, in that, although in general individuals within groups showed significant similarity in their personality 'types', repeatability estimates were relatively low, indicating that there is sufficient behavioural variation within groups to facilitate niche specialisation. However, I found no evidence for a higher level of behavioural dissimilarity in larger groups, suggesting that niche specialisation does not facilitate increasing group size in this species.

Continuing the line of investigation begun in Chapter 4, in Chapter 5 I further explored patterns of foraging ecology and group size in babblers. Here, using a direct indicator of foraging niche (prey delivered to young in the nest), I tested two related hypotheses regarding how groups might optimise resource acquisition within a given area, in response to resource competition. The first hypothesis was that individuals would specialise, relative to their group mates, in the prey types they delivered to nestlings, and that specialisation would be positively associated with increasing group size. Next, I tested the hypothesis that larger groups would deliver a greater diversity of prey types. This would indicate that larger groups are more generalist in their foraging, either because individuals become more generalist in larger groups, or because of increasing numbers of specialists. I found evidence that in some groups, individuals did specialise to some extent in the prey types they used, relative to their group mates. However, variation among individuals in these groups was generally very low. Moreover, as in Chapter 4, I found no evidence that differences among individuals increased with group size. These results further suggest that niche specialisation is not a means through which babblers are able to achieve larger group sizes.

Several key points emerge from the studies outlined above. In the following sections, I discuss these points and possible directions for further research.

6.2 Niche specialisation and DoL, mediated by personality variation, could be key to increasing group size in social species

Although very much an emerging area of study, there is growing evidence to suggest that personality variation could play a key role in mediating both foraging niche specialisation, and DoL, in social-living species. Thus, this could be an as yet underexplored factor in increasing group size, and ultimately the rise of social complexity. In a recent review, Toscano *et al.* (2016) proposed 5 main pathways through which personality could affect niche specialisation:

(1) influencing activity levels during foraging; (2) varying responses to risk; (3) social factors; (4) spatial factors and (5) physiological drivers of foraging niche. This provides a framework for further study. Meanwhile, although much less work has so far explored personality variation as a mediator of DoL, here too, studies are beginning to emerge (see Kühbandner, Modlmeier and Foitzik, 2014; Pamminger *et al.*, 2014; Wright, Holbrook and Pruitt, 2014). Moreover, in both vertebrate and invertebrate examples of DoL in which no link with personality variation has yet been made, personality theory suggests that the latter could be predicted to affect observed labour divisions. DoL represents one of the highest forms of social complexity, and further investigation into the potentially important role that personality variation may play in its rise, could greatly increase our understanding of how and when this phenomena does, and does not, emerge. As I have shown in Chapter 3 (also see 6.3 below), the study of personality variation is also in development. One critical element in this development will be to apply what we are discovering about consistent differences in behaviour, to novel socio-ecological contexts. Niche specialisation and DoL represent a potentially exciting avenue of investigation in this regard.

6.3 Issues with the use of standardised assays in neophobic and skittish species

During the past two decades, there has been a proliferation of research into personality variation, and this phenomena has now been explored in a diverse array of taxa, ranging from invertebrates to humans (Nettle, 2006; Kralj-Fišer and Schuett, 2014). This research has revealed that personality variation can have important evolutionary and ecological consequences, and in an effort to identify general patterns, and allow comparisons across taxonomic groups, there has been a move to establish a standardised methodology through which personality variation can be assessed. While, in general, this is a desirable development, several issues have also been raised with this standardised approach (e.g. Burns, 2008; Dammhahn and Almeling, 2012; Beckmann and Biro, 2013; Carter *et al.*, 2013; Kerman *et al.*, 2016). One such issue, which so far has largely been overlooked, is that species-specific socio-ecology can be an important consideration in how behavioural responses to standardised assays are captured and interpreted. In particular, it is likely that different species will perceive the same assay in different ways (Carter *et al.*, 2013). In Chapter 3 of this thesis, for example, I have shown that in the highly neophobic and skittish chestnut-crowned babbler, the artificial testing conditions presented by commonly used personality assays are likely to all be associated with a high level of risk. Thus in this case, these tests appear to elucidate variation in response to such risky situations, rather than in the range of personality traits which they have previously been used to test, generally labelled boldness, exploration and activity level (Brown, Jones and Braithwaite, 2005; Quinn and Cresswell, 2005; Guillette *et al.*, 2009; Julien Cote *et al.*, 2010; Le Vin *et al.*, 2011; Edelaar *et al.*, 2012; Kerman *et al.*, 2016; Perals *et al.*, 2017).

Misinterpreting behavioural responses to standardised assays, due to a failure to take socio-ecology and temperament into account, could have two main implications. First, it could lead to false inferences regarding the likely way observed personality variation will manifest in ecologically relevant situations. Take one of the behavioural measures I used in the novel-environment assay as an example. In great-tits (*Parus major*), research indicates that individuals that make more movements in a standardised arena are those that are more willing to enter novel and potentially risky environments, being both more dispersive and more likely to locate new foraging patches (Dingemanse *et al.*, 2003; van Overveld and Matthysen, 2010). In contrast, in babblers it seems that making more movements indicates aversion to such novel and potentially risky situations (Chapter 3). Thus, this leads to a different set of hypotheses regarding how highly ‘active’ individuals will behave in socio-ecological contexts such as dispersal, or foraging under predation risk: in babblers, individuals that make more movements would be predicted to be less dispersive and forage in known areas with lower risk.

Second, misinterpreting behavioural responses to standardised assays could impair comparative assessments of personality variation across species, and thus our ability to identify general patterns regarding the selective drivers of personality, and it's role in ecological and evolutionary processes (Dingemanse and Réale, 2005; Kralj-Fišer and Schuett, 2014). For example, another of the assays I conducted, latency to enter a novel environment, has often been used as a measure of willingness to be exposed to risk (i.e. boldness): shorter latencies are generally taken to indicate relative boldness (Brown, Jones and Braithwaite, 2005; Cote *et al.*, 2010; Beckmann and Biro, 2013; Kerman *et al.*, 2016; Perals *et al.*, 2017). However, in babblers, associations between this and other behaviours suggest that shorter latencies in fact indicate relative aversion to risky situations (Chapter 3). Had I accepted the 'classic' interpretation of latency, and in a subsequent study comparing latency to enter a novel environment with boldness towards a predator, found that short latencies were negatively associated with willingness to approach the predator, I might have erroneously concluded that in this species, the evolutionary drivers of boldness in a novel environment and boldness towards predators were uncoupled.

The past two decades have seen personality variation transition from a peripheral field of study, viewed by some with marked scepticism, to an important part of evolutionary and behavioural ecology research. However, it is still a developing field, and ultimately of course, the relevance any field depends on reliable results. Researchers must therefore respond dynamically to challenges to established methodological paradigms.

6.4 Consistent differences in an inconsistent environment: foraging ecology in a cooperative breeding bird

A main aim of this thesis was to investigate the relationship between foraging ecology and group size in my model study system, the chestnut-crowned babbler. This is a species which expresses a high degree of sociality, and in which selection on increasing group size would be expected. Thus, this is a prime system in which to test predictions regarding the factors mediating group size in social vertebrates. In Chapter 5, I used a direct measure of foraging niche (prey delivered to nestlings) to investigate the foraging ecology of this species, at the intra-group level. I found that 3 types of prey accounted for the vast majority of food delivered, and that these tended to be obtained through two foraging techniques. Thus I identified the range of resources utilised, and also two ways in which babblers could, in principle, specialise to a foraging niche: (1) specialising to a prey type or (2) specialising to a foraging technique. I predicted that to reduce competition, larger groups might either utilise a greater range of resources, or show a higher degree of niche specialisation within groups. However, analysis showed that there was no difference among groups in the range of prey types utilised. Further, in only a minority of groups were individual differences in foraging niche apparent, and where they were, variation among individuals was very low. Moreover, there was no relationship between the degree of inter-individual variation and group size. We are therefore presented with 2 questions: why is there no relationship between group size and either generalisation or specialisation, and why do we only find limited evidence of consistent niche specialisation within groups *per se*?

The first of these questions is likely explained by the number of foraging niches which are available. The finding that babblers did utilise a wide variety of prey types, but that only 3 constituted the vast majority of food delivered to young, suggests that babblers in general are already exploiting the full range of available prey, but that only 3 of these occur in abundance.

Thus, there is no opportunity for groups, large or small, to add new prey types to their diet. Meanwhile, that the modal size of groups in this study was 5 (mean = 5.2) shows that that in most, it is not possible for all individuals to specialise on different resources, and the degree of overlap among individuals will inevitably be greater in larger groups.

Next, I suggest that the low levels of intragroup specialisation, and the lack of evidence for increasing generalisation in larger groups, are likely explained by the highly unpredictable nature of the babblers' environment. Which prey are available, and when, is contingent on rainfall, which is highly erratic (Russell, 2016; Sorato, Griffith and Russell, 2016) and both theoretical and empirical research predicts that there will be selection against specialising on unpredictable resources (Overington, Dubois and Lefebvre, 2008; Terraube *et al.*, 2011). Meanwhile, adopting a generalist foraging strategy is contingent on there being an array of prey types of sufficient abundance available. This is because to avoid competition *via* generalisation, each individual must meet their energetic demands by sampling from a range of prey types, while not exhausting any one: a strategy which may not be possible in unpredictable and/or harsh environments, where species (and thus prey) diversity is commonly lower (Connell, 1980).

Thus it seems that the lack of either generalist or specialist foraging strategies, in response to competition generated by increasing group size, is due to the harsh, unpredictable environment in which babblers live. This has important implications for the rise of social complexity in social vertebrates generally.

6.5 Comparing vertebrate and invertebrate sociality

Given that increasing evidence suggests that intragroup foraging specialisations can be important in increasing group size, and thus in the rise of social complexity in vertebrates, it is interesting to compare vertebrate systems with social insects, which achieve large group sizes and advanced forms of social complexity, generally without such specialisations. I suggest there are two key and related factors which differ between vertebrates and social insects, which may explain this apparent contradiction. Firstly, insects have lower energetic requirements, meaning that food availability is less often a constraint on group size. This is illustrated by the relative energetic requirements of a social insect such as the fire ant (*Solenopsis invicta*), compared with a small passerine bird: the latter has been found to use 0.96 kcal per day, per gram, while the former requires only 0.16 kcal per day, per gram of colony biomass (Macom and Porter, 1995; DEFRA, 2002). Secondly, the fecundity of reproductives in social insects means that group sizes can increase rapidly to the level where full division of labour can develop (Tschinkel, 1988), at which point it becomes more efficient for a particular caste of workers to gather food for the whole colony, rather than for each individual to forage independently (Arnan *et al.*, 2011; Ferguson-Gow *et al.*, 2014). For these reasons, I suggest the role of intragroup foraging niche specialisation to is likely to be specific to vertebrate societies.

6.6 Broader implications for vertebrate sociality

In the introduction to this thesis (Chapter 1), I posed a question: what are the constraints on social complexity in vertebrates? Given that, with the exception of primates, the most complex vertebrate examples of sociality tend to be cooperative breeders, and that larger group sizes are thought to be a critical precursor to more complex forms of sociality (Bourke, 1999; Ferguson-Gow *et al.*, 2014; Dunbar, 2018), in essence this question becomes, what are the factors mediating group size in cooperative vertebrates? In this thesis, I have found evidence to suggest that a key constraint on the capacity of chestnut-crowned babblers to develop ways of reducing the costs of increasing resource competition, caused by increasing group size, is the unpredictability and harshness of their environment. Increasingly, evidence suggests that there is a general association between cooperative breeding in vertebrates and such challenging environments. This means that, the conditions which drive the rise of basic forms of social complexity, and those which might lead to more complex forms, are antagonistic to one-another. Further research is required to explore this in a greater number of species, but if these patterns do prove to be general, returning back to the initial question posed, it seems that this paradox may be a critical element constraining the rise of social complexity in vertebrates.

REFERENCES

Anderson, C., & Ratnieks, F. L. W. (1999). Task partitioning in insect societies. I. Effect of colony size on queueing delay and colony ergonomic efficiency. *The American Naturalist*, *154*(5), 521–535.

Arnan, X., Ferrandiz-Rovira, M., Pladevall, C., & Rodrigo, A. (2011). Worker size-related task partitioning in the foraging strategy of a seed-harvesting ant species. *Behavioural Ecology and Sociobiology*, *65*, 1881-1890.

Arnold, K. E., Owens, I. P. F., & Goldizen, A. W. (2005). Division of labour within cooperatively breeding groups. *Behaviour*, *142*(11/12), 1577–1590.

Ashton, B. J., Ridley, A. R., Edwards, E. K., & Thornton, A. (2018). Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature*, *554*, 364.

Barrick, M. R., & Mount, M. K. (1991). The big five personality dimensions and job performance: a meta-analysis. *Personnel Psychology*, *44*, 1–26.

Bateman, A. W., Lewis, M. A., Gall, G., Manser, M. B., & Clutton-Brock, T. H. (2015). Territoriality and home-range dynamics in meerkats, *Suricata suricatta*: a mechanistic modelling approach. *Journal of Animal Ecology*, *84*, 260–271.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Bebbington, K., & Hatchwell, B. J. (2016). Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology*, *27*(2), 652–659.

Beckmann, C., & Biro, P. A. (2013). On the validity of a single (boldness) assay in personality research. *Ethology*, *119*(11), 937–947.

Bell, A. M. (2007). Future directions in behavioural syndromes research. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1611), 755–61.

Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*(4), 771–783.

Bell, A. M., & Sih, A. (2007). Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, *10*(9), 828–834.

Bennett, A. F. (1987). Interindividual variability: an underutilized resource. In M. E. Feder, A. F. Bennett, W. W. Burggren, & R. B. Huey (Eds.), *New directions in ecological physiology* (pp. 147–169). Cambridge, UK: Cambridge University Press.

Bergmüller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, *25*, 504–511.

Biro, P. A. (2012). Do rapid assays predict repeatability in labile (behavioural) traits? *Animal Behaviour*, *83*, 1295–1300.

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, *23*(7), 361–368.

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology & Evolution*, *25*(11), 653–659.

Blumstein, D. T., & Daniel, J. C. (2003). Red kangaroos (*Macropus rufus*) receive an antipredator benefit from aggregation. *Acta Ethologica*, *5*, 95–99.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135.

Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M., & Svanbäck, R. (2002). Measuring individual-level resource specialization. *Ecology*, *83*(10), 2936–2941.

Bourke, A. F. G. (1999). Colony size, social complexity and reproductive conflict in social insects. *Journal of Evolutionary Biology*, *12*, 245–257.

Briffa, M., Rundle, S. D., & Fryer, A. (2008). Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1640), 1305–11.

Brotherton, P. N. M., Clutton-Brock, T. H., O'Riain, M. J., Gaynor, D., Sharpe, L., Kansky, R., & McIlrath, G. M. (2001). Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioral Ecology*, *12*(5), 590–599.

Brown, C., Jones, F., & Braithwaite, V. (2005). In situ examination of boldness–shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, *70*(5), 1003–1009.

Browning, L. E., Patrick, S. C., Rollins, L. A., Griffith, S. C., & Russell, A. F. (2012). Kin selection, not group augmentation, predicts helping in an obligate cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 3861–3869.

Browning, L. E., Young, C. M., Savage, J. L., Russell, D. J. F., Barclay, H., Griffith, S. C., & Russell, A. F. (2012). Carer provisioning rules in an obligate cooperative breeder: prey type, size and delivery rate. *Behavioural Ecology and Sociobiology*, *66*, 1639–1649.

Brust, V., Wuerz, Y., & Krüger, O. (2013). Behavioural flexibility and personality in zebra finches. *Ethology*, *119*(7), 559–569.

Burns, J. G. (2005). Impulsive bees forage better: the advantage of quick, sometimes inaccurate foraging decisions. *Animal Behaviour*, *70*(6), e1–e5.

Burns, J. G. (2008). The validity of three tests of temperament in guppies (*Poecilia reticulata*). *Journal of Comparative Psychology*, *122*(4), 344–356.

Burns, J. G., & Dyer, A. G. (2008). Diversity of speed-accuracy strategies benefits social insects. *Current Biology*, *18*(20), R953–R954.

Careau, V., & Garland, T. (2012). Performance, personality, and energetics: correlation, causation, and mechanism. *Physiological and Biochemical Zoology*, *85*(6), 543–571.

Careau, V., Thomas, D., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, *117*(5), 641–653.

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, *88*(2), 465–475.

Carter, A. J., Marshall, H. H., Heinsohn, R., & Cowlishaw, G. (2014). Personality predicts the propensity for social learning in a wild primate. *Peer J*, *2*, e283.

Case, T. J., & Gilpin, M. E. (1974). Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America*, *71*(8), 3073–3077.

Chapman, C. A. (1990). Ecological constraints on group size in three species of neotropical primates. *Folia Primatologica*, *55*(1), 1–9.

Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, *36*, 59–70.

Chazarreta, L., Ojeda, V., & Lammertink, M. (2012). Morphological and foraging behavioral differences between sexes of the Magellanic woodpecker (*Campephilus magellanicus*). *Ornitologia Neotropical*, *23*, 529–544.

Chittka, L., Dyer, A. G., Bock, F., & Dornhaus, A. (2003). Bees trade off foraging speed for accuracy. *Nature*, *424*(6947), 388.

Clarke, F. M., & Faulkes, C. G. (2001). Intracolony aggression in the eusocial naked mole-rat, *Heterocephalus glaber*. *Animal Behaviour*, *61*, 311–324.

Cockrem, J. F. (2007). Stress, corticosterone responses and avian personalities. *Journal of Ornithology*, *148*, 169–178.

Coleman, K., & Wilson, D. S. (1998). Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, *56*(4), 927–936.

Connell, J.H. (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, *35*, 131–138.

Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A., & Griffin, A. S. (2017). Cooperation facilitates the colonization of harsh environments. *Nature Ecology & Evolution*, *1*(57).

Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 383–90.

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 4065–4076.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T., & Sih, A. (2010). Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1571–1579.

Covas, R., & Griesser, M. (2007). Life history and the evolution of family living in birds. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 1349–1357.

Crane, J. M. S., Savage, J. L., & Russell, A. F. (2016). Diversity and function of vocalisations in the cooperatively breeding chestnut-crowned babbler. *Emu*, *16*(3), 241–253.

Creel, S., & Marusha Creel, N. (1995). Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, *50*, 1325–1339.

Dall, S. R. X., Bell, A. M., Bolnick, D. I., & Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, *15*(10), 1189–1198.

Dall, S. R. X., Houston, A. I., & McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*(8), 734–739.

Dammhahn, M., & Almeling, L. (2012). Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Animal Behaviour*, *84*, 1131–1139.

Darimont, C. T., Paquet, P. C., & Reimchen, T. E. (2009). Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *Journal of Animal Ecology*, *78*, 126–133.

Darwin, C. (1859). On the origin of the species by natural selection.

David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour*, *81*, 219–224.

Denny, A. J., Wright, J., & Grief, B. (2001). Foraging efficiency in the wood ant, *Formica rufa*: is time of the essence in trail following? *Animal Behaviour*, *62*(1), 139–146.

Dingemanse, N. J., Both, C., Drent, P. J., Oers, K. Van, & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, *64*, 929–938.

Dingemanse, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*, *270*(1516), 741–747.

Dingemanse, N. J., Bouwman, K. M., van de Pol, M., van Overveld, T., Patrick, S. C., Matthysen, E., & Quinn, J. L. (2012). Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *Journal of Animal Ecology*, *81*(1), 116–126.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., & Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, *76*(6), 1128–1138.

Dingemanse, N., & Réale, D. (2005). Natural selection and animal personality. *Behaviour*, *142*(9), 1159–1184.

DiRienzo, N., Niemelä, P. T., Skog, A., Vainikka, A., & Kortet, R. (2015). Juvenile pathogen exposure affects the presence of personality in adult field crickets. *Frontiers in Ecology and Evolution*, *3*, 1–10.

Dochtermann, N. A., & Dingemanse, N. J. (2013). Behavioral syndromes as evolutionary constraints. *Behavioral Ecology*, *24*(4), 806–811.

Doolan, S. P., & Macdonald, D. W. (1996). Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology*, *239*, 697–716.

Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Realized heritability of personalities in the great tit (Parus major). *Proceedings of the Royal Society B: Biological Sciences*, *270*(1510), 45–51.

Duca, C., & Marini, M. Â. (2014). Territorial system and adult dispersal in a cooperative-breeding tanager. *The Auk*, *131*(1), 32–40.

Dunbar, R. I. M. (2018). Social structure as a strategy to mitigate the costs of group living: a comparison of gelada and guereza monkeys. *Animal Behaviour*, *136*, 53–64.

Eals, M., & Silverman, I. (1994). The Hunter-Gatherer theory of spatial sex differences: proximate factors mediating the female advantage in recall of object arrays. *Ethology and Sociobiology*, *15,*(2), 95–105.

Eckel, C. C., & Grossman, P. J. (2008). Men, women and risk aversion: experimental evidence. In *Handbook of Experimental Economics Results* (Vol. 1, pp. 1061–1073).

Edelaar, P., Serrano, D., Carrete, M., Blas, J., Potti, J., & Tella, J. L. (2012). Tonic immobility is a measure of boldness toward predators: an application of Bayesian structural equation modeling. *Behavioral Ecology*, *23*(3), 619–626.

Elwood, R. W., Stoilova, V., McDonnell, A., Earley, R. L., & Arnott, G. (2014). Do mirrors reflect reality in agonistic encounters? A test of mutual cooperation in displays. *Animal Behaviour*, *97*, 63–67.

Emlen, J. M. (1966). The role of time and energy in food preference. *The American Naturalist*, *100*(916), 611–617.

Emlen, S. T. (1982). The evolution of helping. I. An ecological constraints model. *The American Naturalist*, *119*(1), 29–39.

Exnerová, A., Hotová, K., Dová, S., Fučíková, E., Drent, P., & Tys, P. Š. (2010). Personality matters: individual variation in reactions of naive bird predators to aposematic prey. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1682), 723–728.

Favati, A., Leimar, O., & Løvlie, H. (2014). Personality predicts social dominance in male domestic fowl. *PLoS One*, *9*(7), p.e103535.

Ferguson-Gow, H., Sumner, S., Bourke, A. F. G., & Jones, K. E. (2014). Colony size predicts division of labour in attine ants. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20141411.

Fontaine, C., Collin, C. L., & Dajoz, I. (2008). Generalist foraging of pollinators: diet expansion at high density. *Journal of Ecology*, *96*(5), 1002–1010.

Fox, R. A., Ladage, L. D., Roth II, T. C., & Pravosudov, V. V. (2009). Behavioural profile predicts dominance status in mountain chickadees, *Poecile gambeli*. *Animal Behaviour*, *77*, 1441–1448.

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 1785–1801.

Gaston, A. J. (1973). The ecology and behaviour of the long-tailed tit. *Ibis*, *115*(3), 330–351.

Gaston, A. J. (1978). The evolution of group territorial behavior and cooperative breeding. *The American Naturalist*, *112*(988), 1091–1100.

Gordon, D. M. (1995). The expandable network of ant exploration. *Animal Behaviour*, *50*, 995–1007.

Goulson, D., & Osborne, J. L. (2009). Foraging range and the spatial distribution of worker bumble bees. In S. Jarau & M. Hrncir (Eds.), *Food Exploitation by Social Insects: Ecological, Behavioural, and Theoretical Approaches* (1st ed., pp. 97–111). Boca Raton, Fl: CRC Press.

Griesser, M., Drobniak, S. M., Nakagawa, S., & Botero, C. A. (2017). Family living sets the stage for cooperative breeding and ecological resilience in birds. *PLoS Biology*, *15*(6), p.e2000483.

Griffen, B. D., Toscano, B. J., & Gatto, J. (2012). The role of individual behavior type in mediating indirect interactions. *Ecology*, *93*(8), 1935–1943.

Grüter, C., Menezes, C., Imperatriz-Fonseca, V. L., & Ratnieks, F. L. W. (2012). A morphologically specialized soldier caste improves colony defense in a neotropical eusocial bee. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(4), 1182–1186.

Guillette, L. M., Hahn, A. H., Hoeschele, M., Przyslupski, A.-M., & Sturdy, C. B. (2015). Individual differences in learning speed, performance accuracy and exploratory behaviour in black-capped chickadees. *Animal Cognition*, *18*(1), 165–178.

Guillette, L. M., Reddon, A. R., Hurd, P. L., & Sturdy, C. B. (2009). Exploration of a novel space is associated with individual differences in learning speed in black-capped chickadees, *Poecile atricapillus*. *Behavioural Processes*, *82*, 265–270.

Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*, 1–16.

Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, *7*, 17–52.

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, *2*, e616.

Hatchwell, B. J., Anderson, C., Ross, D. J., Fowlie, M. K., & Blackwell, P. G. (2001). Social organization of cooperatively breeding long-tailed tits: kinship and spatial dynamics. *Journal of Animal Ecology*, *70*(5), 820–830.

Hatchwell, B. J., & Komdeur, J. (2000). Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, *59*, 1079–1086.

Hatchwell, B. J., Russell, A. F., Fowlie, M. K., & Ross, D. J. (1999). Reproductive success and nest-site selection in a cooperative breeder: effect of experience and a direct benefit of helping. *Source: The Auk*, *116*(2), 355–363.

Hatchwell, B. J., Russell, A. F., Maccoll, A. D. C., Ross, D. J., Fowlie, M. K., & Mcgowan, A. (2004). Helpers increase long-term but not short-term productivity in cooperatively breeding long-tailed tits. *Behavioral Ecology*, *15*(1), 1–10.

Heinze, J., & Schrempf, A. (2008). Aging and reproduction in social insects – A mini-review. *Gerontology*, *54*, 160–167.

Hirschenhauser, K., Wittek, M., Johnston, P., & Möstl, E. (2008). Social context rather than behavioral output or winning modulates post-conflict testosterone responses in Japanese quail (*Coturnix japonica*). *Physiology & Behavior*, 457–463.

Hixon, M. A. (1980). Food production and competitor density as the determinants of feeding territory size. *The American Naturalist*, *115*(4), 510–530.

Holbrook, S. J., & Schmitt, R. J. (1992). Causes and consequences of dietary specialization in surfperches: patch choice and intraspecific competition. *Ecology*, *73*(2), 402–412.

Hughes, W. O. H., Oldroyd, B. P., Beekman, M., & Ratnieks, F. L. W. (2008). Ancestral monogamy shows kin selection is key to the evolution of eusociality. *Science*, *320*, 1213–1216.

Janson, C. H., & van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: methods. *Behaviour*, *105*(1/2), 165–186.

Jarvis, J. U. M. (1981). Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science*, *212*(4494), 571–573.

Jarvis, J. U. M., & Bennett, N. C. (1993). Eusociality has evolved independently in two genera of bathyergid mole-rats - but occurs in no other subterranean mammal. *Behavioral Ecology and Sociobiology*, *33*, 253–260.

Jennions, M. D., & Macdonald, D. W. (1994). Cooperative breeding in mammals. *Trends in Ecology & Evolution*, *9*(3), 89–93.

Jetz, W., & Rubenstein, D. R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, *21*(1), 72–78.

Judd, T. M., & Sherman, P. W. (1996). Naked mole-rats recruit colony mates to food sources. *Animal Behaviour*, *52*(5), 957–969.

Kerman, K., Sieving, K. E., Mary, C. S., & Avery, M. L. (2016). Evaluation of boldness assays and associated behavioral measures in a social parrot, monk parakeet (*Myiopsitta monachus*). *Behaviour*, *153*, 1817–1838.

Koenig, W. D., Pitelka, F. A., Carmen, W. J., Mumme, R. L., & Stanback, M. T. (1992). The evolution of delayed dispersal in cooperative breeders. *The Quarterly Review of Biology*, *67*(2), 111–150.

Komdeur, J., Richardson, D. S., Hammers, M., Eikenaar, C., Brouwer, L., & Kingma, S. A. (2017). The evolution of cooperative breeding in vertebrates. In *eLS* (pp. 1–11). Chichester: John Wiley & Sons Ltd.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., van Der Vegt, B. J., van Reenen, C. G., Hopster, H., … Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, *23*(7), 925–935.

Korb, J., & Heinze, U. (2016). Major hurdles for the evolution of sociality. *Annual Review of Entomology*, *61*, 297–316.

Kralj-Fišer, S., & Schuett, W. (2014). Studying personality variation in invertebrates: why bother? *Animal Behaviour*, *91*, 41–52.

Kre, J. G. (1999). Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy*, *80*(4), 1114–1129.

Kruuk, H. (1978). Foraging and spatial organisation of the European badger, *Meles meles L. Behavioral Ecology and Sociobiology*, *4*, 75–89.

Kruuk, H., & Macdonald, D. W. (1985). Group territories of carnivores: empires and enclaves. In R. M. Sibly & R. H. Smith (Eds.), *Behavioural Ecology. Ecological Consequences of Adaptive Behaviour*. Oxford: Blackwell.

Kühbandner, S., Modlmeier, A. P., & Foitzik, S. (2014). Age and ovarian development are related to worker personality and task allocation in the ant *Leptothorax acervorum*. *Current Zoology*, *60*(3), 392–400.

Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A., & Ydenberg, R. C. (2010). The effect of personality on social foraging: shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 601–608.

Layman, C. A., Quattrochi, J. P., Peyer, C. M., & Allgeier, J. E. (2007). Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecology Letters*, *10*, 937–944.

Le Vin, A. L., Mable, B. K., Taborsky, M., Heg, D., & Arnold, K. E. (2011). Individual variation in helping in a cooperative breeder: relatedness versus behavioural type. *Animal Behaviour*, *82*(3), 467–477.

Lessells, C. M., & Boag, P. T. (1987). Unrepeatable repeatabilities: a common mistake. *The Auk*, *104*(1), 116–121.

Macarthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*(916), 603–609.

Maccoll, A. D. C., & Hatchwell, B. J. (2003). Sharing of caring: nestling provisioning behaviour of long-tailed tit, *Aegithalos caudatus*, parents and helpers. *Animal Behaviour*, *66*, 955–964.

MacColl, A. D. C., & Hatchwell, B. J. (2002). Temporal variation in fitness pay-offs promotes cooperative breeding in long-tailed tits *Aegithalos caudatus*. *The American Naturalist*, *160*(2), 186–194.

Magrath, R. D. (2001). Group breeding dramatically increases reproductive success of yearling but not older female scrubwrens: a model for cooperatively breeding birds? *Journal of Animal Ecology*, *70*(3), 370–385.

Marchetti, K., & Price, T. (1989). Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological Reviews*, *64*(1), 51–70.

Marino, J. (2003). *Spatial Ecology of the Ethiopian Wolf, Canis simensis.* PhD thesis, University of Oxford, UK.

Martin, J. G. A., Nussey, D. H., Wilson, A. J., & Réale, D. (2011). Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models. *Methods in Ecology and Evolution*, *2*(4), 362–374.

Martin, J. G. A., & Réale, D. (2008). Temperament, risk assessment and habituation to novelty in eastern chipmunks, Tamias striatus. *Animal Behaviour*, *75*(1), 309–318.

Marx, K. (1867). *Capital (Vol. I)*. Mark Harris.

McBurney, D. H., Gaulin, S. J. C., Devineni, T., & Adams, C. (1997). Superior spatial memory of women: stronger evidence for the Gathering Hypothesis. *Evolution and Human Behavior*, *18*, 165–174.

McCowan, L. S. C., Mainwaring, M. C., Prior, N. H., & Griffith, S. C. (2015). Personality in the wild zebra finch: exploration, sociality, and reproduction. *Behavioral Ecology*, *26*(3), 735–746.

Mellgren, R. L., & Ropert, T. J. (1986). Spatial learning and discrimination of food patches in the European badger (*Meles meles L.*). *Animal Behaviour*, *34*, 1129–1134.

Michelena, P., Sibbald, A. M., Erhard, H. W., & McLeod, J. E. (2009). Effects of group size and personality on social foraging: the distribution of sheep across patches. *Behavioral Ecology*, *20*(1), 145–152.

Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., … Rillig, M. C. (2014). Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, *4*(18), 3514–3524.

Morse, D. H. (1974). Niche breadth as a function of social dominance. *The American Naturalist*, *108*(964), 818–830.

Nakagawa, S., & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, *82*(4), 591–605.

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews*, *85*(4), 935–956.

Nakahashi, W., & Feldman, M. W. (2014). Evolution of division of labor: emergence of different activities among group members. *Journal of Theoretical Biology*, *348*, 65–79.

Näslund, J., & Johnsson, J. I. (2016). State-dependent behavior and alternative behavioral strategies in brown trout (*Salmo trutta L.*) fry. *Behavioral Ecology and Sociobiology*, *70*(12), 2111–2125.

Nelson-Flower, M. J., Hockey, P. A. R., O'Ryan, C., Raihani, N. J., du Plessis, M. A., & Ridley, A. R. (2011). Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied babbler. *Behavioral Ecology*, *22*(3), 559–565.

Nettle, D. (2006). The evolution of personality variation in humans and other animals. *American Psychologist*, *61*(6), 622–631.

O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, *1*(2), 118–122.

O'Reilly, K. M., & Wingfield, J. C. (2001). Ecological factors underlying the adrenocortical response to capture stress in arctic-breeding shorebirds. *General and Comparative Endocrinology*, *124*, 1–11.

O'Riain, M. J., & Jarvis, J. U. M. (1997). Colony member recognition and xenophobia in the naked mole-rat. *Animal Behaviour*, *53*(3), 487–498.

Oers, K. Van, & Sinn, D. L. (2013). Quantitative and molecular genetics of animal personality. In C. Carere & D. Maestripieri (Eds.), *Animal Personalities: Behavior, ehysiology, and Evolution* (pp. 149–200). Chicago; London: University of Chicago Press.

Ostfeld, R. S. (1982). Foraging strategies and prey switching in the California sea otter. *Oecologia*, *53*(2), 170–178.

Overington, S. E., Dubois, F., & Lefebvre, L. (2008). Food unpredictability drives both generalism and social foraging: a game theoretical model. *Behavioral Ecology*, *19*, 836–841.

Pamminger, T., Foitzik, S., Kaufmann, K. C., Schü, N., & Menzel, F. (2014). Worker personality and its association with spatially structured division of labor. *PLoS One*, *9*(1), e79616.

Perals, D., Griffin, A. S., Bartomeus, I., & Sol, D. (2017). Revisiting the open-field test: what does it really tell us about animal personality? *Animal Behaviour*, *123*, 69–79.

Pietrewicz, A. T., & Kamil, A. C. (1979). Search image formation in the blue jay (*Cyanocitta cristata*). *Science*, *204*, 1332–1333.

Pigozzi, G. (1989). Digging behaviour while foraging by the European badger, *Meles meles*, in a Mediterranean habitat. *Ethology*, *83*, 121–128.

Portelli, D. J., Barclay, H., Russell, D. J. F., Griffith, S. C., & Russell, A. F. (2009). Social organisation and foraging ecology of the cooperatively breeding chestnut-crowned babbler (*Pomatostomus ruficeps*). *Emu*, *109*(2), 153–162.

Powell, E. C., & Taylor, L. A. (2017). Specialists and generalists coexist within a population of spider-hunting mud dauber wasps. *Behavioral Ecology*, *28*(3), 890–898.

Pöysä, H. (1992). Group foraging in patchy environments: the importance of coarse-level local enhancement. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *23*(2), 159–166.

Pruitt, J. N., Stachowicz, J. J., & Sih, A. (2012). Behavioral types of predator and prey jointly determine prey survival: potential implications for the maintenance of within-species behavioral variation. *The American Naturalist*, *179*(2), 217–227.

Quinn, J. L., & Cresswell, W. (2005). Personality, anti-predation behaviour and behavioural plasticity in the chaffinch. *Behaviour, 142*(9/10), 1377–1402.

Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A., & Sheldon, B. C. (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of Animal Ecology*, *78*(6), 1203–1215.

Quinn, J.L., Cole, E.F., Bates J., Payne, R.W., & Cresswell, W. (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society of London B: Biological Sciences*, *279*, 1919–1926.

R Core Team. (2016). R: A language and environment for statistical vomputing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.r-project.org

Radford, A. N., & Du Plessis, M. A. (2003). Bill dimorphism and foraging niche partitioning in the green woodhoopoe. *Journal of Animal Ecology*, *72*(2), 258–269.

Radford, A. N., & Ridley, A. R. (2006). Report recruitment calling: a novel form of extended parental care in an altricial species. *Current Biology*, *16*, 1700–1704.

Raihani, N. J., Nelson-Flower, M. J., Golabek, K. A., & Ridley, A. R. (2010). Routes to breeding in cooperatively breeding pied babblers *Turdoides bicolor*. *Journal of Avian Biology*, *41*(6), 681–686.

Raihani, N. J., Nelson-Flower, M. J., Moyes, K., Browning, L. E., & Ridley, A. R. (2010). Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. *Journal of Animal Ecology*, *79*, 44–52.

Raihani, N. J., & Ridley, A. R. (2008). Experimental evidence for teaching in wild pied babblers. *Animal Behaviour*, *75*, 3–11.

Rangassamy, M., Dalmas, M., Féron, C., Gouat, P., & Rödel, H. G. (2015). Similarity of personalities speeds up reproduction in pairs of a monogamous rodent. *Animal Behaviour*, *103*, 7–15.

Ratnieks, F. L. W., & Anderson, C. (1999). Task partitioning in insect societies. *Insectes Sociaux*, *46*, 95–108.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 4051–4063.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318.

Reeve, H. K., Westneatt, D. F., Noont, W. A., Sherman, P. W., & Aquadrot, C. F. (1990). DNA“ fingerprinting” reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. *Proceedings of the National Academy of Sciences of the United States of America*, *87*, 2496–2500.

Ridley, A. R. (2016). Southern pied babblers: The dynamics of conflict and cooperation in a group-living society. In W. D. Koenig & J. L. Dickinson (Eds.), *Cooperative Breeding in vertebrates: Studies of ecology, evolution, and behavior.* (pp. 115–132). Cambridge: Cambridge University Press.

Ridley, A. R., Nelson-Flower, M. J., & Thompson, A. M. (2013). Is sentinel behaviour safe? An experimental investigation. *Animal Behaviour*, *85*, 137–142.

Riley, J. R., Greggers, U., Smith, A. D., Reynolds, D. R., & Menzel, R. (2005). The flight paths of honeybees recruited by the waggle dance. *Nature*, *435*, 205–207.

Rissing, S. W. (1981a). Foraging specializations of individual seed-harvester ants. *Behavioral Ecology and Sociobiology*, *9*, 149–152.

Rissing, S. W. (1981b). Prey preferences in the desert horned lizard: influence of prey foraging method and aggressive behavior. *Ecology*, *62*(4), 1031–1040.

Robertson, A., McDonald, R. A., Delahay, R. J., Kelly, S. D., & Bearhop, S. (2014). Individual foraging specialisation in a social mammal: the European badger (*Meles meles*). *Oecologia*, *176*(2), 409–421.

Robertson, A., McDonald, R. A., Delahay, R. J., Kelly, S. D., & Bearhop, S. (2015). Resource availability affects individual niche variation and its consequences in group-living European badgers *Meles meles*. *Oecologia*, *178*(1), 31–43.

Rollins, L. A., Browning, L. E., Holleley, C. E., Savage, J. L., Russell, A. F., & Griffith, S. C. (2012). Building genetic networks using relatedness information: a novel approach for the estimation of dispersal and characterization of group structure in social animals. *Molecular Ecology*, *21*(7), 1727–1740.

Rood, J. P. (1975). Population dynamics and food habits of the banded mongoose. *African Journal of Ecology*, *13*, 89–111.

Roughgarden, J. (1972). Evolution of niche width. *The American Naturalist*, *106*(952), 683–718.

Rudin, F. S., & Briffa, M. (2012). Is boldness a resource-holding potential trait? Fighting prowess and changes in startle response in the sea anemone, *Actinia equina*. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1904–1910.

Russell, A. F. (2016). Chestnut-crowned babblers: dealing with climatic adversity and uncertainty in the Australian arid zone. In W. D. Koenig & J. L. Dickinson (Eds.), *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution and Behaviour.* (pp. 150–164). Cambridge, MA: Cambridge University Press.

Russell, A. F., Portelli, D. J., Russell, D. J. F., & Barclay, H. (2010). Breeding ecology of the chestnut-crowned babbler: a cooperative breeder in the desert. *Emu*, *110*(4), 324–331.

Sakal, R. R., & Rohlf, F. J. (1995). *Biometry: The principles and practice of statistics in biological research.* (3rd editio). WH Creman, San Francisco.

Schmid-Hempel, P., & Schmid-Hempel, R. (1984). Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Insectes Sociaux*, *31*(1), 345–360.

Schuett, W., & Dall, S. R. X. (2009). Sex differences, social context and personality in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, *77*(5), 1041–1050.

Schuett, W., Dall, S. R. X., & Royle, N. J. (2011). Pairs of zebra finches with similar "personalities" make better parents. *Animal Behaviour*, *81*, 609–618.

Schuett, W., Dall, S. R. X., Wilson, A. J., & Royle, N. J. (2013). Environmental transmission of a personality trait: foster parent exploration behaviour predicts offspring exploration behaviour in zebra finches. *Biology Letters*, *9*, p.20130120.

Schuett, W., Tregenza, T., & Dall, S. R. X. (2010). Sexual selection and animal personality. *Biological Reviews*, *85*, 217–246.

Shackleton, D. M., & Shafak, C. C. (1984). A review of the social behavior of feral and wild sheep and goats. *Journal of Animal Science*, *58*(2), 500–509.

Sharp, S. P., & Hatchwell, B. J. (2005). Individuality in the contact calls of cooperatively breeding long-tailed tits (*Aegithalos caudatus*). *Behaviour*, *142*(11/12), 1559–1575.

Shen, S.-F., Emlen, S. T., Koenig, W. D., & Rubenstein, D. R. (2017). The ecology of cooperative breeding behaviour. *Ecology Letters*, *20*(6), 708–720.

Sheppard, C. E., Inger, R., McDonald, R. A., Barker, S., Jackson, A. L., Thompson, F. J., … Marshall, H. H. (2018). Intragroup competition predicts individual foraging specialisation in a group-living mammal. *Ecology Letters*.

Sibbald, A. M., & Hooper, R. J. (2004). Sociability and the willingness of individual sheep to move away from their companions in order to graze. *Applied Animal Behaviour Science*, *86*, 51–62.

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: a behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(2762–2772).

Sillero-Zubiri, C., & Gottelli, D. (1995). Diet and feeding behavior of Ethiopian wolves (*Canis simensis*). *Journal of Mammalogy*, *76*(2), 531–541.

Silverman, I., & Eals, M. (1992). Sex differences in spatial abilities: evolutionary theory and data. In J. H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture.* (pp. 533–549). New York: Oxford University Press.

Smith, A. (1776). *An inquiry into the nature and causes of the wealth of nations.*

Snaith, T. V, & Chapman, C. A. (2007). Primate group size and interpreting socioecological models: do folivores really play by different rules? *Evolutionary Anthropology*, *16*, 94–106.

Sorato, E., Griffith, S. C., & Russell, A. F. (2016). The price of associating with breeders in the cooperatively breeding chestnut-crowned babbler: foraging constraints, survival and sociality. *Journal of Animal Ecology*, *85*, 1340–1351.

Sorato, E., Gullett, P. R., Creasey, M. J. S., Griffith, S. C., & Russell, A. F. (2015). Plastic territoriality in group-living chestnut-crowned babblers: roles of resource value, holding potential and predation risk. *Animal Behaviour*, *101*, 155–168.

Sorato, E., Gullett, P. R., Griffith, S. C., & Russell, A. F. (2012). Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Animal Behaviour*, *84*(4), 823–834.

Stevenson, P. R., & Castellanos, M. C. (2000). Feeding rates and daily path range of the Colombian woolly monkeys as evidence for between-and within-group competition. *Folia Primatologica*, *71*, 399–408.

Svanbäck, R., & Bolnick, D. I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 839–844.

Svendsen, G. E., & Armitage, K. B. (1973). Mirror-image stimulation applied to field behavioral studies. *Ecology*, *54*(3), 623–627.

Sweeney, K., Cusack, B., Armagost, F., O'Brien, T., Keiser, C. N., & Pruitt, J. N. (2013). Predator and prey activity levels jointly influence the outcome of long-term foraging bouts. *Behavioral Ecology*, *24*(5), 1205–1210.

Tebbich, S., Taborsky, M., Fessl, B., & Blomqvist, D. (2001). Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society B: Biological Sciences*, *268*, 2189–2193.

Terraube, J., Arroyo, B., Madders, M., & Mougeot, F. (2011). Diet specialisation and foraging efficiency under fluctuating vole abundance: a comparison between generalist and specialist avian predators. *Oikos*, *120*(2), 234–244.

Thornton, A., & Clutton-Brock, T. (2011). Social learning and the development of individual and group behaviour in mammal societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 978–87.

Thornton, A., & Malapert, A. (2009). Experimental evidence for social transmission of food acquisition techniques in wild meerkats. *Animal Behaviour*, *78*, 255–264.

Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science*, *313*, 227–229.

Tian, L., & Zhou, X. (2014). The soldiers in societies: defense, regulation, and evolution. *International Journal of Biological Sciences*, *10*(3), 296–308.

Tinker, M. T., Bentall, G., & Estes, J. A. (2008). Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(2), 560–565.

Tinker, M. T., Mangel, M., & Estes, J. A. (2009). Learning to be different: acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specializations. *Evolutionary Ecology Research*, *11*, 841–869.

Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Cristián, J. M. (2016). Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia*, *182*, 55–69.

Traniello, J. F. A. (1989). Foraging strategies of ants. *Annual Review of Entomology*, *34*, 191–210.

Tschinkel, W. R. (1988). Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta*. *Behavioral Ecology and Sociobiology*, *22*, 103–115.

van Oers, K., De Jong, G., & Noordwijk, A. J. Van. (2005). Contribution of genetics to the study of animal personalities : a review of case studies. *Behaviour*, *142*(9–10), 1191–1212.

van Oers, K., Klunder, M., & Drent, P. J. (2005). Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioural Ecology*, *16*(4), 716–723.

van Overveld, T., & Matthysen, E. (2010). Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters*, *6*(2), 187–90.

Verbeek, M. E. M., Drent, P. J., & Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, *48*, 1113–1121.

Wang, M.-Y., Brennan, C. H., Lachlan, R. F., & Chittka, L. (2015). Speed-accuracy trade-offs and individually consistent decision making by individuals and dyads of zebrafish in a colour discrimination task. *Animal Behaviour*, *103*, 277–283.

White, S. L., Wagner, T., Gowan, C., & Braithwaite, V. A. (2017). Can personality predict individual differences in brook trout spatial learning ability? *Behavioural Processes*, *141*, 220–228.

Whittingham, M. J., Butler, S. J., Quinn, J. L., & Cresswell, W. (2004). The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos*, *106*(2), 377–385.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*(3/4), 262–300.

Wrangham, R. W., Gittleman, J. L., & Chapman, C. A. (1993). Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behavioral Ecology and Sociobiology*, *32*, 199–209.

Wright, C. M., Holbrook, C. T., & Pruitt, J. N. (2014). Animal personality aligns task specialization and task proficiency in a spider society. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(26), 9533–7.

Wrona, F. J., & Jamieson Dixon, R. W. (1991). Group size and predation risk: a field analysis of encounter and dilution effects. *The American Naturalist*, *137*(2), 186–201.

Young, C. M., Browning, L. E., Savage, J. L., Griffith, S. C., & Russell, A. F. (2013). No evidence for deception over allocation to brood care in a cooperative bird. *Behavioral Ecology*, *24*(1), 70–81.