

The causes and consequences of individual variation in cognitive ability in the cooperatively  
breeding Australian magpie (*Cracticus tibicen dorsalis*)

Ben Ashton MBiolSci



This thesis is presented for the degree of Doctor of Philosophy of The University of Western  
Australia

Centre for Evolutionary Biology

School of Biological Sciences

2017

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The work described in this thesis was funded by an international postgraduate research scholarship (IPRS), awarded to Ben Ashton, and an ARC Discovery grant awarded to Amanda Ridley & Alex Thornton (DP140101921)

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## ABSTRACT

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The long-held belief that primates were the pinnacle of intelligence was only brought into question relatively recently, as an explosion of research in the field of comparative cognition revealed remarkable cognitive capacities in other, non-primate species. Evidence of birds being capable of future planning, deception and tool manufacture raised a number of important questions, the most pressing of these being; what conditions favour the evolution of cognition?

Factors governing the evolution of intelligence are poorly understood; conflicting evidence derived primarily from comparative studies argue in favour of either environmental or social explanations. However, more recently an intraspecific approach to the study of cognition has been championed. The ecological and phylogenetic confounds associated with comparative studies can be nullified by focusing on the causes and consequences of individual variation in cognitive ability *within* species. Rather than dismissing intraspecific variation in cognitive ability as noise, a focus on this variation has the potential to reveal profound insights into cognitive evolution by linking cognitive variation to fitness consequences. Critically, very few attempts have been made to address the effect of *sociality* on the causes and consequences of individual variation in cognition, particularly so in wild populations of animals. My research aims to help resolve this by investigating the causes and consequences of individual variation in cognitive performance in the cooperatively breeding Western Australian magpie (*Cracticus tibicen dorsalis*).

In Chapter 2 I investigated the causes of individual variation in cognitive performance, and found that group size was the strongest predictor of general intelligence, providing evidence for a robust link between sociality and cognitive performance. To determine the direction of causality in the observed relationship between group size and cognitive performance, I quantified cognitive performance in fledglings at 100, 200, and 300 days post-fledging (Chapter 3). Group size was the strongest predictor of general intelligence at 200 and 300 days post-fledging, suggesting that group size has a causal effect on the development of cognitive traits. In order to determine the

consequences of individual variation in cognitive traits, I investigated the relationship between the measures of general intelligence gained from the second chapter, and three indicators of female fitness (average number of nestlings, fledglings and juveniles produced each year, Chapter 4). We found that general intelligence was the strongest predictor of all three measures of female fitness. This provides evidence for a selective benefit of increased general intelligence, and demonstrates how natural selection may act upon general intelligence.

A potential benefit of living in larger groups is that it may lead to the solution of novel problems more quickly. In light of the relationship I found between group size and general intelligence, I sought to investigate this relationship in Australian magpies (Chapter 5). I presented a novel foraging task to magpie groups, and found that innovative behaviour emerged more rapidly in larger groups, and through social learning, spread more quickly in larger groups. These results provide a unique link between the emergence, spread and establishment of innovative behaviour in a wild population of animals.

In conclusion, my research has shed light on how group size may have a causal effect on the development of cognition, which in turn affects the reproductive success of individuals.

Furthermore, I found evidence of how group size facilitates the emergence, spread and establishment of local traditions. Together, these findings provide evidence of how sociality may mediate the evolution of cognition in a wild population of animals.

## TABLE OF CONTENTS

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<b>Abstract</b>	<b>iii</b>
<b>Contents</b>	<b>v</b>
<b>Acknowledgements</b>	<b>viii</b>
<b>Authorship declaration</b>	<b>x</b>
<b>Chapter one: Introduction</b>	<b>2</b>
1.1 The evolution of intelligence	3
1.2 An intraspecific approach to the study of cognition	6
1.3 The consequences of individual variation in cognition	6
1.4 Studying cognition in the wild	7
1.5 Bird brain: insult or compliment?	9
1.6 Study system: The Australian magpie	10
1.7 Thesis structure	13
1.8 References	14
<b>Chapter two: General intelligence is linked to group size in a cooperative breeder</b>	<b>22</b>
2.1 Abstract	24
2.2 Main text	25
2.3 References	30
2.4 Supplementary material	36
<b>Chapter three: The influence of rearing group size on cognitive development in a group-living bird</b>	<b>60</b>
3.1 Abstract	62

3.2 Introduction	63
3.3 Methods	64
3.4 Results	70
3.5 Discussion	74
3.6 References	77
3.7 Supplementary material	83
<b>Chapter four: General intelligence influences reproductive success in the wild</b>	<b>92</b>
4.1 Abstract	94
4.2 Introduction	95
4.3 Methods	97
4.4 Results	103
4.5 Discussion	105
4.6 References	107
4.7 Supplementary materials	113
<b>Chapter five: Larger group sizes facilitate the emergence and spread of innovative behaviour in a group living bird</b>	<b>118</b>
5.1 Abstract	120
5.2 Introduction	121
5.3 Methods	123
5.4 Results	127
5.5 Discussion	130
5.6 References	133
5.7 Supplementary materials	137

<b>Chapter six: Discussion</b>	140
6.1 Introduction	142
6.2 Main findings	142
6.3 Talking points arising from this thesis	145
6.4 Conclusion	149
6.5 References	150

## ACKNOWLEDGEMENTS

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It seems that this journey started a long time ago in the Kalahari. I'd like to thank the Kalahari Meerkat Project and Tom Flower for giving me the opportunity to carry out field work in an incredible place; this proved beyond all doubt that I wanted to pursue a career as a biologist, and fuelled my passion for this topic.

I owe a huge amount to my supervisors Mandy and Alex. I have been incredibly lucky in that they are both exceptionally knowledgeable and supportive. Despite being pregnant or on maternity leave, Mandy would always get manuscripts back swiftly. Alex, although being seven (or eight) hours behind, always made time to skype and chat- these would always be enjoyable, and usually contained a sprinkling of inspiring quotes from the Big Lebowski: "*well, that's just their opinion, man*" (I resisted the temptation to put these in the thesis). I look forward to continuing working with both of you. Thank you to the rest of the research group; Lizzie, Kate, Stephanie, Phil, Mel and Kyana. Of course, a big thanks to my research assistants, Emily, Amy, and Margot. I'm very grateful for all the sleep you sacrificed!

I'd like to thank all of the close friends I have made at UWA rugby club, you have helped make my time here truly special; whether this was playing with you on the rugby field or having beers with you on the hill (or any number of Perth's drinking establishments). I'd also like to thank everyone in the CEB, both for their support and their friendship. I have many fond memories, from lunchtime BBQs at the foreshore, to our regular forays into Varsity (I'm convinced we've doubled their turnover). In particular I'd like to thank Bruno and Rowan for helping me with stats when they undoubtedly had better things to be doing with their time, my long-suffering office mate Lizzie, who despite me consistently playing pranks on her, put up with me, and Rob, with whom I probably spent more time at the WACA than I should have. Thanks for being awesome.




I'd also like to thank Eleanor Russell and the late Ian Rowley who introduced us to the magpie population. Eleanor was always generous with her time and advice; both of which proved invaluable. I hope you enjoy reading this thesis. I'd also quickly like to thank the magpies- despite your reputation, you did not swoop me once, and my eyesight is still intact. You also provided me with hours of entertainment.


I'd like to thank *all* my family. In particular, thank you Mum, Dad and Laura for inspiring me to pursue this career, and for supporting me. Whether it's been me deciding to swan off to South Africa for a couple of years, or move to Perth, you have always been genuinely excited and supportive. Admittedly, it has provided you with a couple of cracking holidays. Last of all, and most importantly, I would like to thank Inês; thank you for being you, your love and support is unwavering (even when you haven't had your morning coffee!).

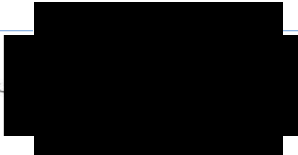
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This thesis contains work that has been prepared for publication.

Details of the work: General intelligence linked to group size in a cooperative breeder	
Location in thesis: Chapter 2	
Student contribution to work: 80%	
Co-author signatures and dates:	 20/02/17

Details of the work: The influence of rearing group size on cognitive development in a group-living bird	
Location in thesis: Chapter 3	
Student contribution to work: 80%	
Co-author signatures and dates:	 20/02/17

Details of the work: General intelligence influences reproductive success in the wild	
Location in thesis: Chapter 4	
Student contribution to work: 80%	
Co-author signatures and dates:	 20/02/17

Details of the work: Larger group sizes facilitate the emergence and spread of innovative behaviour in a group living bird	
Location in thesis: Chapter 5	
Student contribution to work: 80%	

Co-author signatures and dates:

[Redacted signature]

20/02/17

Student signature:

[Redacted signature]

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I, Amanda Ridley certify that the student statements regarding their contribution to each of the works listed above are correct

Coordinating supervisor signature:

[Redacted signature]

Date: 20/02/17



## CHAPTER ONE

### Introduction



## Chapter 1: General introduction

### 1.1 The evolution of intelligence

Planning for the future<sup>1</sup>, episodic memory<sup>2</sup>, understanding third party relations<sup>3</sup>; these are a few of a number of examples of cognitive processes that, until relatively recently, were thought to be unique to humans<sup>4</sup>. However, evidence accumulated over the past couple of decades has demonstrated that some nonhuman animals are capable of these cognitively demanding behaviours<sup>1,2,5,6</sup>. As a result it is becoming increasingly apparent that the anthropocentric view of cognition is becoming more obsolete<sup>4</sup>. The traditional view that primate cognition is at the pinnacle of a linear ladder of intelligence has been replaced by the idea of a convergent model<sup>7,8</sup>, whereby selective pressures in distantly related species have led to some species having cognitive abilities much closer to primates than previously thought possible<sup>9</sup>. Naturally, this has stimulated a whole raft of questions, the most pressing being: what conditions favour the evolution of intelligence?

Cognition is defined as the “mechanisms by which animals acquire, process, store and act on information from the environment”<sup>10</sup>, and encompasses a broad range of behaviours; it is therefore unsurprising that studies in this field cover a broad range of subjects, ranging from fundamental mechanisms of cognition, such as perception and learning, to physical cognition and social cognition. Although there is no consensus on a precise definition of intelligence, it is perhaps best viewed as a phenomenon “allowing individuals to devise flexible solutions to problems they meet”<sup>11</sup>. This includes the ability to recall knowledge gained from past experiences to guide behaviour in both familiar and novel contexts<sup>11</sup>; intelligence therefore requires the use of many cognitive traits.

Social and environmental challenges are hypothesised to be the predominant factors driving cognitive evolution. However, studies addressing the potential role of these factors have produced highly conflicting results<sup>12-14</sup>. Three environmental factors in particular have been argued to be selective pressures influencing cognition: resource availability, habitat complexity, and seasonality<sup>14</sup>.

Food availability and habitat complexity can have a large influence on the foraging behaviour of species<sup>15</sup>; if both of these factors are unpredictable, foraging can present considerable spatial and temporal cognitive challenges, which may favour the development of greater cognitive abilities<sup>10</sup>.

Frugivorous spider monkeys (*Ateles geoffroyi*), whose primary food source is ephemeral and unpredictable, have larger brains compared to the leaf-eating howler monkey (*Alouatta palliate*), whose food source is ubiquitous<sup>15</sup>. This is supported by a recent phylogenetic analysis by DeCasien *et al.*<sup>13</sup> which found a strong relationship between frugivory and brain size. Coupled with evidence of strong links between brain size and cognitive ability<sup>16-20</sup>, this provides support for a foraging theory of intellect. A foraging theory of intellect has also been used to explain how episodic memory influences food cache recovery in Western scrub jays<sup>2</sup> (*Aphelocoma californica*). Similarly, episodic memory allows grey-cheeked mangabeys (*Lophocebus albigena*) to take into account the effect of previous weather conditions when making foraging decisions<sup>21</sup>. However, if the “taxonomic net” is cast further afield, it is difficult to find support for environmental hypotheses for the evolution of intelligence outside of primates and birds. Further work needs to be carried out on a greater taxonomic range to truly determine the effect of resource availability on the evolution of cognition.

Although not necessarily mutually exclusive from the potential effects of resource availability and environmental heterogeneity, seasonality has also been hypothesised to select for increased cognitive ability<sup>22,23</sup>. Seasonal changes in climatic conditions mean some species migrate whilst others endure the harsher environments<sup>22,23</sup>. Both scenarios may create situations which select for elevated cognitive performance<sup>22,23</sup>. Migratory birds have increased levels of long-term spatial memory<sup>24-26</sup> (although note Sayol *et al.*<sup>14</sup> found migratory birds have smaller brains), whilst non-migratory species are often forced to cache food in winter, resulting in elevated spatial memory<sup>27-29</sup>.

A comparative analysis of brain size in 1,200 bird species found larger brained birds are more likely to occur in areas with greater environmental variation, adding support to the idea of seasonality favouring increased levels of cognition<sup>14</sup>.

Due to the fact many small-brained species face the same ecological challenges hypothesised to favour increased levels of cognition, ecological theories of intellect are often considered an insufficient explanation for interspecific differences in cognition<sup>30</sup>. The novel concept of social intelligence was first introduced over 50 years ago by Alison Jolly<sup>31</sup>, although it is arguably Nick Humphrey's seminal paper, "the social function of intellect"<sup>30</sup>, that is recognised as giving rise to the social intelligence hypothesis (SIH), and the resulting research in this area. The SIH posits that the challenges associated with group living gives rise to advanced cognitive abilities<sup>32</sup>. Since the SIH was conceptualised, an abundance of literature has demonstrated how living in groups can present cognitive challenges<sup>33</sup>. The need to possess behavioural flexibility, maintain and coordinate multiple relationships, monitor other group members, and recognise suitable cooperative partners, are a few of a number of factors unique to social animals that are hypothesised to be selective pressures requiring advanced cognition<sup>33,34</sup>.

The majority of evidence supporting the SIH is derived from comparative studies on primates and birds<sup>35-37</sup>, relating between-species or between-population differences in brain size or cognitive performance to differences in social organisation or life history<sup>12,36-40</sup>. Several proxies of social complexity have been found to correlate with cognitive performance or measures of brain size or brain composition<sup>12,36,38,39</sup>. Group size and neocortex size positively correlate in anthropoid primates<sup>12</sup>, the presence of long term pair bonds is associated with large brain size in corvids<sup>36</sup>, and primates experiencing fission-fusion dynamics outperform primates living in more cohesive groups in inhibition tasks<sup>39</sup>. In addition, comparative studies have also revealed social species perform better than solitary species in a number of tasks; namely the highly social pinyon jay (*Gymnorhinus cyanocephalus*) outperforms the non-social western scrub jay in transitive inference and reversal learning tasks<sup>38,40</sup>. Similarly, pinyon jays also outperformed the solitary Clark's nutcracker (*Nucifraga columbiana*) in a reversal learning task<sup>40</sup>. However, there are a number of studies reporting findings inconsistent with the social intelligence hypothesis (reviewed in Holekamp<sup>41</sup>); for example Sayol et al.'s<sup>14</sup> comprehensive analysis found no relationship between mating system and brain size in birds,



and one of the largest avian brains is found in the non-social owl<sup>42</sup>. It is apparent further work needs to be carried out to determine the explanatory power of the social intelligence hypothesis; a productive approach may be to focus on the causes of intraspecific variation in cognitive performance.

## **1.2 An intraspecific approach to the study of cognition**

An intraspecific approach to the study of cognitive evolution has recently garnered momentum, particularly among behavioural ecologists. A focus on individual differences in cognitive performance within species allows the causes and consequences of variation in cognitive ability to be quantified<sup>43-47</sup>. This is in contrast to an interspecific approach, where variation in cognitive performance within species is often disregarded as “noise”<sup>44</sup>. This detracts from the potentially vital insights that may be gained by focusing on the causes of variation, and linking cognitive variation to fitness consequences. Ignoring intraspecific variation in cognition may also give an inaccurate representation of the general cognitive abilities of species. Much like Usain Bolt is unlikely to be representative of the running speed for the majority of the human race, a focus on the top set of performers in a cognitive test may not be representative of the species. As has already been demonstrated in other fields, an intraspecific approach to the study of evolution has the potential to answer fundamental questions, and this approach is already starting to produce exciting results regarding cognitive evolution<sup>48,49</sup>.

More specifically, studies adopting an intraspecific approach have provided evidence for the SIH. Social network size correlates with brain size in macaques<sup>49</sup> (as has been found in humans<sup>50-52</sup>), and rearing group size correlates with brain size in cichlids<sup>48</sup>. However, critically, the relationship between group size and cognitive performance in *wild* populations is unknown.

## **1.3 The consequences of individual variation in cognitive performance**

Despite there being a number of hypotheses for the evolution of cognition, very little is known about the consequences of this variation. Investment in cognitive traits is metabolically costly<sup>12</sup>, and it is therefore predicted that any investment should confer a fitness benefit. However, two issues have hampered progress in this field. Firstly, many of the studies attempting to investigate the relationship between cognitive ability and fitness have used measures of problem-solving performance, usually derived from the presentation of novel foraging tasks, as a proxy for cognition<sup>53-56</sup>. The cognitive processes underlying problem-solving are poorly understood, and the potential for non-cognitive factors to influence performance cannot be excluded; the use of this problem solving paradigm has therefore been widely criticised<sup>43,44,47</sup>. Secondly, of those studies that have used robust measures to explore the relationship between cognition and fitness, very few have been carried out on wild populations of animals<sup>57-60</sup>, where conditions are argued to be most ecologically relevant<sup>44</sup>. Together, this has led to equivocal and ambiguous results. In order to truly determine what factors shape cognitive evolution, the relationship between robust measures of individual cognitive performance and fitness need to be investigated in wild populations. Once this has been achieved we will be able to understand how natural selection may act on cognition. However, thus far empirical data is scarce (although see<sup>57-60</sup>).

#### **1.4 Studying cognition in the wild**

In order to quantify and analyse variation in cognitive traits in ecologically relevant contexts, it is vital to carry out tests on wild populations of animals, as selective pressures are likely to be vastly different in captive conditions compared to natural conditions<sup>47</sup>. Studying the causes of individual variation in cognitive traits in the wild has the potential to be a fruitful endeavour that could complement experimental manipulations on captive populations. However, quantifying cognitive traits in wild populations of animals is littered with hurdles<sup>43</sup>. The need for tests to quantify well-understood cognitive traits is paramount; in order to do this psychologically grounded psychometric tests targeting clearly defined cognitive traits are required<sup>44,61</sup>. Psychometric tests were originally

designed to measure intelligence in humans<sup>62</sup>. In human psychometric testing, performance across tests is usually correlated, and a general cognitive factor (commonly called general intelligence (*g*)), typically accounts for around 30% of the total variance in test performance<sup>63,64</sup>. A few ground-breaking studies have conducted psychometric testing on wild animals, such as research on New Zealand robins<sup>65</sup> (*Petroica longipes*), black-capped chickadees<sup>27</sup> (*Poecile atricapillus*), spotted bowerbirds<sup>59</sup> (*Chlamydera maculata*), and song sparrows<sup>60</sup> (*Melospiza melodia*). However, although there is evidence of general intelligence in a wide range of taxa<sup>59,65-68</sup>, there are few examples of it being recorded in wild populations (although see<sup>59,65</sup>).

One of the challenges associated with conducting psychometric tests on animals, particularly in the wild, is ensuring the cognitive trait of interest is being quantified, while accounting for extraneous confounding variables<sup>43</sup>. To ensure this, in addition to using established psychologically grounded tests, multiple tests are needed to test for repeatability of performance, and thus determine if performance reflects true cognitive variation or noise due to other contextual variables<sup>44,61</sup>.

Quantifying the same cognitive trait multiple times can be achieved by presenting individuals with psychometric tasks that are visually distinct from one another, but causally identical<sup>61</sup>. For example, multiple colour associative learning tests can be carried out using different combinations of colours.

It is becoming increasingly apparent that in order to successfully address key questions of cognitive evolution, an interdisciplinary approach is needed. This represents a problem in itself; transferring rigorous psychometric tests from laboratory controlled conditions used in psychology to the field raises a number of issues<sup>44</sup>. Psychometric tests carried out in laboratories are able to carefully control conditions; this is virtually impossible in wild populations of animals. This means that factors such as past experience cannot be controlled for. For example, when carrying out a colour associative learning task, certain colours may be more salient because of positive interactions test subjects may have previously had with that colour; likewise certain colours may be associated with negative experiences<sup>43</sup>. Although it is not possible to control for all past experience in wild animals,

efforts can be made to minimise the potential impact; a suggestion to address the issue of past experience with colours is to use greyscale shades, or extreme shades of one colour, such as light blue and dark blue<sup>43</sup>. Another factor that is particularly hard to control for in wild populations is issues of satiety, which in turn can affect processes such as motivation or persistence to interact with a cognitive task<sup>43</sup>. It is possible to minimise the effects of satiation by ensuring experiments are carried out as close as possible to when individuals begin foraging each day, and it is also possible to incorporate measures of persistence and motivation (such as the time spent interacting with a task before giving up, or the number of attempts made to solve a task) into analyses investigating factors affecting performance. Although it is apparent that studying the evolutionary ecology of cognition in the wild will be a challenging task, given the potential insights that may be gained, it is a worthwhile endeavour<sup>69,70</sup>.

### **1.5 Bird brain: insult or compliment?**

If you were to wind the clock back 100 years, and tell the anatomist Ludwig Edinger that you were proposing to study the evolution of cognition with an avian model system, you would have been ridiculed. Edinger incorrectly described the organisation of avian brains, suggesting it was largely composed of striatum, leading to the erroneous conclusion that birds were incapable of advanced cognitive processes<sup>4</sup>. This supposition remained commonplace well into the 20<sup>th</sup> century, before research began to emerge of what the avian brain was truly capable of<sup>4</sup>.

There is considerable interspecific variation in the cognitive capabilities of birds<sup>14,71</sup>, and given the notorious demise of the archetypal dim-witted bird, the dodo (*Raphus cucullatus*), it is easy to envisage why terms such as “bird-brained” appeared. However, once the exploits of Alex the African grey parrot<sup>72</sup> (*Psittacus erithacus*) and Betty the New Caledonian crow<sup>73</sup> (*Corvus moneduloides*) were thrust into the public consciousness, an explosion of cognitive research began to demonstrate that certain bird species were capable of cognitive processes thought only possible by primates<sup>4</sup>. Since

then it has been demonstrated that birds are capable of manufacturing tools<sup>5,73</sup>, deception<sup>74</sup>, and self recognition<sup>75</sup>.

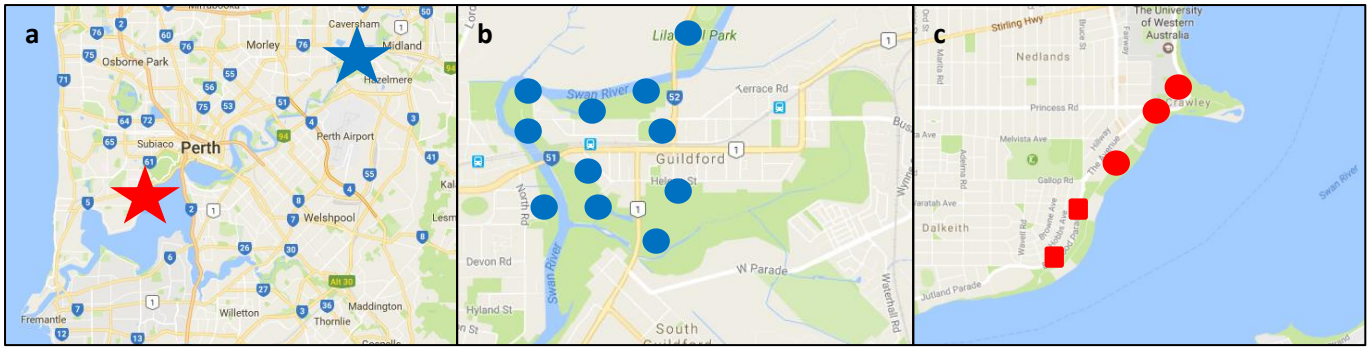
Not only is it apparent that there is a large amount of variation in the cognitive ability of different bird species, but there is also a large amount of bird species that live in social groups, or breed cooperatively<sup>76</sup>. Given the tractable nature of a number of these species, it is probable that a number of them may represent an excellent opportunity to study the relationship between sociality and cognition. In doing so, key questions posed by the social intelligence hypothesis may be resolved using an intraspecific approach.

### **1.6 Study system: the Australian magpie**

I have adopted an intraspecific approach to study the causes and consequences of cognitive performance in the Australian magpie (Western Australian subspecies *Cracticus tibicen dorsalis*). The Western Australian magpie is a large passerine (300-400g) occurring in territorial groups of 2-15 individuals, and unlike other subspecies of the Australian magpie, breeds cooperatively<sup>77-79</sup>. Within these groups there is plural breeding: all females attempt to breed at least once a year (although they rarely re-nest after a successful breeding attempt), and some failed breeders become helpers<sup>80</sup>. This is relatively rare in cooperative breeders<sup>76</sup>, and therefore presents a unique opportunity to study the relationship between cognition and reproductive fitness in a cooperative breeder. Alloparental care occurs; multiple females and males provision offspring, and the mother and multiple males incubate nests<sup>77</sup>. Despite the cooperative nature of the study species, rates of extra-group paternity in the study population are the highest recorded for any bird species (>80%)<sup>78</sup>. The Australian magpie is also renowned for its “corvid-like” cognitive abilities, with anecdotal evidence of tool use, such as manipulating bin lids and tap faucets<sup>79</sup>. A combination of these factors makes the Western Australian magpie an ideal species to study the relationship between sociality and the causes and consequences of individual variation in cognitive performance.

A ringed, habituated population of magpies was established by Eleanor Russell and Ian Rowley in Guildford, Western Australia, in 1995. Although their research concluded in 2007, a strong foundation for further research remained. Research on the study population resumed in 2013, and the study population currently consists of 14 habituated “core” groups ranging in size from 2-12 individuals, located at the University of Western Australia campus, and in the suburb of Guildford (Figure 1.1). Magpie group size has remained stable, and all individually identifiable birds have remained in the same group since research resumed in 2013, and those that were ringed by Eleanor Russell or Ian Rowley prior to 2007 have also remained in the same group. The study population is comprised of over 80 individuals, and the majority of these individuals are colour-ringed and individually identifiable. Territories inhabited by the study population typically include open grassland and parklands. The habituated nature of the study population allows close behavioural observations, and controlled presentations of psychometric tasks. In addition to the 14 “core” groups, there are two “peripheral” groups, which contain no ringed individuals, but are in the process of being habituated. The peripheral groups were used in one of the analyses in Chapter 5 (*“does innovative behaviour emerge more rapidly in larger groups?”*). For details of the group composition of the study population, and which groups were used in each data chapter, please refer to Table 1.1.

Data collected on the study population includes weekly behavioural focals that quantify aggressive and social interactions, as well as foraging efficiency. A life-history database is maintained that records any significant life-history events, such as any breeding activity, and the presence or absence of individuals in a group. Body mass is collected by weighing individuals that step onto top pan scales in return for a small crumb of mozzarella.



**Figure 1.1** (a) the location of the Guildford (blue star) and University of Western Australia (red star) study populations, (b) the location of the Guildford study population groups, (c) the location of the University of Western Australia groups. Circular dots represent “core” groups, square dots represent “peripheral” groups.

**Table 1.1** The group composition of the study population, including which groups were used in each data chapter.

Group Identity	Group size	Group type	Chapter			
			2	3	4	5
LRR	2	Peripheral	X	X	X	✓
KMO	3	Core	✓	✓	✓	✓
PR	3	Core	✓	X	✓	✓
SBB	5	Core	✓	✓	✓	✓
LHP	6	Core	✓	✓	✓	✓
RVD	6	Core	✓	✓	✓	✓
SS	6	Core	✓	✓	✓	✓
GON	6	Core	✓	✓	X	✓
NH	7	Core	✓	✓	✓	✓
MBG	7	Core	✓	✓	✓	✓
BWY	8	Core	✓	✓	✓	✓
ESC	10	Core	✓	✓	✓	✓
KMP	10	Core	✓	✓	✓	✓
CPC	11	Core	✓	✓	✓	✓
FSQ	11	Peripheral	X	X	X	X
FMR	12	Core	✓	✓	✓	✓

## 1.7 Thesis structure

In this thesis I used an intraspecific approach to quantify the causes and consequences of individual variation in cognitive ability. In Chapter 2, I investigated the causes of individual variation in adult cognitive performance by quantifying four cognitive traits and determining the factors affecting variation in performance. Factors included in analyses were group size, neophobia, sex, body mass and foraging efficiency. I also examined the relationship in performance across different cognitive tasks to determine if there is evidence for a general intelligence factor underpinning performance. In order to ensure that robust measures of cognitive ability were being quantified, and to control for non-cognitive confounding factors, I carried out a second battery of cognitive tasks on adults two weeks later, quantifying the same traits. These results are discussed in Chapter 2. In light of the results of Chapter 2, I wanted to determine if rearing group size affects the development of cognitive traits. With this in mind, I quantified the same four cognitive traits we recorded for the adult population in fledglings, at 100, 200 and 300 days post-fledging. These results are discussed in Chapter 3.

To help unravel the evolutionary consequences of individual variation in cognitive performance, and determine if there is the potential for natural selection to act on cognitive traits, I looked at the relationship between cognitive performance and three indicators of fitness: the number of hatched clutches per year, the number of fledglings per year, and the number of fledglings surviving to independence per year. These results are discussed in Chapter 4. Finally, I investigated the relationship between group size and the emergence of innovative solutions to novel problems. Although the relationship between innovative tendencies and cognition are unclear, a potential consequence of variation in cognitive performance is that it may result in benefits associated with solving novel problems. These results are discussed in Chapter 5.

Please note chapters are formatted according to where they have been submitted for publication, resulting in the structure of Chapter 2 being slightly different to that of Chapters 3-5.



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## CHAPTER TWO

### General intelligence is linked to group size in a cooperative breeder



*Submitted to Science for publication*



## 2.1 Abstract

The social intelligence hypothesis posits that the challenges of social life are key drivers of cognitive evolution. Whilst comparative studies provide support for this hypothesis at the species level, it is not known whether *intraspecific* variation in social structure affects cognitive performance in wild animal populations at the individual level. Intraspecific studies are crucial if we are to determine how social structure influences cognition, as it controls for the ecological and phylogenetic confounds associated with interspecific comparisons. We quantified cognitive performance in wild, cooperatively breeding Australian magpies across 14 groups of varying size, using a battery of four psychometric tasks. Individual performance correlated positively across tasks, indicative of a “general intelligence” factor, and critically, group size showed strong positive associations with performance across all tasks, whereas morphological variables and neophobia did not. These results highlight the potential effect of group size on the expression of cognitive traits in wild animals.

## 2.2 Main text

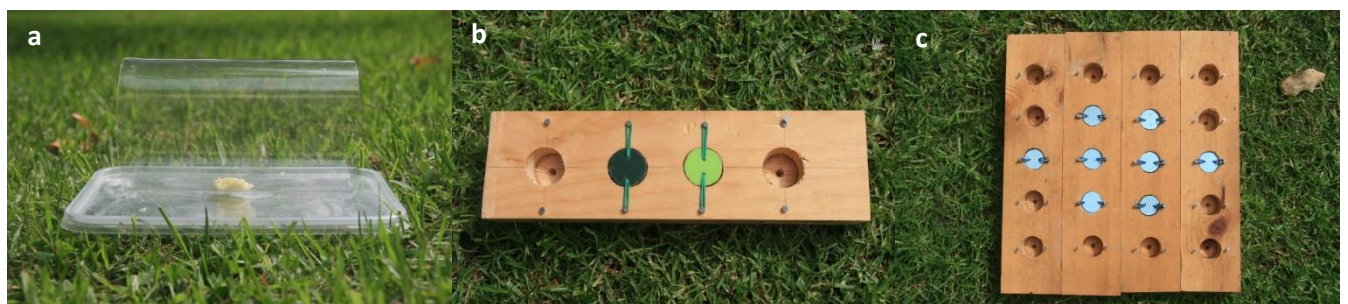
The social intelligence hypothesis (SIH) is a widely accepted explanation for the evolution of intelligence, and posits that the demands of living in complex social systems drive the evolution of sophisticated cognitive abilities<sup>1-3</sup>. Maintaining and coordinating relationships, monitoring third party relationships, and anticipating and reacting strategically to the actions of other group members are argued to be among the cognitively demanding problems unique to social animals<sup>4-6</sup>.

Evidence for the social intelligence hypothesis comes mainly from comparative studies on mammals and birds<sup>7,8</sup>. For instance, measures of brain size and cognitive performance have been shown to correlate with a number of indicators of social complexity, including group size<sup>5,9</sup>, the presence of stable individualized relationships<sup>5,10</sup>, and social systems with fission-fusion dynamics<sup>11</sup>. In addition, social species often outperform asocial species in cognitive tasks<sup>9,12</sup>.

If sociality has a causal effect on cognitive abilities, one may predict differences in social experience to generate intraspecific variation in cognition. Measures of brain structure, which have been found to be good indicators of cognitive ability<sup>13-17</sup>, correlate with social network size in humans<sup>18-20</sup> and captive macaques<sup>21</sup>, and rearing group size in cichlids<sup>22</sup>. Other studies on captive animals have generated conflicting results<sup>23</sup>, but the effects of group size are often confounded by stocking density, aggression or social deprivation<sup>23</sup>. Critically, the relationship between group size and cognitive performance in wild populations are unknown. To determine whether group size is associated with cognition in ecologically relevant contexts, it is critical to examine relationships between group size and cognitive ability in the wild.

We quantified individual cognitive ability in a population of wild Australian magpies (Western Australian subspecies, *Cracticus tibicen dorsalis*) by presenting individuals with a cognitive test battery comprising four different tasks designed to measure performance in behavioural inhibition, associative learning, reversal learning, and spatial memory (Figure 2.1). These domain-general

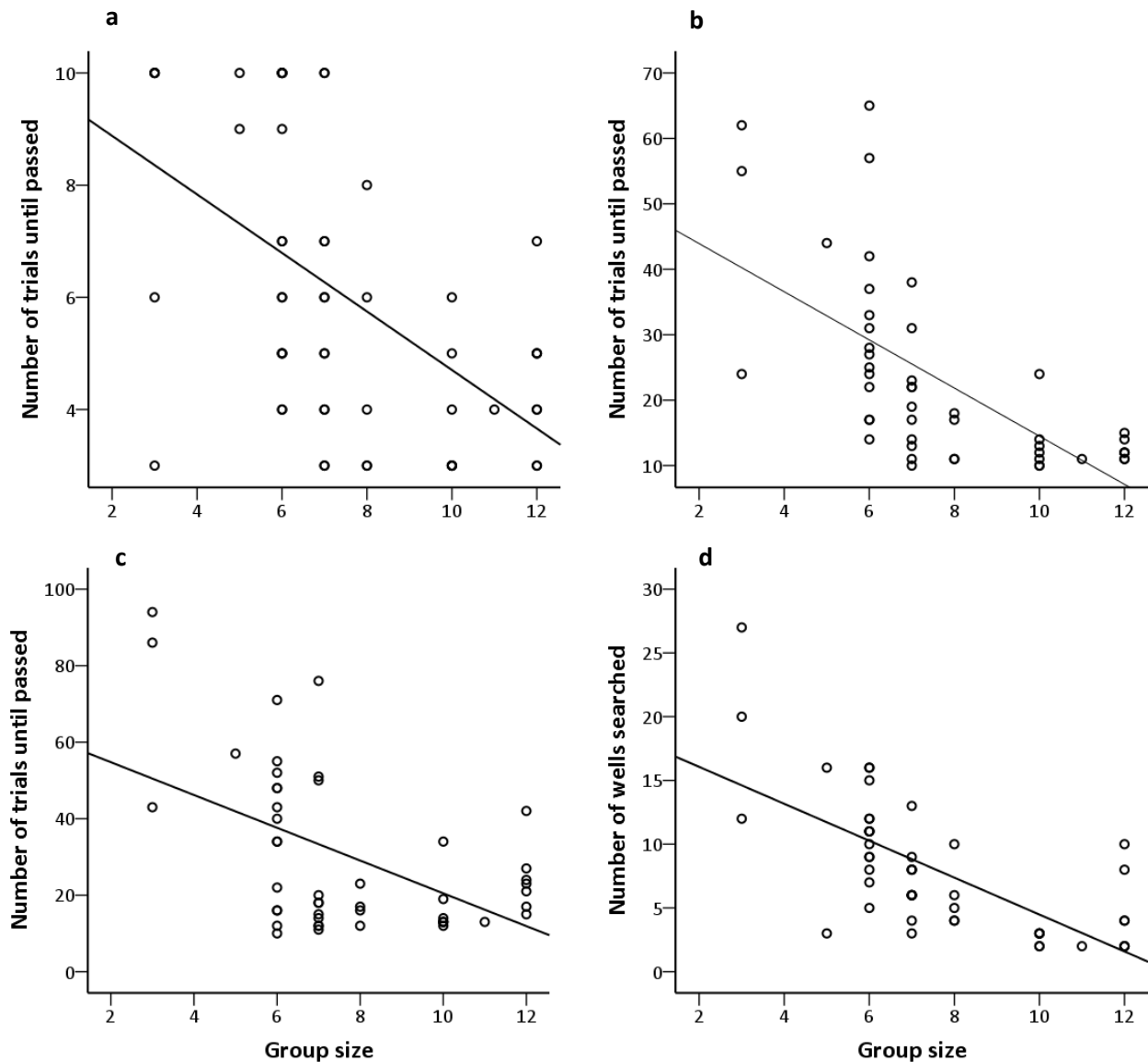
cognitive processes likely play an important role in both social and individual behaviours including foraging, predator avoidance and reproduction<sup>24,25</sup>. We quantified cognitive performance in 56 birds from 14 groups that ranged in size from 3-12 individuals. Western Australian magpies live in stable family groups, and exhibit cooperative behaviours such as territory defence and alloparental care, although extra-group paternity in magpies is the highest recorded for any bird species (>82%)<sup>26</sup>, indicating a high amount of gene flow across groups. Reproductive skew is very low, with all adult females typically attempting to breed each year<sup>27</sup>.



**Figure 2.1** The cognitive test battery used to quantify individual variation in (a) behavioural inhibition (b) associative and reversal learning (c) spatial memory

We found that group size was the strongest predictor of individual performance across all four tasks (Tables S2.1 to S2.4), with individuals from larger groups performing better than those from smaller groups (Figure 2.2). In human psychometric testing, individual performance across psychometric tests is usually correlated, and a general cognitive factor, commonly called general intelligence (*g*), typically accounts for around 30% of the total variance in test performance<sup>28,29</sup>. In non-human animals, general intelligence has been reported across a number of taxa, including honeybees<sup>30</sup>, birds<sup>31,32</sup>, primates<sup>33</sup>, and rodents<sup>34</sup>, though evidence is equivocal and contentious<sup>35,36</sup>. Individual task performance in magpies was significantly positively correlated across all four tasks (Table S2.5), and a principal components analysis (PCA) revealed that performance in all four tasks loaded positively onto the first principal component (PC1; eigenvalue >1). This accounted for 64.6% of the total variance in task performance (Table 2.1), a substantially higher proportion than in previous studies on other species<sup>28-33</sup>, providing strong support for general cognitive performance in

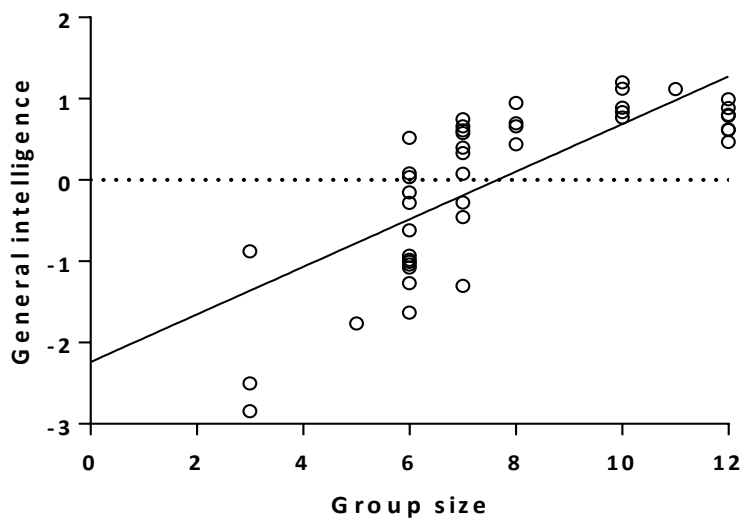
individuals. Furthermore, PC1 was also significantly positively correlated with group size ( $r_s=0.82$ ,  $N=46$ ,  $P<0.0001$ ), indicating a robust relationship between sociality and  $g$  (Figure 2.3). To confirm that task performance was repeatable we ran a second battery of cognitive tasks two weeks later using causally identical, but visually distinctive tasks (see supplementary materials). We found high levels of repeatability in individual performance in all four tasks: behavioural inhibition ( $r=0.806$ ,  $P<0.0001$ ), associative learning ( $r=0.97$ ,  $P<0.0001$ ), reversal learning ( $r=0.975$ ,  $P<0.0001$ ) and spatial memory ( $r=0.932$ ,  $P<0.0001$ ) (Table S2.6), indicating that the tasks provide robust measures of individual cognitive performance, rather than ‘noise’ due to contextual variables.



**Figure 2.2** The relationship between group size and cognitive performance in tasks quantifying (a) behavioural inhibition (b) associative learning (c) reversal learning and (d) spatial memory. Lines represent best fit. Results from the first cognitive test battery.

**Table 2.1** Results of the principal components analysis for magpies that completed all four tasks in the first cognitive test battery. All tasks loaded positively onto the one principal component extracted with an eigenvalue >1. N=46.

Task	PC1
Behavioural inhibition	0.703
Associative learning	0.789
Reversal learning	0.870
Spatial memory	0.841
Eigenvalue	2.582
% of total variance explained	64.56



**Figure 2.3** The relationship between group size and general intelligence

The social intelligence hypothesis is traditionally portrayed as an evolutionary hypothesis. However, our results suggest that social variation may also have important developmental effects on individual cognitive performance. To unequivocally determine causality in the observed relationship between

group size and cognitive performance, experimental manipulations would be necessary; however, this is very difficult on wild populations of animals. Research on humans, chimpanzees and rodents indicate that intelligence is heritable<sup>28,33,37,38</sup>, and studies on a number of species have reported positive associations between measures of cognitive performance and indicators of fitness (<sup>39-41</sup> although see<sup>42</sup>). It is therefore possible that larger groups containing individuals with elevated levels of *g* might form as a result of individuals with elevated levels of *g* producing more offspring. However, the extraordinarily high rates of extra-group paternity in our study population<sup>26</sup> make this explanation unlikely, as extensive gene flow is likely to preclude substantial genetic differentiation between groups. Another possible explanation for the link between cognitive performance and group size is that magpies preferentially join groups containing individuals with similar traits. However, in over four years of life-history data collection we have no evidence of social assortment occurring. It is also worth noting that frequency distributions comparing general intelligence between small and large groups indicate that larger groups do not contain individuals with greater general intelligence due to statistical probability (Figure S2.1). Instead, we suggest that living in larger group sizes has a causal influence on individual cognitive performance.

There are a number of potential explanations for how living in larger groups may lead to increased cognitive performance. First, individuals in larger groups may be less likely to suffer the deleterious effects of nutritional stress on cognitive development<sup>43-45</sup> because increased rates of vigilance and the presence of helpers permit greater foraging success and higher rates of offspring provisioning<sup>46,47</sup>. However, we found no effect of body size or foraging efficiency on cognitive performance (Tables S2.1-S2.4). Moreover, analyses of behavioural focal follows show no effect of group size on offspring provisioning rates (Table S2.7). However, it is worth noting that nutritional quality, rather than quantity, may be important; this possibility needs further investigation.

Second, animals in larger groups may be better able to manifest their cognitive abilities during tests if, for example, they need to spend less time being vigilant or show reduced fear responses towards



test apparatus. However, predation pressure in our study population is negligible, and we recorded no antipredator behaviour during any of the task presentations. In addition, there was no relationship between group size and time spent interacting with the task (supplementary text), and neophobia failed to predict performance in any of the tasks (Tables S2.1 to S2.4).

Consequently, we suggest the cognitive demands of living in larger social groups may lead directly to the development of elevated cognitive performance. There is extensive evidence that cognitive challenges can modify brain regions; the archetypal example being London taxi drivers, whose posterior hippocampi are significantly larger than that of control subjects, due to the navigational demands of their jobs<sup>48</sup>. In a similar way, the challenges of living in larger groups may directly promote improvements in cognitive performance in wild animals. In our study we did not know, for the majority of individuals, the size of the group they grew up in due to most individuals being born before we started observing groups. It is therefore not clear whether any developmental effects of group size on cognition are driven by experiences in early life, in adulthood or both. Determining whether there are particular sensitive periods during which social structure shapes cognition is a key task for future research.

Variation in social structure is widely thought to contribute to cognitive differences between species<sup>1-3</sup>. Our results highlight the role of similar effects *within* species. We show that cooperatively breeding Australian magpies living in larger groups show elevated performance across a battery of four different cognitive tasks, and provide compelling evidence for a general intelligence factor, with strong correlations in individual performance across all tasks. The association between group size and general intelligence cannot be explained by variation in body condition, foraging success, neophobia or attention to the task, suggesting that the challenges of life in large groups may exert a direct causal effect on cognitive development. Cognitive benefits may therefore represent an important but hitherto neglected advantage to living in large groups.

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## 2.4 Supplementary materials

## Materials and methods

### Study site and species

The study took place in the urban grassland areas of Guildford, Western Australia, and the University of Western Australia campus, between October 2015 and February 2016. The study population consists of 14 groups of ringed, habituated Australian magpies (Western Australian subspecies *Cracticus tibicen dorsalis*), ranging in size from 3-12 individuals. Unlike other subspecies within Australia, the Western Australian subspecies breeds cooperatively, and lives in territorial groups where adult group size remains stable<sup>26,49</sup>.

The majority of birds within the study population are colour-ringed and habituated to close human observation, allowing the presentation of cognitive tests to most individuals in every group. Moreover, individuals are trained to hop onto electronic top-pan scales in return for a crumb of mozzarella cheese, allowing collection of daily records of individual body mass. Mozzarella was also used as the food reward in the cognitive test battery. Weekly behavioural focals are carried out on all individuals in the study population<sup>27</sup>, from which foraging efficiency is calculated (defined as the amount of food (measured in grams), caught per minute; biomass of food items was calculated by Edwards<sup>27</sup>).

### Cognitive test battery

We carried out a battery of cognitive tests on 56 adult Australian magpies. The battery consisted of four tasks designed to measure behavioural inhibition, associative learning, reversal learning, and spatial memory (Figure 2.1). We chose these tasks because (i) they target well-understood and widely studied cognitive traits spanning cognitive domains<sup>24,32</sup> and (ii) they are likely to be highly ecologically relevant: spatial memory is likely to be important in remembering locations of resources and territory boundaries<sup>50</sup>, while associative and reversal learning enable the acquisition and flexible readjustment of predictive contingencies between cues in the environment, including



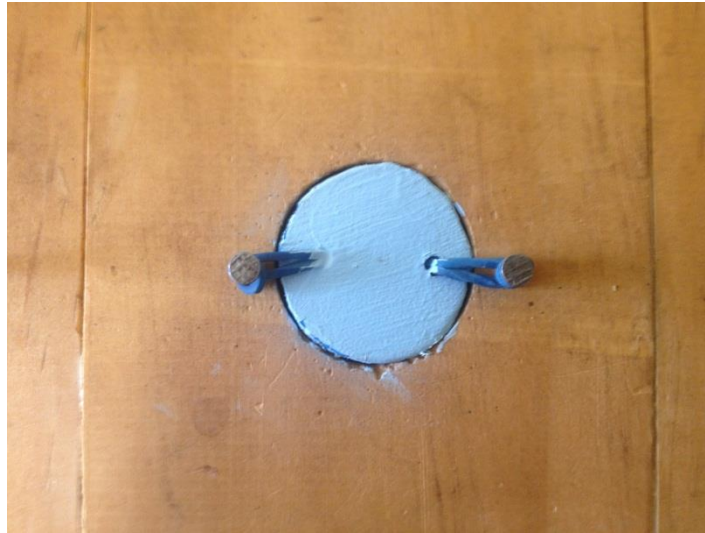
learning from conspecifics' behaviour<sup>24,51,52</sup>. Finally, behavioural inhibition, the ability to inhibit prepotent responses, has been implicated in adaptive decision-making in both social and asocial contexts<sup>11,25,53</sup>. The order in which individuals were tested on the tasks was randomised (except for the reversal learning task, which was always carried out 24hrs after the associative learning task).

To ensure that we were testing individual performance, and to control for the potentially confounding effect of social learning or social interference, all trials were carried out in social isolation. This was achieved by ensuring that no other birds were within 10m of the bird being tested. This was possible as magpies often forage over 10m away from each other. Performance was recorded once an individual started interacting with the task (defined as making contact with the task). If another bird (or another disturbance such as a human) approached within 10m, before the individual started interacting with the task, the trial was discontinued and no cognitive performance data was recorded. If the individual was already interacting with the task, it was permitted to continue the trial until completion. The short nature of the experimental trials meant the focal individual had ample time to complete the trial before the "disturbance" approached much closer. Furthermore, a second observer "shepherded" away any individuals approaching within 10m of the task. This approach meant no trials had to be discontinued once an individual started interacting with the task. Inclement weather did not prevent any trials being carried out. To verify that individuals were tested in isolation, we included "test order" as an explanatory term in the analyses investigating factors affecting performance, to check that individuals tested later within a group did not perform better than those tested earlier. Tasks were placed directly in front of the test subjects. Experiments were run between 0500 and 1000 hours and were recorded live by the observers (B.J.A. and E.K.E.). One observer recorded individual performance, whilst the other recorded neophobia (defined as the time elapsed between the test subject first coming within 5m of the apparatus and first touching the apparatus), and antipredator behaviour within the group. The time spent interacting with the task (defined as the time elapsed between the test subject first and last making contact with the task) was also recorded for the detour-reaching task.

Behavioural inhibition: To quantify behavioural inhibition we presented individuals with a detour reaching task<sup>53</sup>. This consisted of a transparent open-ended cylinder (13cm length, 5cm diameter, Figure 2.1a) in which a food reward was placed in the centre. Test subjects were presented with the task such that the open ends of the cylinder were facing away from the individual's direction of gaze. A trial was deemed successful if the test subject inhibited the prepotent response of pecking the transparent cylinder, and detoured around to the open ends of the cylinder to gain access to the food reward. Once an individual successfully detoured to the open ends of the cylinder without pecking the transparent walls 3 times in a row, it was considered to have passed the behavioural inhibition experiment. The number of trials taken to pass was the measure of success. Trials were carried out at one-minute intervals with a maximum of 10 trials, and when possible, all trials were carried out on the same day. Other studies using the detour-reaching task commonly include a training phase in which test subjects are presented with an opaque tube before being exposed to the transparent tube (e.g. Boogert *et al.*<sup>53</sup>). We did not include the opaque phase in our study because it generates difficulties in interpretation: success in the transparent condition could be linked to behavioural control, or could result from the continued application of a learned rule: pecking at the open ends of the cylinder was rewarded in the opaque condition, so individuals may persist with this behaviour in the transparent condition.

Associative learning: The associative learning task consisted of a wooden foraging grid (31 x 9 x 4cm) containing two wells (3.5cm diameter, 2.5cm deep, Figure 2.1b). The presence of only two wells allowed experimental trials to be carried out quickly, reducing the chance of non-focal birds detecting and approaching the task. The wells were covered with PVC lids that fitted exactly into the wells, and were held in place by elastic bands that were threaded through drilled holes in the lids and fastened to either side of the well (Figure S2.2). This created an axis on which the lids would swivel when pecked. Birds were first trained to search the wells using a shaping procedure similar to that of Boogert *et al.*<sup>54</sup>: magpies could gain access to a food reward (a small amount of grated mozzarella cheese) by first being exposed to the wells without any lids covering them, secondly with

the lids partially covering the well, and thirdly with the lid fully covering the well. Lid colour in the training phase was yellow, a colour not used in any of the experimental tests. Once a bird had successfully searched the wells when fully covered by lids three times in a row, it moved onto the experimental trials of the associative learning task.



**Figure S2.2** Lids used in the associative learning, reversal learning, and spatial memory tasks were held in place by elastic bands.

During experimental trials the wells were covered by either a dark blue or light blue lid. One of these two colours was randomly assigned to be the rewarded colour for each of the test subjects. We used dark and light shades of one colour, rather than distinct colours (i.e. red vs yellow), in order to minimise any potential effects of past experience with particular colours on task performance<sup>55</sup>.

Following Shaw *et al.*<sup>32</sup>, test subjects were allowed to search both wells in the first trial to demonstrate that only one of the wells contained a food reward. In all subsequent trials, the bird was only allowed to search one well before the task was removed. Test subjects had a maximum of one minute to complete the task. There was a minimum interval of one minute between trials (mean + SD= 1.06 ± 0.35 minutes; range = 1-6 minutes), and a maximum of 50 trials per individual per day; differences in inter-trial interval were unrelated to group size ( $r_s=0.048$ ,  $P=0.121$ ,  $N=1027$  trials).

Trials were continued the following day if the maximum number of trials was reached. We ensured

that the baited well was pseudo-randomised, and not on the same side of the foraging grid for more than 3 consecutive trials, to ensure that colour was the cue being associated with a food reward, rather than the side of the grid. Following Shaw *et al.*'s<sup>32</sup> rationale, an individual was considered to have passed the task when it pecked the rewarded colour in 10 out of 12 consecutive trials (10/12 correct represents a significant deviation from random binomial probability; binomial test:  $P=0.039$ ).

Reversal learning: 24hrs after the completion of the associative learning task individuals were tested on a reversal learning task. The same foraging grid was presented to individuals; the only difference being the colour of the rewarded lid was reversed from that of the associative learning task.

Otherwise the experimental protocol and the criteria for passing were exactly the same as the associative learning task described above.

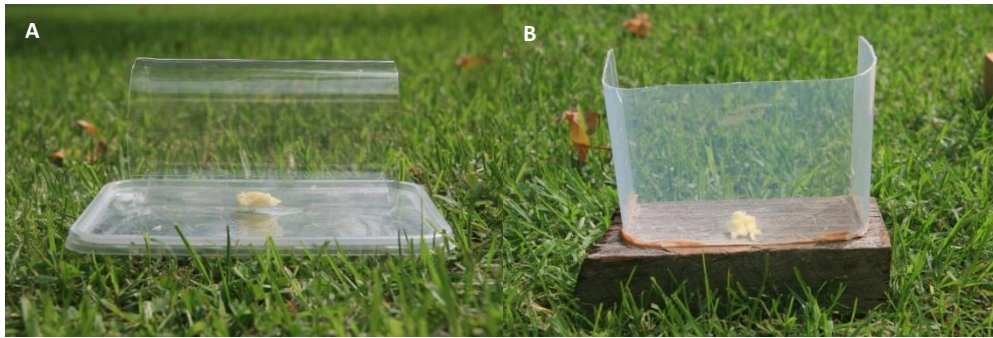
Spatial memory: The spatial memory task consisted of a wooden foraging grid (40 x 36 x 4.5cm) containing 8 wells (3.5cm diameter, 2.5cm deep). The wells were arranged in three rows, the first containing 2 wells, the second 4, and third 2 (Figure 2.1c). All wells were equidistant from one another (6cm). The wells were covered with lids exactly like those used in the associative and reversal learning experiments, so no training phase was necessary. Following Shaw *et al.*'s<sup>32</sup> protocol, the experiment consisted of five phases. One of the 8 wells was randomly chosen to be the baited well containing a food reward in all phases of the experiment. The first phase was a "baseline" trial whereby individuals searched the foraging grid for the baited well. Once the test subject had located and eaten the food reward, the foraging grid was removed. Five minutes after the baseline trial, the second "training" phase was carried out, whereby the same well was baited, and the test subjects had to search for the food reward again. The third and fourth phases were experimental trials where test subjects were presented with the foraging grid 24hrs and 48hrs after the training phase respectively. The cumulative number of wells searched before locating the rewarded well in the third and fourth phases of the experiment was the spatial memory score, thus larger scores indicate poorer performance. To control for olfactory cues the foraging grid was

presented a fifth time (5 minutes after the 48hr post-training phase trial), rotated 180 degrees, and without a baited well. The foraging grid would appear identical to the magpie, but the position of the previously baited well would be on the opposite side of the grid compared to the other phases of the experiment. If the test subject had remembered the location of the rewarded well in the experimental phases, one would predict that it would search the well opposite the previously baited well. If the test subjects were using olfactory cues to locate the rewarded well one would predict that the previously baited well would be searched first.

#### Repeatability of cognitive performance

One of the challenges associated with conducting psychometric tests on animals, particularly in the wild, is ensuring the cognitive trait of interest is being quantified, while accounting for extraneous confounding variables<sup>55</sup>. To ensure this, in addition to using established psychologically grounded tests, we ran a second battery of cognitive tests on individuals to test for repeatability of performance, and thus determine if our measures reflect true cognitive variation rather than noise due to other contextual variables. To examine repeatability, we re-tested all individuals on a second test battery comprised of causally identical but visually distinct versions of each of the four tasks from the first test battery. This ensured the cognitive demands of the second test battery were identical to the first test battery. The second test battery was carried out two weeks after the first test battery.

In the associative and reversal learning task the colour of lids was changed to dark green and light green. In the spatial memory task the location of the rewarded well was changed from the first test battery. In the behavioural inhibition task, rather than using an open ended cylinder, a transparent curved wall (30cm length, 10cm height, Figure S2.3b) was presented with the food reward located behind that. Other than these changes in the appearance of the tasks, the protocol and criteria for passing were exactly the same as the first cognitive test battery.



**Figure S2.3** The task used to measure behavioural inhibition in (a) the first cognitive test battery and (b) the second cognitive test battery, whereby test subjects had to detour around the transparent Perspex wall in order to gain access to the food reward.

### Statistical analyses

To determine the factors influencing individual variation in cognitive ability we analysed cognitive performance using generalised linear mixed models (glmm) with either a poisson distribution with a logarithmic link (behavioural inhibition), or a negative binomial distribution with a logarithmic link to account for over-dispersion (associative learning, reversal learning and spatial memory). Cognitive performance was measured as the number of trials taken to pass the task or the number of wells searched. In addition to the potential cognitive demands of living in larger social groups, it is possible that indirect effects of group size on energy intake and task attention could generate group size effects on cognitive performance<sup>56,57</sup>. For this reason neophobia (recorded for each task, and defined as the time taken to interact with the task once being within 5m of it), body mass, and foraging efficiency (defined as the amount of food biomass, measured in grams, consumed per minute when foraging; recorded during behavioural focals carried outside of experimental trials) were included as explanatory terms in the analysis, as well as sex, the sex ratio of males to females in the group, the order tested within the group, and group size. Group identity was included as a random term in all models.

In avian research it is common to use the residuals of a regression of body mass on tarsus length as a measure of body condition<sup>58</sup>. We only had measures of tarsus length for a subset of individuals in

the study population (N=27). However, tarsus length and body mass did not correlate ( $r=0.226$ ,  $N=27$ ,  $P=0.258$ ), we therefore included both measures as separate explanatory variables in analyses for this subset of individuals (Tables S2.8-S2.11). Dominance status was not included as an explanatory variable as there is not a clear dominance hierarchy within magpie groups. Age and immigration status were not included as explanatory variables because the fledge date and natal origins of the majority of adults in our population are unknown. We note that among the birds whose complete life-history is known (N=19 individuals), there has been no movement between groups.

We analysed our data using a model selection process; terms were ranked in order of their corrected quasi-information criterion (QICc) values (the lowest QICc value has the greatest explanatory power<sup>59</sup>). If a term was more than two QICc units smaller than any other term, then this was judged to explain the observed relationship in the data better than any other term. If there was more than one term with  $\Delta\text{QICc} < 2$  from the 'best' term, had confidence intervals that did not intersect zero, and explained more variation than the basic model (the model containing no predictors, just the constant and the random terms), then model averaging was carried out on this "top set" of models *sensu* Symonds and Moussalli<sup>60</sup>. All statistical analyses were carried out using IBM SPSS Statistics software (version 22).

To explore the relationship in performance across tasks, we conducted Spearman rank pairwise correlations between all four tasks. To determine if a general cognitive factor explained cognitive performance across all four tasks, we performed a Principal Components Analysis (PCA) with a varimax rotation. Only principal components with an eigenvalue  $>1$  were extracted from the analysis. Total variance in task performance accounted for in the first principal component extracted is used as a measure of general intelligence. A general intelligence factor has been argued to exist when all tasks load positively onto the first principal component and explain  $>30\%$  of total task variance<sup>34</sup>. Following Shaw et al.<sup>32</sup>, to assess whether the tasks loaded onto the first principal

component by chance we compared the mean and standard deviation of the first component factor loadings to the 95% confidence intervals of the means and standard deviations of the first component factor loadings from 10,000 simulations. For each simulation, performance within each task was randomised between individuals (using the `randomizeMatrix` function in the `picante` R package<sup>61</sup>), a PCA was performed, and the mean and standard deviation of the first component factor loadings were obtained. The 95% confidence intervals were then calculated from the stored means and standard deviations from all the simulations.

Statistical analyses used to calculate estimates of repeatability in cognitive performance between the first and second cognitive test batteries were carried out in R (version 3.1.1, <http://www.r-project.org>) with the `rptR` package<sup>62</sup> using a linear mixed model repeatability estimate, with a restricted maximum likelihood function (`reml`).

### **Supplementary text**

In total 56 magpies participated in the cognitive test battery. Of these, 46 participated in all four tasks: 56 participated in the behavioural inhibition task, 48 in the associative and reversal learning tasks, and 49 in the spatial memory task. Seven individuals that took part in the behavioural inhibition task did not take part in the other three tasks because part of their territory became inaccessible due to construction work in the area. One bird died of natural causes during the fieldwork, meaning the sample size of the associative and reversal learning tasks was reduced to 48.

The number of days required to carry out the behavioural inhibition task ranged from 1-3 (mean  $\pm$  SD =  $1.4 \pm 0.484$ , N=56), the number of days required to carry out the associative learning task ranged from 1-5 (mean  $\pm$  SD =  $1.4 \pm 0.824$ , N=48), and the number of days required to carry out the reversal learning task ranged from 1-5 (mean  $\pm$  SD =  $1.4 \pm 0.987$ , N=48). Due to the nature of the spatial memory task, all trials were completed over the course of three days.



The number of trials taken to pass the behavioural inhibition task ranged from 3-10 (mean  $\pm$  SD =  $6.02 \pm 2.569$ , N=56), the number of trials taken to pass the associative learning task ranged from 10-65 (mean  $\pm$  SD =  $22.77 \pm 14.393$ , N=48), the number of trials taken to pass the reversal learning task ranged from 10-94 (mean  $\pm$  SD =  $30.12 \pm 21.242$ , N=48), and the number of wells searched in the spatial memory task ranged from 2-27 (mean  $\pm$  SD =  $7.88 \pm 5.294$ , N=49). Using an equation developed from a hypergeometric distribution assuming sampling without replacement (equation 8 in Tille *et al*<sup>63</sup>), searching any more than 4.5 wells in the spatial memory task constituted searching randomly. Overall, in the 24h experimental trial, magpies did not search significantly less than random (mean  $\pm$  SD =  $4.265 \pm 3.094$ ; one sample t-test:  $t=-0.531$ ,  $P=0.598$ ). However, in the 48h experimental trial, magpies searched significantly fewer wells than would be expected if searching was random (mean  $\pm$  SD =  $3.612 \pm 2.928$ ; one sample t-test:  $t=-2.122$ ,  $P=0.039$ ), suggesting that, on average, magpies remembered where the food was located. There was no significant difference in the number of wells searched between the 48h trial (mean  $\pm$  SD =  $3.759 \pm 3.280$ , N=29) and final 48h + 5 minute trial (mean  $\pm$  SD =  $3.414 \pm 2.457$ , N=29; paired t-test:  $t=1.069$ ,  $P=0.294$ ), indicating magpies did not rely on odour cues to locate food rewards in the spatial memory task.

The order in which individuals were tested within the group did not predict cognitive performance (Tables S2.1 to S2.4), suggesting that individuals tested later in the group did not learn the task by observing individuals tested earlier in the group. If individuals were paying attention to the presence of the task within the group, one may predict that later test subjects may show less neophobia than earlier test subjects. There was no relationship between order tested and neophobia in any of the cognitive tasks; behavioural inhibition ( $r_s=-0.226$ ,  $P=0.094$ , N=56), associative learning ( $r_s=-0.114$ ,  $P=0.440$ , N=48), reversal learning ( $r_s=-0.114$ ,  $P=0.440$ , N=48), and spatial memory ( $r_s=-0.196$ ,  $P=0.178$ , N=49). Together, these results provide convincing evidence that individuals were tested in isolation.

There was no relationship between time spent interacting with the task (recorded for the detour reaching task only) and group size ( $r_s = -0.058$ ,  $P = 0.287$ ,  $N = 337$  trials), suggesting the observed relationship between group size and cognitive performance wasn't due to task attention.

An analysis on a subset of individuals revealed there was no effect of body mass or tarsus length on cognitive performance (Tables S2.8-S2.11). This provides further evidence that morphological variables did not contribute to cognitive performance.

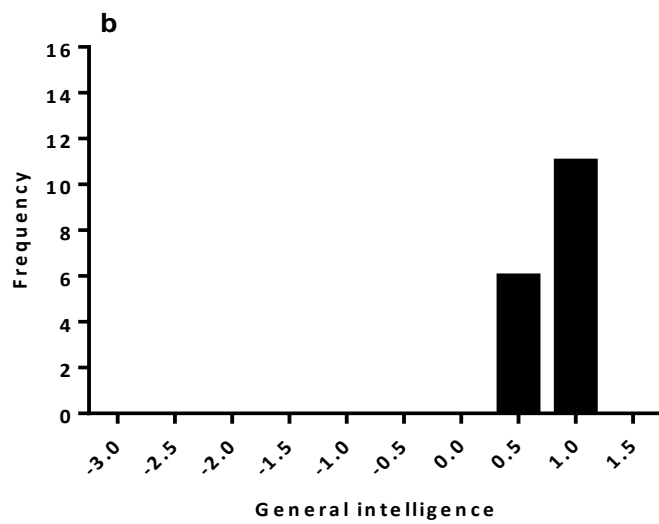
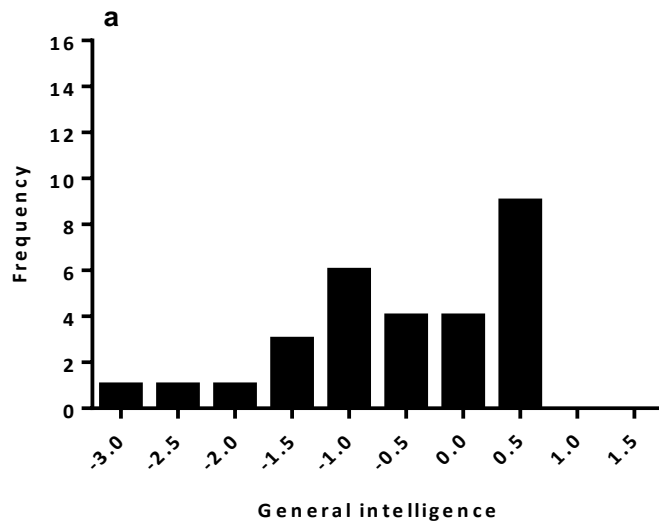
The results obtained from the PCA were highly unlikely to occur due to chance- the mean of the variable loadings obtained from the first principal component (0.8) was larger than the 95% confidence intervals of the simulated means (0.01, 0.57). Furthermore, the standard deviation of the variable loadings obtained from the first principal component (0.07) was smaller than the 95% confidence intervals of the simulated standard deviations (0.17, 0.7), indicating there was much less variation in the variable loadings obtained from the first principal component than by chance.

Finally, it is possible that measures of repeatability between the two cognitive test batteries were influenced by learning. Although the tasks were changed between the first and second cognitive test batteries, it is possible that rule-learning by individuals enhanced performance. In order to investigate this, paired t-tests between performance in the first and second cognitive test batteries were carried out. Performance was not significantly different between the first and second behavioural inhibition tasks ( $t = 0.82$ ,  $P = 0.416$ ,  $N = 56$ ), but individuals performed significantly better in the second cognitive test battery in the associative learning ( $t = 3.001$ ,  $P = 0.004$ ,  $N = 46$ ), reversal learning ( $t = 2.021$ ,  $P = 0.049$ ,  $N = 46$ ), and spatial memory tasks ( $t = 2.856$ ,  $P = 0.006$ ,  $N = 46$ ).

Although individuals performed better in three out of the four tasks in the second cognitive test battery, it is worth noting that the difference in performance, although significant, was very small.

The average number of trials taken to pass the associative learning task in the first cognitive test battery was 22.7, compared to 20.4 in the second cognitive test battery. The average number of trials taken to pass the reversal learning task in the first cognitive test battery was 30.1, compared to

29.7 in the second cognitive test battery. The average number of wells searched in the spatial memory task in the first cognitive test battery was 7.8, compared to 7.4 in the second cognitive test battery. With this in mind, I conclude that learning had a very minor effect on performance in the second cognitive test battery.



**Figure S2.1.** Frequency distribution of general intelligence in (a) small groups (<8 individuals), N=29, and (b) large groups (>8 individuals), N=17.

**Table S2.1** Full model set (top) and top model set (bottom) of candidate terms affecting performance in a behavioural inhibition task using model selection. The top set includes models within 2 QICc values of the best model. N=56 individuals. Group identity was included as a random term.

Term	QICc	$\Delta$ QICc
Group size	44.805	0
Group size+Neophobia <sub>1</sub>	46.673	1.868
Sex*Group size	47.609	2.804
Sex+Group size	48.015	3.21
Basic	61.235	16.43
Body mass	61.281	16.476
Order tested	61.445	16.64
Body mass+Foraging efficiency	61.997	17.192
Body mass*Foraging efficiency	62.131	17.326
Sex ratio	62.213	17.408
Group size*Neophobia	62.381	17.576
Foraging efficiency	62.544	17.739
Sex	62.667	17.862
Neophobia	63.071	18.266
Neophobia*body mass	63.143	18.338
Neophobia*Sex ratio	63.204	18.339
Neophobia+body mass	63.209	18.404
Sex+Foraging efficiency	63.224	18.419
Neophobia*Foraging efficiency	63.227	18.422
Sex+body mass	63.303	18.498
Sex*body mass	63.609	18.804
Sex*Foraging efficiency	63.901	19.096
Neophobia+Sex ratio	64.196	19.391
Neophobia+Foraging efficiency	64.225	19.42
Sex+Sex ratio	64.312	19.507
Sex+Neophobia	64.511	19.706
Sex*Sex ratio	65.970	21.165
Sex*Neophobia	66.01	21.205

Parameter	Estimate	Standard error	Confidence intervals
Group size	-0.092	0.0176	-0.126, -0.058

<sub>1</sub>although within two QICc of the top model, not included in top model set as the confidence intervals intersected zero.

**Table S2.2** Full model set (top) and top model set (bottom) of candidate terms affecting performance in an associative learning task using model selection. The top set includes models within 2 QICc values of the best model. N=48 individuals. Group identity was included as a random term.

Term	QICc	$\Delta$ QICc
Group size	10.778	0
Group size+Neophobia <sub>1</sub>	12.777	1.999
Sex*Group size	14.486	3.698
Sex+Group size	14.479	3.701
Basic	16.446	5.658
Order tested	17.897	7.119
Group size*Neophobia	18.069	7.281
Body mass*Foraging efficiency	18.229	7.451
Foraging efficiency	18.268	7.48
Sex ratio	18.313	7.535
Neophobia*Foraging efficiency	18.388	7.6
Neophobia	18.423	7.635
Neophobia*body mass	18.429	7.641
Neophobia*Sex ratio	18.440	7.662
Body mass	18.43	7.642
Sex	19.091	8.303
Body mass+Foraging efficiency	20.235	9.455
Neophobia+Foraging efficiency	20.260	9.482
Neophobia+Sex ratio	20.311	9.533
Sex*Neophobia	20.369	9.581
Neophobia+body mass	20.397	9.619
Sex*Foraging efficiency	20.696	9.908
Sex+Foraging efficiency	20.848	10.07
Sex+Body mass	20.913	10.135
Sex*Body mass	20.955	10.167
Sex+Neophobia	21.000	10.222
Sex+Sex ratio	21.07	10.292
Sex*Sex ratio	21.319	10.541

Parameter	Estimate	Standard error	Confidence intervals
<b>Group size</b>	<b>-0.162</b>	<b>0.0264</b>	<b>-0.214, -0.111</b>

<sub>1</sub>although within two QICc of the top model, not included in top model set as the confidence intervals intersected zero.

**Table S2.3** Full model set (top) and top model set (bottom) of candidate terms affecting performance in a reversal learning task using model selection. The top set includes models within 2 QICc values of the best model. N=48 individuals. Group identity was included as a random term.

Term	QICc	$\Delta$ QICc
Group size	18.41	0
Group size+Neophobia <sub>1</sub>	20.408	1.998
Sex+Group size	20.792	2.382
Sex ratio	21.072	2.662
Sex*Group size	21.362	2.952
Basic	21.455	3.045
Sex	22.066	3.656
Order tested	22.085	3.675
Sex+Sex ratio	22.859	4.449
Body mass	23.018	4.608
Neophobia+Sex ratio	23.047	4.637
Sex*Neophobia	23.065	4.655
Group size*Neophobia	23.152	4.742
Neophobia*Foraging efficiency	23.26	4.85
Neophobia	23.358	4.948
Neophobia*body mass	23.391	4.981
Foraging efficiency	23.446	5.036
Neophobia*Sex ratio	23.452	5.042
Body mass*Foraging efficiency	23.452	5.042
Sex+Foraging efficiency	23.995	5.585
Sex+Neophobia	24.056	5.646
Sex+body mass	24.060	5.65
Sex*Sex ratio	24.120	5.71
Sex*Body mass	24.194	5.784
Sex*Foraging efficiency	24.607	6.197
Neophobia+Body mass	24.984	6.574
Body mass+Foraging efficiency	25.015	6.605
Neophobia+Foraging efficiency	25.358	6.948

Parameter	Estimate	Standard error	Confidence intervals
Group size	-0.121	0.0523	-0.224, -0.019

<sub>1</sub>although within two QICc of the top model, not included in top model set as the confidence intervals intersected zero.

**Table S2.4** Full model set (top) and top model set (bottom) of candidate terms affecting performance in a spatial memory task using model selection. The top set includes models within 2 QICc values of the best model. N=49 individuals. Group identity was included as a random term.

Term	QICc	$\Delta$ QICc
Group size	13.652	0
Group size+Neophobia <sub>1</sub>	15.652	2.000
Sex*Group size	17.467	3.815
Sex+Group size	17.629	3.977
Basic	20.784	7.132
Body mass	21.732	8.08
Sex ratio	21.907	8.345
Neophobia	22.035	8.383
Neophobia*Foraging efficiency	22.116	8.464
Neophobia*Body mass	22.124	8.472
Order tested	22.546	8.894
Group size*Neophobia	22.548	8.896
Neophobia*Sex ratio	22.653	9.001
Foraging efficiency	22.774	9.122
Body mass*Foraging efficiency	22.784	9.132
Neophobia+Body mass	23.411	9.759
Neophobia+Sex ratio	23.548	9.896
Sex	23.688	10.036
Body mass+Foraging efficiency	23.732	10.08
Neophobia+Foraging efficiency	24.015	10.363
Sex+Neophobia	24.864	11.212
Sex+Body mass	25.006	11.354
Sex*Body mass	25.015	11.363
Sex+Sex ratio	25.304	11.652
Sex*Neophobia	25.534	11.882
Sex+Foraging efficiency	25.683	12.031
Sex*Sex ratio	25.836	12.274
Sex*Foraging efficiency	26.125	12.473

Parameter	Estimate	Standard error	Confidence intervals
Group size	-0.183	0.0481	-0.277, -0.089

<sub>1</sub>although within two QICc of the top model, not included in top model set as the confidence intervals intersected zero.



**Table S2.5** Spearman rank correlation matrix of cognitive performance between all four tasks in the cognitive test battery.

		Behavioural inhibition	Associative learning	Reversal learning
Associative learning	rs	0.382		
	P	0.008		
	N	47		
Reversal learning	rs	0.433	0.485	
	P	0.002	<0.0001	
	N	47	48	
Spatial memory	rs	0.425	0.594	0.472
	P	0.003	<0.0001	0.001
	N	48	47	47

**Table S2.6** Estimations of repeatability between the first cognitive test battery and the second cognitive test battery

Task	Repeatability	SE	Confidence intervals	P
Behavioural inhibition	0.806	0.049	0.691, 0.882	<0.0001
Associative learning	0.970	0.01	0.946, 0.983	<0.0001
Reversal learning	0.975	0.008	0.954, 0.986	<0.0001
Spatial memory	0.932	0.021	0.879, 0.963	<0.0001

**Table S2.7** Full set of parameters used to explain variation in the proportion of time helpers invested in young. Data based on 108, 1-2 hour observations of 19 helpers over two breeding seasons. Reproduced from Pike <sup>49</sup> with permission.

Model	AICc	$\Delta$ AICc
Chick age	-144.18	0
Chick age+Sex	-141.93	2.25
Basic	-138.93	5.25
Group size	-138.01	6.17
Chick age*Sex+ Group size	-137.83	6.35
Group size+Sex	-137.02	7.16
Sex	-136.75	7.43
Chick age+Group size	-130.1	14.08

**Table S2.8** The effect of tarsus length and body mass on performance in a detour reaching task. N=27 individuals. Group identity was included as a random term.

Term	QICc	$\Delta$ QICc
Tarsus <sub>1</sub>	33.697	0
Basic	33.991	0.294
Mass*Tarsus	34.279	0.582
Tarsus*Foraging efficiency	35.456	1.759
Tarsus+Neophobia	35.549	1.852
Tarsus+Foraging efficiency	35.612	1.915
Body mass+Tarsus	35.69	1.993
Body mass*Foraging efficiency	35.821	2.124
Body mass	35.839	2.142
Body mass*Neophobia	35.991	2.294
Tarsus*Neophobia	35.991	2.294
Tarsus*Sex	36.923	3.226
Tarsus+Sex	36.976	3.279
Body mass+Foraging efficiency	37.617	3.920
Body mass+Neophobia	37.839	4.142
Body mass*Sex	39.671	5.974
Body mass+Sex	39.75	6.053

<sub>1</sub>although explained more variation than the basic model, this term is not considered significant as the confidence intervals intersected zero.

**Table S2.9** The effect of tarsus length and body mass on performance in an associative learning task. N=27 individuals. Group identity was included as a random term.

Term	QICc	$\Delta$ QICc
Basic	8.898	0
Tarsus	9.88	0.982
Mass	10.551	1.653
Mass+Tarsus	10.594	1.696
Mass*Neophobia	10.612	1.714
Tarsus*Neophobia	10.689	1.791
Body mass*Tarsus	10.743	1.845
Body mass*Foraging efficiency	10.831	1.933
Tarsus*Foraging efficiency	10.891	1.993
Tarsus+Neophobia	11.786	2.888
Tarsus+Foraging efficiency	11.876	2.978
Body mass+Neophobia	12.343	3.445
Body mass+Foraging efficiency	12.472	3.574
Tarsus*Sex	12.65	3.752
Tarsus+Sex	12.696	3.798
Body mass*Sex	13.06	4.162
Body mass+Sex	13.086	4.188

**Table S2.10** The effect of tarsus length and body mass on performance in a reversal learning task. N=27 individuals. Group identity was included as a random term.

Term	QICc	$\Delta$ QICc
Basic	8.432	0
Mass*Tarsus	10.097	1.665
Tarsus	10.173	1.741
Body mass	10.27	1.838
Tarsus*Neophobia	10.351	1.919
Body mass*Neophobia	10.356	1.924
Tarsus*Foraging efficiency	10.387	1.955
Body mass*Foraging efficiency	10.409	1.977
Body mass+Tarsus	12.096	3.664
Tarsus+Neophobia	12.139	3.707
Tarsus+Foraging efficiency	12.16	3.728
Body mass+Neophobia	12.178	3.746
Body mass+Foraging efficiency	12.239	3.807
Tarsus+Sex	14.097	5.665
Tarsus*Sex	14.103	5.671
Body mass*Sex	14.127	5.695
Body mass+Sex	14.141	5.709

**Table S2.11** The effect of tarsus length and body mass on performance in a spatial memory task. N=27. Group identity was included as a random term.

Term	QICc	$\Delta$ QICc
Basic	10.662	0
Tarsus*Foraging efficiency	11.849	1.187
Body mass*Foraging efficiency	11.944	1.282
Tarsus	12.356	1.694
Body mass*Tarsus	12.362	1.7
Body mass	12.514	1.852
Body mass*Neophobia	12.588	1.926
Tarsus*Neophobia	12.609	1.947
Tarsus+Foraging efficiency	13.709	3.047
Body mass+Foraging efficiency	13.74	3.078
Body mass+Tarsus	14.318	3.656
Tarsus+Neophobia	14.399	3.737
Body mass+Neophobia	14.452	3.79
Body mass*Sex	15.955	5.293
Tarsus*Sex	15.961	5.299
Body mass+Sex	15.968	5.306
Tarsus+Sex	15.987	5.325

## CHAPTER THREE

### The influence of rearing group size on cognitive development in a group living bird



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### 3.1 Abstract

Early developmental conditions can have a substantial impact on an individual's life, including the development of cognition. The prevailing explanation for the evolution of cognition, the social intelligence hypothesis (SIH), theorises that cognitive ability evolved as a consequence of the pressures of living in social groups. The SIH is traditionally portrayed as an evolutionary hypothesis, and receives support from comparative studies; however the possibility that sociality has an influence on cognitive development remains untested in wild populations of animals. In order to determine the effect of rearing group size on the development of cognition, we quantified cognitive ability in Australian magpie fledglings (Western Australian subspecies *Cracticus tibicen dorsalis*) at 100, 200, and 300 days post-fledging. Cognitive ability was quantified using a battery of four psychometric tasks, designed to measure behavioural inhibition, associative learning, reversal learning, and spatial memory. We found that at 100 days post-fledging there was no effect of group size on cognitive performance. However, at both 200 days and 300 days post-fledging there was a significant positive relationship between group size and cognitive performance. Together, our results provide evidence of an interaction between group size and age tested, whereby individuals from larger groups perform better than individuals from smaller groups at older ages. We provide the first evidence for a relationship between rearing group size and the development of individual cognitive ability in a wild population of animals.

### 3.2 Introduction

The rearing environment of animals can have a profound impact on an individual's life. Unfavourable rearing conditions have been shown to influence survivorship and health<sup>1</sup>, future reproductive success<sup>2</sup>, the acquisition of mating territories<sup>3</sup>, migratory behaviour<sup>4</sup>, and the development of emotional responses and social behaviour<sup>5</sup>.

As well as behavioural, physiological, and life history traits, there is also evidence to suggest conditions experienced early in life can affect the development of cognition. Compensatory growth resulting from nutritional stress during development was found to reduce adult performance in an associative learning task in zebra finches (*Taeniopygia guttata*)<sup>(6, although see 7)</sup>. Similarly, evidence from cleaner wrasse (*Labroides dimidiatus*) and rodents<sup>8,9</sup> suggest that complex habitats can have positive impacts on the development of cognitive traits, whereas ecologically simple environments hinder cognitive development. This is further supported by evidence that environmental enrichment contributes to cognitive development in captive animals<sup>10</sup>. Moreover, environmental change has been found to promote cognitive development in fish<sup>11</sup>, whereby fluctuating conditions promote greater learning abilities.

Although there is evidence indicating that nutritional and ecological factors impact the development of cognitive traits, the effect of the social environment on the development of cognitive ability in wild populations of nonhuman animals is less clear. This is perhaps surprising considering that living in complex social environments is commonly argued to be a key driver of the evolution of cognitive traits<sup>12-14</sup>. The Social Intelligence Hypothesis is primarily supported by interspecific comparisons relating differences in cognitive performance or brain size to differences in social complexity, including group size<sup>15-21</sup>. However, the effect of the social environment on the *development* of cognition has received relatively little attention. If, as predicted by the SIH, there is a relationship between sociality and cognitive ability, it may be hypothesised that rearing group size may also have a causal effect on the development of cognitive performance in individuals.

There is increasing support for the argument that an intraspecific approach to the study of cognition, focusing on individual variation in cognitive traits, is fundamental if we are to determine how sociality may influence the evolution and development of cognition. Evidence from studies on apes have found an effect of social complexity on the development of vocal comprehension<sup>22</sup>, however, there have been few studies that directly measure the effect of group size on the development of cognition<sup>23–25</sup>. However, two studies have produced compelling results: rearing group size was found to determine brain size in cichlids<sup>25</sup> (*Neolamprologus pulcher*), and experimental manipulations of group size promoted changes in neural circuits in young adult rhesus macaques<sup>23</sup> (*Macaca mulatta*). In contrast no effect of rearing environment was found on the development of spatial learning ability in tree shrews<sup>26</sup> (*Egernia striolata*). Critically, no studies have been carried out on wild populations of animals, where findings are likely to be most ecologically relevant<sup>27,28</sup>. However, group size predicted general intelligence in adult Australian magpies (Chapter 2), raising the possibility that rearing group size has an influence on the development of cognition in magpie fledglings.

We quantified cognitive performance in Australian magpies (Western Australian subspecies *Cracticus tibicen dorsalis*) at three ages: 100, 200, and 300 days post-fledging. At 100 days post-fledging behavioural inhibition and spatial memory was quantified, and at 200 and 300 days post-fledging behavioural inhibition, associative learning, reversal learning, and spatial memory were quantified. The Australian magpie is a cooperatively breeding bird renowned for corvid-like cognitive abilities<sup>29</sup>, thus it is an ideal species to study the relationship between sociality and the development of cognition.

### 3.3 Methods

**Study site and population.** The Australian magpie is a large passerine (250-400g), occurring in territorial groups of two to 15 individuals<sup>30</sup>. Unlike other subspecies of the Australian magpie, the Western Australian subspecies is sexually dichromatic, and breeds cooperatively, with evidence of

alloparental care in both sexes<sup>30-33</sup>. The Australian magpie also has exceptionally high rates of extra group paternity - analyses carried out on the study population revealed extra group paternity rates of over 80%, the highest recorded for any bird species<sup>30</sup>. Nestlings generally fledge 3-4 weeks after hatching<sup>29</sup>, and are nutritionally dependent on other group members for food until at least five weeks post-fledging, although they receive a decreasing amount of parental and alloparental care up to 6 months post-fledging<sup>29</sup>. Individuals are considered juveniles three months post-fledging, and adults one year post-fledging.

The study took place in two suburbs of Perth, Crawley (University of Western Australia campus) and Guildford, Western Australia, from January 2015 to September 2016. The study population consists of 14 groups of magpies ranging in size from three to 12 individuals (excluding fledglings). The majority of individuals in the study population are ringed and habituated to close observation (<2m), allowing detailed behavioural observations to be carried out, as well as the presentation of psychometric tasks to individuals.

**Cognitive tasks.** In order to quantify individual variation in cognitive ability, and determine whether there is a relationship between rearing group size on cognitive performance, we presented fledglings with a battery of four cognitive tasks at three ages: 100, 200 and 300 days post-fledging (Figure 3.1). Cognitive testing commenced at 100 days post-fledging because by this stage individuals spend the majority of their time foraging independently. The cognitive test batteries consisted of tasks designed to quantify four cognitive traits; behavioural inhibition, associative learning, reversal learning, and spatial memory. The cognitive test batteries used at each age category contained causally identical but visually distinct versions of each of the four tasks testing these traits. This ensured the same cognitive traits were tested at each age, whilst making sure the tasks were not the same in appearance, minimising the potentially confounding effect of memory.

In order to quantify behavioural inhibition at 100 days post-fledging we presented individuals with a detour reaching task, whereby a transparent open-ended cylinder (13cm length, 5cm diameter,

Figure 3.1a) containing a food reward (a small crumb of mozzarella cheese), was placed in front of the test subject. The task was presented such that the open ends of the cylinder were facing away from the test subject's direction of gaze; this was easily achievable due to the habituated nature of the study population. Individuals were considered to have passed a trial when they inhibited the prepotent response of pecking the transparent cylinder, and detoured around to the open ends to gain access to the food reward. Individuals were considered to have passed the experiment when they successfully completed three trials consecutively. The number of trials taken to reach this criterion was the behavioural inhibition score. At 200 days post-fledging, rather than using a transparent open ended cylinder, a transparent curved wall was presented with a food reward located behind that (32cm length, 12cm height, Figure 3.1d). At 300 days post-fledging individuals were presented with a detour reaching task consisting of a transparent "umbrella", whereby a food reward could be accessed by detouring underneath the transparent Perspex (55cm circumference, 8cm height, Figure 3.1g). Other than the slight differences in appearance, the criterion for passing the behavioural inhibition tasks at 200 and 300 days post-fledging was exactly the same as that of the first detour-reaching task presented at 100 days post-fledging.

Spatial memory was quantified at 100 days post-fledging by presenting individuals with a wooden foraging grid (40 x 26 x 4cm) containing six wells (3.5cm diameter, 2.5cm deep) covered with lids exactly like those used in the associative and reversal learning tasks, except they were black in colour (Figure 3.1c). One of the six wells was randomly assigned to be the rewarded location for all phases of the experiment. The spatial memory experiment consisted of two phases; firstly the grid was presented in a "baseline trial" whereby individuals were able to search for the rewarded location. A "memory trial" was carried out five minutes later, where individuals were presented with the foraging grid in the exact same arrangement a second time. The number of wells searched before locating the food reward in the memory trial was the spatial memory score. At 200 and 300 days post-fledging the same experiment was carried out, although it was ensured that a different well was randomly assigned to be the rewarded location (Figure 3.1f and 3.1i).

Associative and reversal learning were not quantified at 100 days post-fledging because individuals took a prohibitive amount of trials to complete the tasks (no individuals passed within 20 trials). Associative learning was quantified at 200 days post-fledging by presenting test subjects with a wooden foraging grid (41 x 35 x 4cm) containing 20 wells (3.5cm diameter, 2.5cm deep), covered with 20 plastic lids; 10 a light blue colour and 10 a dark blue colour (Figure 3.1e). We used dark and light shades of one colour, rather than distinct colours (i.e. red vs yellow), in order to minimise any potential effects of past experience with particular colours on task performance<sup>34</sup>. Wells covered with lids of one colour were randomly assigned to be rewarded for the duration of the trials, whereby when pecked, a food reward could be accessed (for details on how the lids work see Chapter 1 and Figure S3.1). Test subjects were considered to have passed the associative learning task when they chose the rewarded well in eight out of the first nine wells searched; this represents a significant deviation from binomial probability (binomial test:  $P = 0.039$ ). The number of trials taken to reach this criterion was the associative learning score. At 300 days post-fledging rather than light and dark blue lids, light and dark green lids were used (Figure 3.1h). Other than the change in lid colour, all protocols and criteria for passing remained the same.

At each developmental stage (200 and 300 days post-fledging), reversal learning was quantified 24 hours after the successful completion of the associative learning task. The protocol and criteria for passing the reversal learning tasks were exactly the same as the associative learning task, except that the previously unrewarded colours were now rewarded.

To ensure that individual cognitive ability was being quantified, and to control for the potentially confounding effects of social learning and social interference, it was ensured that all trials were carried out on individuals in isolation. This was achievable as individuals often forage over 10 metres away from each other. In addition, by 100 days post-fledging, fledglings start to forage independently, making experimentation in isolation a lot easier. All trials were carried out as close to sunrise as possible (between 05:00am and 10:00am) to control for satiation.



**Figure 3.1** Cognitive test batteries presented to individuals at 100 (a-c), 200 (d-f), and 300 (g-i) days post-fledging, containing four tasks designed to quantify behavioural inhibition (a, d, g), associative and reversal learning (b, e, h), and spatial memory (c, f, i). Individuals were unable to complete the associative and reversal learning tasks at 100 days post-fledging (b).

**Statistical analyses.** A series of generalised linear mixed models (GLMMs) were carried out to determine factors affecting cognitive performance in each of the tasks. A model selection approach was used to determine the most significant predictors of performance in each of the cognitive tasks<sup>35</sup>. Terms were ranked in order of their quasi-information criterion (QICc), the lowest values having the greatest explanatory power. If a term was more than two QICc units smaller than any other term, then this was considered the ‘best term’ to explain the variation in the data. If one term or more was within two QICc units of the “best term”, had confidence intervals that did not intersect zero, and explained more variation than the basic model (the null model containing no predictors), then model averaging was carried out on this “top set” of models<sup>36</sup>.

At 100 days post-fledging, the response terms used were cognitive performance; in the detour reaching task this was the number of trials until passed, and in the spatial memory task it was the number of wells searched. As these were count data, generalised linear mixed models with a poisson distribution were used. The relationship between performance in the detour-reaching task and the spatial memory task was also examined using a spearman rank correlation. At 200 and 300 days post-fledging, principal components analyses (PCA), using a varimax rotation were carried out to determine if a general cognitive factor, akin to the “general intelligence” commonly reported in human psychometric studies <sup>37</sup>, accounted for performance across all four tasks. General intelligence is argued to occur if all tasks load positively onto the first principal component extracted with an Eigenvalue over one, and accounts for over 30% of total variance in task performance <sup>38,39</sup>. If evidence of general intelligence was found in magpie fledglings (as for the adults; see Chapter 1), then the measures of general intelligence gained from the first principal component were used as the response term for analyses investigating factors affecting cognitive performance at 200 and 300 days post-fledging.

Explanatory terms included in the models were neophobia (defined as the latency in seconds between an individual first approaching the array to within 5m and first interacting with it), body mass, what stage of the breeding season (early or late), the presence or absence of siblings (from the same brood), group size, and the sex ratio of adult males to females in the group. We were unable to include provisioning rate from adults to fledglings as an explanatory term in analyses as this data was only available for a small subset of individuals. Group ID was included as a random term in all models.

Factors affecting performance across all ages were analysed for each of the four cognitive traits quantified, using generalised linear mixed models. Four separate analyses were carried out, with cognitive performance used as the response terms. An additional two analyses were carried out, firstly to determine factors affecting performance across all ages for both behavioural inhibition and



spatial memory (associative and reversal learning were omitted from this analysis as we only quantified performance at 200 and 300 days post-fledgling in these traits). Secondly, we investigated factors affecting general intelligence measured at 200 and 300 days post-fledgling. Group ID and individual ID were included as random terms. Explanatory terms included were those used for the previous analyses. A model selection approach was used to determine the most significant terms affecting performance. The relationship between mother and offspring cognitive performance was investigated using spearman rank correlations to investigate whether there may be heritable variation in cognitive performance (see supplementary materials).

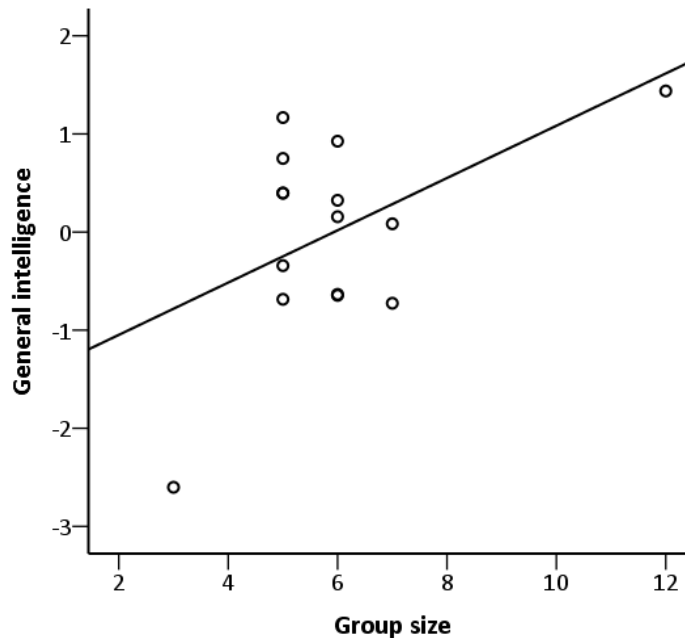
All statistical analyses were carried out using IBM SPSS Statistics software (version 22).

### 3.4 Results

**Factors affecting cognitive performance at 100 days post-fledgling.** 21 fledglings completed the behavioural inhibition and spatial memory tasks at 100 days post-fledgling. The number of trials taken to pass the behavioural inhibition task ranged from 4-10 (mean  $\pm$  SD =  $8.38 \pm 2.061$ ), and the number of wells searched in the spatial memory task ranged from 1-6 (mean  $\pm$  SD =  $3.2 \pm 1.881$ ). It is worth noting that despite their young age, 43% of individuals passed the behavioural inhibition task, and 70% of individuals located the food reward in the spatial memory task through non-random sampling (searching over 3.5 wells constitutes searching randomly; calculated using equation 8 from Tille *et al.*<sup>40</sup>). No predictors explained more variation in cognitive performance in the behavioural inhibition task than the basic model (the null model containing no predictors, Table S3.5). Sex ratio and neophobia were the strongest predictors of performance in the spatial memory task, whereby there was a negative relationship between neophobia and spatial memory, and a positive relationship between a male-biased group sex ratio and spatial memory (Table S3.6, Figure 3.2). There was no effect of group size on performance in either task (Tables S3.5-S3.6), and individual performance was not significantly correlated across the two tasks ( $r_s = -0.381$ ,  $N = 20$ ,  $P = 0.097$ ).



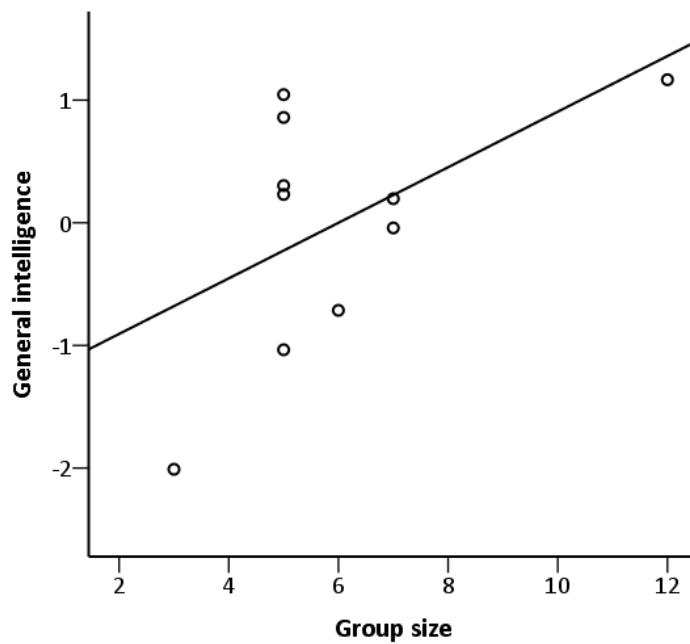
at 200 days post-fledging. Group size was the strongest predictor of general intelligence at 200 days post-fledging, whereby individuals in larger groups recorded a higher value for general intelligence compared to those from smaller groups (Table S3.7, Figure 3.3).



**Figure 3.3** The relationship between general intelligence and group size at 200 days post-fledging. N=15.

**Factors affecting performance at 300 days post-fledging.** 10 fledglings completed the cognitive test battery at 300 days post-fledging. It is worth noting the decreasing sample size of fledglings tested from 100 days post-fledging onwards is due to the high rates mortality in fledglings. The number of trials taken to pass the behavioural inhibition task ranged from 3-10 (mean  $\pm$  SD =  $7.20 \pm 2.741$ ), the number of trials taken to pass the associative learning task ranged from 2-10 (mean  $\pm$  SD =  $5.20 \pm 3.084$ ), the number of trials taken to pass the reversal learning task ranged from 2-10 (mean  $\pm$  SD =  $4.50 \pm 2.506$ ), and the number of wells searched in the spatial memory task ranged from 1-6 (mean  $\pm$  SD =  $2.30 \pm 1.636$ ). A PCA provided evidence of a general intelligence factor; performance in all four tasks positively correlated (Table S3.3), and loaded onto the first principal component extracted with an Eigenvalue over one, accounting for over 80% of total variance in task performance (Table S3.4).

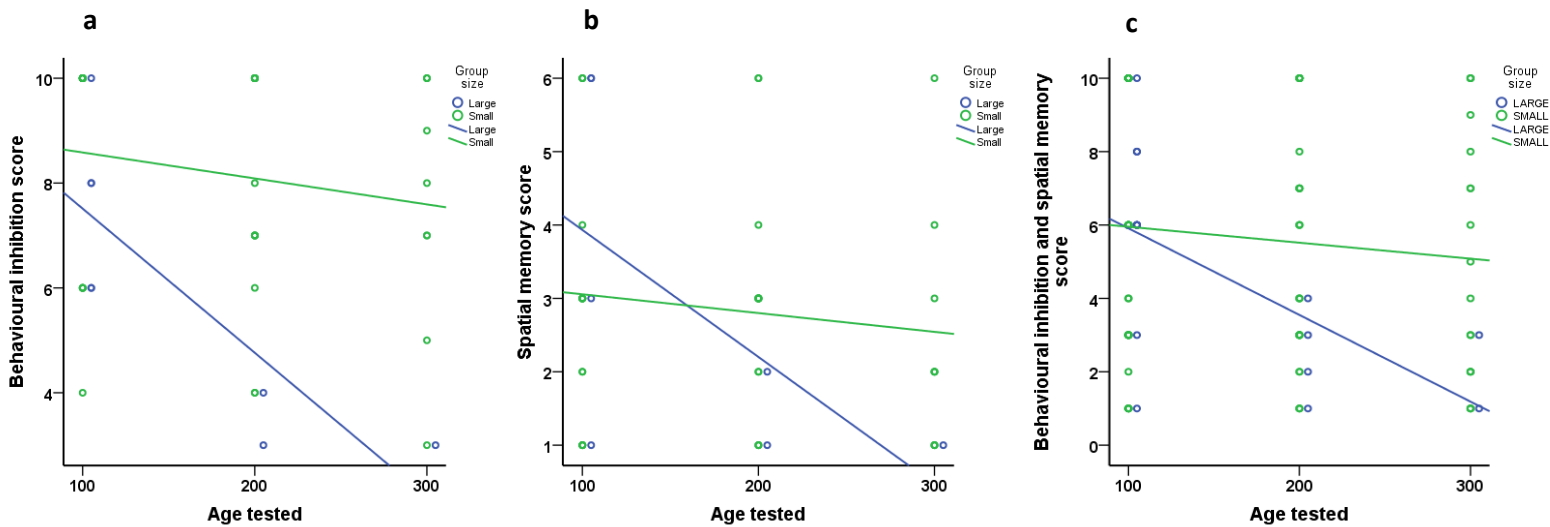
We used the measures of general intelligence gained from PC1 as the response term for analyses investigating factors affecting cognitive performance at 300 days post-fledging. Similar to the result at 200 days post-fledging, group size was the strongest predictor of general intelligence at 300 days post-fledging, whereby individuals from larger groups had greater general intelligence compared to individuals from smaller groups (Table S3.8, Figure 3.4).



**Figure 3.4** The relationship between group size and general intelligence in individuals 300 days post fledging. N=10.

**Factors affecting cognitive performance over time.** An interaction between age tested and group size was the strongest predictor for longitudinal cognitive performance (100 to 300 days post-fledging) in the behavioural inhibition (Table S3.9, Figure 3.5a) and spatial memory tasks (Table S3.12, Figure 3.5b). This finding remained the same when spatial memory and behavioural inhibition performance was analysed together (Table S3.13, Figure 3.5c). Group size was the strongest predictor for longitudinal performance (200 and 300 days post-fledging) in the associative learning

(Table S3.10) and reversal learning tasks (Table S3.11). Group size was also the strongest predictor for general intelligence over time (Table S3.14).



**Figure 3.5** The developmental trajectory of Australian magpies at 100, 200, and 300 days post-fledging in two cognitive traits: **(a)** behavioural inhibition (N=48 trials) **(b)** spatial memory (N=46 trials), and **(c)** behavioural inhibition and spatial memory combined (N=94 trials). Small group=1-7 individuals, Large group size=>8 individuals.

### 3.5 Discussion

In comparison to behavioural and physiological traits, the effect of the early rearing environment on the development of cognitive traits in wild animals has received little attention, and the effect of group size on the development of cognitive traits is particularly poorly understood. In order to understand how sociality may mediate the development of cognitive performance, it is critical to understand the effect of the rearing environment on cognitive development.

We found that group size had no effect on cognitive performance at 100 days post-fledging, but had a significant positive effect at 200 and 300 days post-fledging. This may be because group size has a causal effect on cognitive development, suggesting the social environment has a large influence on the development of general intelligence, or it may be because any heritable variation of general intelligence only emerges later in life. When analysed longitudinally, we found an interaction between age tested and group size on cognitive performance in the behavioural inhibition and

spatial memory tasks, whereby individuals from larger group sizes performed better at older ages compared to those from smaller groups at older ages. Group size remained the strongest predictor for performance in the associative learning and reversal learning tasks when analysed longitudinally. It is possible that there was no significant effect of an interaction between age tested and group size when analysing the longitudinal performance of associative and reversal learning because these tasks were only carried out at 200 and 300 days post-fledging. The effect of group size only emerged at 200 days post-fledging in the other tasks; not being able to include performance at 100 days post-fledging may therefore reduce the chances of detecting any possible interaction. This might also be the reason why there was no interaction between age tested and group size when the measures of general intelligence were analysed longitudinally.

We also provide evidence of a general intelligence factor in magpie fledglings, complementing our finding in adult magpies (Chapter 1). This is the first evidence for general intelligence in juvenile nonhuman animals, and adds support to a growing body of evidence for general intelligence being present in nonhuman animals<sup>41-43</sup>, although few studies have documented this in birds<sup>44,45</sup>.

However, individual performance was not correlated across tasks at 100 days post-fledging. This may be due to the fact that we were only able to carry out two of the four tasks on individuals at this age, although it is also possible that general intelligence only emerges later in life.

There are a number of potential reasons that might explain the relationship between group size and the developmental changes in cognition. There may be a nutritional benefit of living in larger groups, which leads to increased investment in neural tissue<sup>46-48</sup>. Therefore, rather than the proposed cognitive demands associated with group living, it may be increased foraging efficiency, or increased alloparental care in larger groups that drive the positive relationship between group size and cognitive performance. Although we were unable to include foraging efficiency as an explanatory term in our analyses, a separate analysis on the adults in the study population found there was no relationship between group size and offspring provisioning<sup>32</sup>, and there was also no effect of body

mass on fledgling or adult cognitive performance. This would suggest the observed relationship in magpie fledglings is not driven by a nutritional advantage of living in larger group sizes.

An alternative explanation for the observed positive relationship between group size and general intelligence in magpie fledglings is that individuals with greater general intelligence create larger groups. There is a strong positive relationship between group size and general intelligence in adult Australian magpies (Chapter 1) as well as fledglings; however, the direction of causality in this relationship is debatable. If there is a positive relationship between general intelligence and reproductive success, and general intelligence is heritable, larger groups containing both adults and fledglings with greater general intelligence may be formed. This hypothesis is not far-fetched; there is evidence for cognition, and general intelligence in particular, being highly heritable<sup>37,38,42,49</sup>, and there is also some (albeit limited) evidence of positive relationships between cognitive ability and indicators of fitness<sup>50,51</sup>, although see<sup>45,52</sup>). However, here we provide evidence that the positive relationship between group size and general intelligence only emerges after 200 days post-fledging in the natal group; suggesting group size may have a causal effect on cognitive development. In addition, there were no significant correlations between the cognitive performance of mothers and their offspring.

It has been hypothesised that living in large groups actively promotes cognitive development<sup>12</sup>. Maintaining and coordinating multiple relationships, and reacting strategically to the behaviour of other group members, have been hypothesised to be cognitively demanding selective pressures in group-living animals<sup>53,54</sup>. Although comparative studies have found a relationship between group size and cognitive performance<sup>15-20</sup>, intraspecific studies, controlling for the phylogenetic and ecological confounds associated with comparative studies, are much rarer (see<sup>23,25</sup>). The high rate of extra-group paternity in the study population indicates the fathers of fledglings are not likely to be part of the natal group<sup>30</sup>, suggesting any heritable component of general intelligence is likely to have been inherited from parents belonging to groups of varying size, and thus from parents with varying

levels of general intelligence . This, together with the absence of a nutritional effect on cognitive development, and a lack of evidence for individuals with greater general intelligence forming larger groups, suggests that fledglings reared in larger groups may have developed higher levels of cognition due to (at least in part), the pressures of the social environment. Fledglings in larger groups may form a greater number of social bonds, and have a larger social network, compared to fledglings from smaller groups. In addition, the presence of plural breeding in Australian magpies may increase the frequency of within group conflict in larger groups. As a result, behavioural flexibility may be particularly important for fledglings in larger groups in order avoid costly confrontations. Together these cognitively demanding features of group living<sup>16,23</sup> may drive cognitive development in fledglings living in larger groups.

Our results provide the first evidence for a positive relationship between rearing group size and cognitive development in a wild population of animals, highlighting the importance of the social environment on the development of cognition. This finding seems particularly pertinent in the current climate of anthropogenic change, where plastic cognitive responses may be particularly important in enabling animals to cope with rapid changes in their environment, including the social environment<sup>55</sup>.

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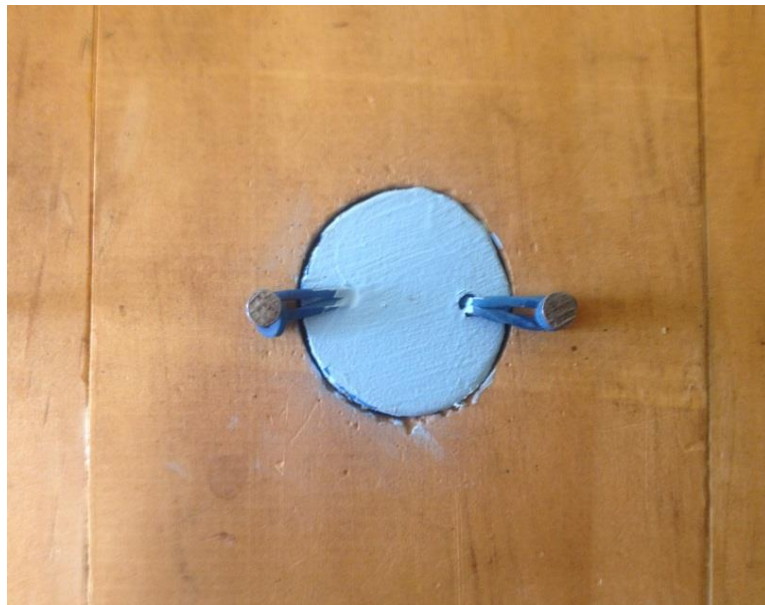
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### 3.7 Supplementary materials

#### Supplementary text

Spearman rank correlations between mother and offspring cognitive performance were carried out. Cognitive performance data for mothers were taken from Chapter 1. A correlation between mother behavioural inhibition score and offspring behavioural inhibition score at 100 days post-fledging was carried out (100 days post-fledging:  $r_s=0.119$ ,  $P=0.648$ ). No other correlations between mother and offspring were carried out at this age, as the task used to quantify spatial memory in adults was slightly different to that of fledglings (see Chapter 1 methods). Associative learning and reversal learning were not quantified in fledglings 100 days post-fledging. Spearman rank correlations between offspring general intelligence and mother general intelligence were carried out at 200 (N=17, 200 days post-fledging:  $r_s=0.2$ ,  $P=0.579$ , N=10) and 300 days post-fledging (300 days post-fledging:  $r_s=0.07$ ,  $P=0.881$ , N=7).



**Figure. S3.1** The lids used in the associative learning, reversal learning, and spatial memory tasks. The lids are held in place by elastic bands creating a “swivelling” axis when pecked.

**Table S3.1** Spearman rank correlation matrix of cognitive performance between all four tasks in the cognitive test battery at 200 days post fledging.

		Behavioural inhibition	Associative learning	Reversal learning
Associative learning	rs	0.314		
	P	0.255		
	N	15		
Reversal learning	rs	0.367	0.973	
	P	0.178	<0.0001	
	N	15	15	
Spatial memory	rs	0.391	0.495	0.54
	P	0.134	0.061	0.038
	N	16	15	15

**Table S3.2** Results of the principal components analysis for magpies that completed all four tasks at 200 days post fledging. All tasks loaded positively onto the one principal component extracted with an eigenvalue >1.

Task	PC1
Behavioural inhibition	0.571
Associative learning	0.916
Reversal learning	0.941
Spatial memory	0.737
Eigenvalue	2.593
% of total variance explained	64.837

**Table S3.3** Spearman rank correlation matrix of cognitive performance between all four tasks in the cognitive test battery at 300 days post fledging.

		Behavioural inhibition	Associative learning	Reversal learning
Associative learning	rs	0.521		
	P	0.123		
	N	10		
Reversal learning	rs	0.534	0.92	
	P	0.112	<0.0001	
	N	10	10	
Spatial memory	rs	0.505	0.889	0.962
	P	0.136	0.001	<0.0001
	N	10	10	10

**Table S3.4** Results of the principal components analysis for magpies that completed all four tasks at 300 days post fledging. All tasks loaded positively onto the one principal component extracted with an eigenvalue >1.

Task	PC1
Behavioural inhibition	0.675
Associative learning	0.947
Reversal learning	0.972
Spatial memory	0.957
Eigenvalue	3.215
% of total variance explained	80.363



**Table S3.5** Full model set (top) and top model set (bottom) of candidate terms affecting performance in a behavioural inhibition task in individuals 100 days post-fledging, using model selection. The top set includes models within 2 QICc values of the best model. N=21 individuals. Group ID was included as a random term.

Term	QICc	$\Delta$ QICc
Basic	12.921	0
Neophobia	13.208	0.287
Body mass	13.512	0.591
Breeding season	13.572	0.651
Siblings	14.768	1.847
Groupsize	14.837	1.916
Sex ratio	14.921	2

Parameter	Estimate	Standard error	Confidence intervals	P value
Basic	2.216	0.0545	2.019, 2.233	0

**Table S3.6** Full model set (top) and top model set (bottom) of candidate terms affecting performance in a spatial memory task in individuals 100 days post-fledging, using model selection. The top set includes models within 2 QICc values of the best model. N=21 individuals. Group ID was included as a random term.

Term	QICc	$\Delta$ QICc
Sex ratio	18.948	0
Neophobia	19.889	0.941
Basic	23.4	4.452
Breeding season	24.023	5.525
Body mass	24.538	6.04
Group size	24.554	5.606
Siblings	25.232	6.284

Parameter	Estimate	Standard error	Confidence intervals	P value	$w_i$
Sex ratio	-0.348	0.1683	-0.677, -0.018	0.039	0.62
Neophobia	0.038	0.0094	0.02, 0.056	<0.0001	0.38

**Table S3.7** Full model set (top) and top model set (bottom) of candidate terms affecting general intelligence in individuals 200 days post-fledging, using model selection. The top set includes models within 2 QICc values of the best model. N=15 individuals.

Term	QICc	$\Delta$ QICc
Group size	14.242	0
Basic	16	1.758
Sex ratio	16.685	2.443
Breeding season	17.011	2.769
Body mass	17.159	2.917
Siblings	17.673	3.431
Neophobia	18	3.758

Parameter	Estimate	Standard error	Confidence intervals	P value	$w_i$
Group size	-0.266	0.1157	-0.493, -0.04	0.02	0.71
Basic	4.93E-19	0.2613	-0.512, 0.512	1	0.29

**Table S3.8** Full model set (top) and top model set (bottom) of candidate terms affecting general intelligence in individuals 300 days post-fledging, using model selection. The top set includes models within 2 QICc values of the best model. N=10 individuals.

Term	QICc	$\Delta$ QICc
Group size	10.332	0
Sex ratio <sub>1</sub>	10.18	-0.152
Basic	11	0.668
Body mass	12.037	1.705
Neophobia	12.448	2.116
Breeding season	12.533	2.201
Siblings	12.988	2.656

Parameter	Estimate	Standard error	Confidence intervals	P value	$w_i$
Group size	-0.227	0.0912	-0.405, -0.048	0.013	0.58
Basic	-4.55E-17	0.3006	-0.589, 0.589	1	0.42

<sub>1</sub>although within two QICc of the top model, not included in top model set as the confidence intervals intersected zero.

**Table S3.9** Full model set (top) and top model set (bottom) of candidate terms affecting behavioural inhibition performance across all ages tested. The top set includes models within 2 QICc values of the best model. N=48 trials. Group ID and individual ID were included as random terms.

Parameter	QICc	$\Delta$ QICc		
Age*Group size	36.481	0		
Group size	39.1	2.619		
Breeding season	39.501	3.02		
Neophobia	39.669	3.188		
Group size*Neophobia	39.975	3.494		
Basic	40.173	3.692		
Age*body mass	40.334	3.853		
Age	40.693	4.212		
Body mass	40.8	4.319		
Breeding season*Siblings	41.485	5.004		
Sex ratio	42.163	5.682		
Siblings	42.164	5.683		
Sex ratio*Siblings	43.58	7.099		
Parameter	Estimate	Standard error	Confidence intervals	P value
Age*Group size	0.001	0.000009	0.001, 0.000004	0.017

**Table S3.10** Full model set (top) and top model set (bottom) of candidate terms affecting associative learning performance across all ages tested. The top set includes models within 2 QICc values of the best model. N=25 trials. Group ID and individual ID were included as random terms.

Parameter	QICc	$\Delta$ QICc		
Group size	34.926	0		
Sex ratio	38.224	3.298		
Age*Group size	39.776	4.85		
Body mass	39.84	4.914		
Group size*Neophobia	40.031	5.105		
Sex ratio*Siblings	40.143	5.217		
Basic	40.268	5.342		
Age	40.587	5.661		
Age*Body mass	41.776	6.85		
Neophobia	41.82	6.894		
Breeding season	41.884	6.958		
Siblings	42.25	7.324		
Breeding season*Siblings	45.584	10.658		
Parameter	Estimate	Standard error	Confidence intervals	P value
Group size	-0.147	0.064	-0.272, -0.022	0.022

**Table S3.11** Full model set (top) and top model set (bottom) of candidate terms affecting reversal learning performance across all ages tested. The top set includes models within 2 QICc values of the best model. N=25 trials. Group ID and individual ID were included as random terms.

Parameter	QICc	$\Delta$ QICc
Group size	21.41	0
Age*Group size	24.904	3.494
Breeding season	25.698	4.288
Basic	27.422	6.012
Group size*Neophobia	27.693	6.283
Sex ratio	27.993	6.583
Body mass	28.375	6.965
Age	29.157	7.747
Neophobia	29.285	7.875
Siblings	29.351	7.941
Age*body mass	29.403	7.993
Sex ratio*Siblings	29.917	8.507
Breeding season*Siblings	32.685	11.275

Parameter	Estimate	Standard error	Confidence intervals	P value
Group size	-0.161	0.072	-0.302, -0.02	0.026

**Table S3.12** Full model set (top) and top model set (bottom) of candidate terms affecting spatial memory performance across all ages tested. The top set includes models within 2 QICc values of the best model. N=46 trials. Group ID and individual ID were included as random terms.

Parameter	QICc	$\Delta$ QICc
Age*Group size	42.691	0
Group size	46.701	4.01
Sex ratio*Siblings	47.464	4.773
Age*body mass	47.47	4.779
Neophobia	47.718	5.027
Body mass	48.296	5.605
Age	48.712	6.021
Group size*Neophobia	48.998	6.307
Basic	49.782	7.091
Siblings	50.604	7.913
Sex ratio	50.751	8.06
Breeding season	51.322	8.631
Breeding season*Siblings	53.398	10.707

Parameter	Estimate	Standard error	Confidence intervals	P value
Age*Group size	0.001	0.0001	-0.001, -0.0001	<0.0001

**Table S3.13** Full model set (top) and top model set (bottom) of candidate terms affecting behavioural inhibition and spatial memory performance across all ages tested. The top set includes models within 2 QICc values of the best model. N=94 trials. Group ID and individual ID were included as random terms.

Parameter	QICc	$\Delta$ QICc
Age*Group size	184.545	0
Group size	191.261	6.716
Age*Body mass	192.147	7.602
Body mass	193.376	8.831
Age	193.425	8.88
Basic	195.501	10.956
Breeding season	196.276	11.731
Siblings	196.705	12.16
Sex ratio	197.028	12.483
Neophobia	197.498	12.953
Group size*Neophobia	197.498	12.953
Sex ratio*Siblings	198.523	13.978
Breeding season*Siblings	198.927	14.382

Parameter	Estimate	Standard error	Confidence intervals	P value
Age*Group size	0.0001	0.000009	0.0001, 0.00001	0.001

**Table S3.14** Full model set (top) and top model set (bottom) of candidate terms affecting general intelligence across all ages tested. The top set includes models within 2 QICc values of the best model. N=25 general intelligence scores. Group ID and individual ID were included as random terms.

Parameter	QICc	$\Delta$ QICc
Group size	20.617	0
Breeding season*Siblings	22.623	2.006
Age*Group size	22.856	2.239
Group size*Neophobia	24.406	3.789
Basic	25	4.383
Sex ratio	25.33	4.713
Body mass	25.49	4.873
Breeding season	25.563	4.946
Siblings	26.615	5.998
Neophobia	26.67	6.053
Sex ratio*Siblings	26.8	6.183
Age*body mass	26.886	6.269
Age	26.996	6.379

Parameter	Estimate	Standard error	Confidence intervals	P value
Group size	0.247	0.0986	0.053, 0.440	0.012



## CHAPTER FOUR

### General intelligence influences reproductive success in the wild



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#### **4.1 Abstract**

Investment in cognitive traits is costly, which has led to the hypothesis that there may be benefits associated with increased levels of cognition. Quantifying the benefits associated with greater cognitive abilities is therefore critical when trying to understand how selection may act upon cognitive traits. Despite this, studies investigating the relationship between cognitive ability and indicators of fitness are rare, and those that exist have produced equivocal results. We presented a battery of four cognitive tasks to individuals from 13 groups of wild, cooperatively breeding Australian magpies. We found that individual performance was positively correlated across all four tasks, indicative of a “general intelligence” factor. General intelligence was found to be the strongest predictor of female fitness, whereby females with a higher general intelligence produced more hatched clutches per year, more fledglings per year, and had a higher number of fledglings surviving to independence per year. Our results provide the first empirical evidence for a positive relationship between general intelligence and fitness in a wild population of animals, and highlight how selection may act on cognitive traits.

## 4.2 Introduction

The study of cognition, in particular the causes and consequences of individual variation in cognitive performance, has become a topic of intense research and debate amongst evolutionary ecologists<sup>1-7</sup>. Recent efforts have successfully quantified individual variation in cognitive ability<sup>8-12</sup>; however the consequences of this variation are unclear<sup>4-6</sup>. Investment in cognitive traits can be costly<sup>13-15</sup>, which has led to predictions that this investment may be associated with fitness benefits, as has been found in humans<sup>16</sup>. Higher levels of general intelligence in humans has been found to predict indicators of fitness, such as mental and physical health, and longevity<sup>16</sup>. However, it has also been suggested that the relationship between cognition and fitness is unlikely to be straightforward<sup>5</sup>; cognition may not be a unitary trait, and the selection pressures acting upon cognitive traits may vary both spatially and temporally. Therefore, selection acting upon cognitive traits that are used across multiple behaviours may lead to a trade-off, with selection acting upon the optimal outcome of all these behaviours, not just one.

Studies investigating the relationship between cognitive performance and fitness in nonhuman animals have typically used measures of problem-solving performance as a proxy for cognitive performance<sup>17-20</sup>. The use of problem-solving tasks in this context has been criticised, as the cognitive traits underlying problem-solving performance are poorly understood<sup>1,4,5,21,22</sup> and variation in success may be driven by non-cognitive factors<sup>4,5,7,21,22</sup>. Moreover, studies using this problem-solving paradigm have yielded conflicting results; some studies report positive relationships between problem-solving performance and fitness<sup>17-19</sup>, and others no relationship<sup>18,20,23</sup>.

The need for tests to reliably assay variation in well-understood cognitive traits is paramount<sup>4,24</sup>. To quantify individual variation in these cognitive traits, multiple psychologically grounded psychometric tests are needed<sup>4,24</sup>. Such tests have rarely been conducted in the wild, and the vast majority have focused on single measures of cognition<sup>4</sup>, and only in satin bowerbirds

(*Ptilonorhynchus violaceus*) and song sparrows (*Melospiza melodia*) has it been attempted to link the variation resulting from these tests to indicators of fitness<sup>10,23</sup>.

Results from laboratory-based studies investigating the relationship between cognitive performance and fitness are also equivocal; some laboratory populations of insects have revealed that better learners have greater reproductive success (reviewed by Dukas<sup>25</sup>), and that selection on learning ability can shape the evolutionary trajectories of populations<sup>26</sup>. In contrast, Mery and Kawecki<sup>27</sup> found a fitness *cost* of learning in *Drosophila melanogaster*. Although logistically they are easier to implement, studies investigating cognitive evolution in captive bred animals may have limited ecological validity because the selection pressures acting upon traits are likely to vary considerably between captive and wild populations<sup>1</sup>. In addition, it may not be possible to test the fitness consequences for long-lived animals in captive conditions.

Studies carrying out psychologically grounded cognitive testing on wild populations of animals, where the context of testing is argued to be most ecologically relevant, are scarce<sup>4,7</sup>. Learning speed correlates positively with foraging success in bumble bees (*Bombus terrestris*)<sup>28</sup>, and there is a positive relationship between survival and spatial memory in African striped mice (*Rhabdomys pumilio*)<sup>29</sup>, but Boogert *et al.*<sup>10</sup> found that song repertoire size in song sparrows, a reliable indicator of fitness in this species, only correlated with one out of the four cognitive traits measured.

Furthermore, contrary to previous findings on bowerbirds<sup>19</sup>, Isden *et al.*<sup>23</sup> found that performance across a battery of cognitive tasks, and the subsequent measure of general intelligence gained from this battery of tasks, failed to predict mating success in spotted bowerbirds (*Chlamydera maculata*).

Whilst evidence for a relationship between cognition and fitness in wild populations is rare, it is worth noting that some of the cognitively demanding features unique to social systems *do* correlate with fitness. For example, there is strong evidence that the strength of social bonds in wild savannah baboons (*Papio cynocephalus*) positively correlates with infant survival<sup>30,31</sup>.

In order to investigate the consequences of individual variation in cognitive performance in a wild populations of animals, we examined the relationship between performance in a battery of four cognitive tasks (detour-reaching, associative learning, reversal learning, and spatial memory, Figure 4.1a-c) and three indicators of fitness in a wild population of cooperatively breeding Australian magpies (Western Australian subspecies *Cracticus tibicen dorsalis*). The average number of clutches hatched per year, the average number of nestlings fledged per year, and the average number of fledglings surviving to independence per year (> three months of age post-fledging) were recorded for each female in the study population, and used as indicators of fitness. The Australian magpie is a large (300- 400g) group-living passerine occurring in territorial groups of 2-15 individuals, that exhibits cooperative behaviours such as alloparental care and territory defence<sup>32,33</sup>. Reproductive skew is very low in Australian magpies, with the majority of females attempting to breed every year<sup>32</sup>. Although both sexes of a social pair will contribute to the rearing of offspring, it is only possible to reliably identify the mother of the brood, due to exceptionally high rates of extra-group paternity in this species (>80% extra-group paternity recorded in the study population; the highest recorded for any bird species<sup>32</sup>). The parentage study<sup>32</sup> was carried out 13 years prior to our study, therefore their analyses could not be used to determine parentage of the current population. For this reason, we were only able record fitness measures for females in the study population (no evidence of egg-dumping in this species means we can be sure that the female that lays the eggs and broods them is the mother). Due to the long-lived nature of the study species (>20 years), we were unable to measure lifetime reproductive success. However, three years of life-history data collection on adult females allowed us to record average values per female for the three measures of fitness used.

### 4.3 Methods

**Study site and population.** The study took place in the Guildford area of Perth and the University of Western Australia campus between November 2012 and February 2016. The study population consists of 14 habituated magpie groups ranging in size from 2-12 individuals. The majority of

individuals in the study population are ringed, and therefore individually identifiable. The study population is habituated to human presence, which allows us to weigh individuals on top-pan scales (in return for a small food reward), giving important information about body mass. The habituated nature of the study population enables us to present individuals with cognitive tasks.

**Cognitive test battery.** We carried out a cognitive test battery on 22 adult female Australian magpies (juveniles were not included as they are not reproductively active<sup>33</sup>). The cognitive test battery consisted of four tasks designed to quantify behavioural inhibition, associative learning, reversal learning and spatial memory respectively (Figure 4.1a-c). These tasks were chosen because they quantify a wide range of well-studied, ecologically relevant cognitive traits<sup>1,12</sup>. Behavioural inhibition is likely to be important for optimal decision-making in social contexts<sup>10,34,35</sup>, associative and reversal learning are likely to be important in learning predictive contingencies in the environment<sup>1,36,37</sup>, and spatial memory is likely to be important for remembering the locations of profitable foraging patches, territory boundaries, and territorial incursions from other groups<sup>38</sup>.



**Figure 4.1** The cognitive test battery used to quantify individual variation in (a) behavioural inhibition (b) associative and reversal learning (c) spatial memory

To ensure that *individual* cognitive performance was being quantified, and to control for the potentially confounding effects of social learning and producer-scrounger effects, all cognitive testing was carried out on individuals in isolation. This was achieved by testing individuals when they were over 10m away from any other individuals- this was achievable as magpies often forage in isolation. A trial was terminated if any social interference occurred during cognitive testing. Due to

the habituated nature of the study population, tasks could be placed directly in front of individuals- performance was then recorded live by the observers (B.J.A and E.K.E). To minimise the effects of satiation and motivation to interact with the task, all trials were carried out between 05:00am and 10:00am, and as close to sunrise as possible. For detailed protocols for cognitive testing see supplementary materials, Chapter 1.

*Behavioural inhibition:* In order to quantify behavioural inhibition, we presented individuals with a detour-reaching task. This consisted of a transparent open-ended cylinder (13cm length, 5cm diameter, Figure 4.1a), in which a food reward was placed in the middle. The cylinder was presented to individuals such that the open ends of the cylinder were facing away from the bird's direction of gaze (this was easily possible due to the habituated nature of the birds). When individuals inhibited the prepotent pecking response at the cylinder, and successfully detoured around to the open ends of the cylinder to access the food reward for three consecutive trials, they were considered to have passed the task. The number of trials taken to reach this criterion was the measure of behavioural inhibition. Test subjects had a maximum of 10 trials to pass this task, otherwise they were considered to have failed. All trials per individual were carried out on the same day, and there was a one-minute interval between trials.

*Associative learning:* To quantify associative learning we presented individuals with a wooden foraging grid (31 x 9 x 4cm) containing two wells (3.5cm diameter, 2.5cm deep, Figure 4.1b). Each well was covered with a PVC lid, which when pecked would reveal a food reward. Individuals were trained to peck the wells using a shaping procedure described by Boogert *et al.*<sup>39</sup>, whereby the grid was presented with the wells covered with yellow lids (a colour not used in the experimental phase of the experiment) in three stages; firstly with the lids not covering the well, secondly with the lids partially covering the well, and finally with the lid fully covering the well. Once test subjects successfully searched for the food three times in a row, when the wells were fully covered, they moved onto the experimental phase of the trial.

During the experimental phases of the trial, the wells in the foraging grid were covered by either a light green or dark green lid. The colour of the rewarded lid was randomly chosen, and the location of the rewarded lid was pseudorandomised between trials. In the first experimental trial, individuals were allowed to search both wells to learn that only one of the wells was rewarded; in all subsequent trials individuals were only allowed to search one well. Individuals were considered to have passed the task when they searched the rewarded well in 10 out of 12 consecutive trials (this represents a significant deviation from binomial probability-  $P=0.039$ ). The number of trials taken to reach this criterion was the measure of success. There were one-minute intervals between trials, and when possible all trials were carried out on the same day.

*Reversal learning:* 24 hours after the associative learning task, individuals were presented with a reversal learning task. All experimental protocols were the same as the associative learning task, apart from the previously unrewarded colour now being the rewarded colour.

*Spatial memory:* Following Shaw *et al.*<sup>12</sup>, in order to quantify spatial memory we presented individuals with a wooden foraging grid (40 x 36 x 4.5cm) containing 8 wells (3.5cm diameter, 2.5cm deep, Figure 4.1c) in which one of the wells was randomly assigned to be the rewarded well throughout the trial. The spatial memory trial consisted of five phases; firstly individuals were presented with the foraging grid and allowed to locate the rewarded well, the grid was then presented a second time five minutes later for the same purpose. 24 hours and 48 hours after the second presentation, the grid was presented a third and fourth time. The cumulative number of wells searched before locating the food reward in these phases was the spatial memory score. A fifth presentation was also carried out to test that olfactory cues were not generating the observed patterns. In order to do this, the grid was presented with no rewarded wells, and rotated 180 degrees (although the grid would still be identical in appearance). If the birds were using olfactory cues to locate the well, one would predict that they search the previously baited well (now located in the opposite position). If the birds remembered the location of the rewarded well from the

experimental phases of the trial, one would predict the birds would search the well opposite the previously baited well (which would appear to be in the same position as the previously baited well from the experimental trials). The results of the fifth presentation in the spatial memory task are discussed in Chapter 2 (supplementary text, supplementary materials).

**Life-history data collection.** In order to obtain measures of fitness for individual birds, we collected life-history data on the study population over three years. This was collected through a combination of behavioural focal observations on individuals, brood observations, and adlib data collected while watching the whole group (for details see Pike<sup>40</sup> and Edwards *et al.*<sup>33</sup>). The extensive life history database developed from these observations allowed us to determine the number of hatched clutches, the number of nestlings that fledged, and the number of fledglings surviving to independence for each adult female in the study population. In addition, the behavioural focal observations, brood observations, and adlib data allowed us to quantify the amount of food adults provisioned to young. Fledglings were considered to have survived to independence when they reached three months post-fledging. At this age, young magpies forage independently and are fed by adults far less frequently<sup>40</sup>. In addition to these three indicators of fitness, we also recorded the number of breeding attempts by females- a breeding attempt was considered to have been made if a female was observed incubating on a nest. Although we have no genetic data confirming the identity of mothers, we assumed the mother was the bird incubating at the nest (there is no evidence of egg-dumping or shared incubation in this subspecies, so there was only ever one female incubating at a given nest). Groups were visited at least once a week during the breeding season; we therefore have very accurate measures of the number of breeding attempts made by individuals, and accurate hatch and fledge dates for all nests. Clutches were considered to have hatched when adults started bringing food to the nest, or if we could see young in the nest. Many nests were upwards of 20m high, and for this reason we were unable to accurately determine clutch size to use as an additional measure of fitness.



**Statistical analyses.** To measure the relationship in individual performance across all four cognitive tasks we carried out Spearman rank pairwise correlations (Table S4.1), and a Principal Components Analysis (PCA) with a varimax rotation (Table S4.2). Principal components with an eigenvalue over one were extracted, and the total variance in task performance accounted for in the first principal component was used to infer whether a general cognitive factor, commonly called general intelligence, was underlying performance across the tasks. General intelligence is typically argued to occur when all tasks load positively onto the first principal component (PC1), and accounts for over 30% of total variance in task performance <sup>41</sup>.

We carried out three separate models to determine the factors affecting the three indicators of fitness we measured: the average number of hatched clutches per year per female, the average number of nestlings fledged per year per female, and the average number of fledglings surviving to independence per year per female. We carried out generalised linear mixed models (glmm), with the fitness measure as the response term, and group ID included as a random term. Explanatory terms included in the models were body mass, foraging efficiency (defined as the amount of food biomass, measured in grams, consumed per minute when foraging- this data was collected as part of the behavioural focals, see Edwards *et al.* <sup>33</sup> for details), group size, the sex ratio of the group, and general intelligence. General intelligence was used as an explanatory term for cognitive performance because the PCA revealed robust evidence for its existence (PC1 accounted for >70% of total variance in task performance, Table S4.2). Dominance status was not included as an explanatory term as this was not always clear among females within magpie groups. We also did not include age because we do not know the exact fledge date for the majority of adult individuals in the population. We adopted a model selection process for analysis. Terms were ranked in order of their corrected Akaike information criterion (AICc) value, with the smallest values having the greatest explanatory power <sup>42</sup>. If a term was more than two AICc units smaller than any other term, it was considered to explain the data better than any other term. If there was one term or more within two AICc of the

“best” term, the confidence intervals of these terms did not intersect zero, and it explained more variation than the basic model (the null model containing no predictors), then model averaging was carried out on this “top set” of models<sup>43</sup>. All statistical analyses were carried out using IBM SPSS Statistics software (version 22).

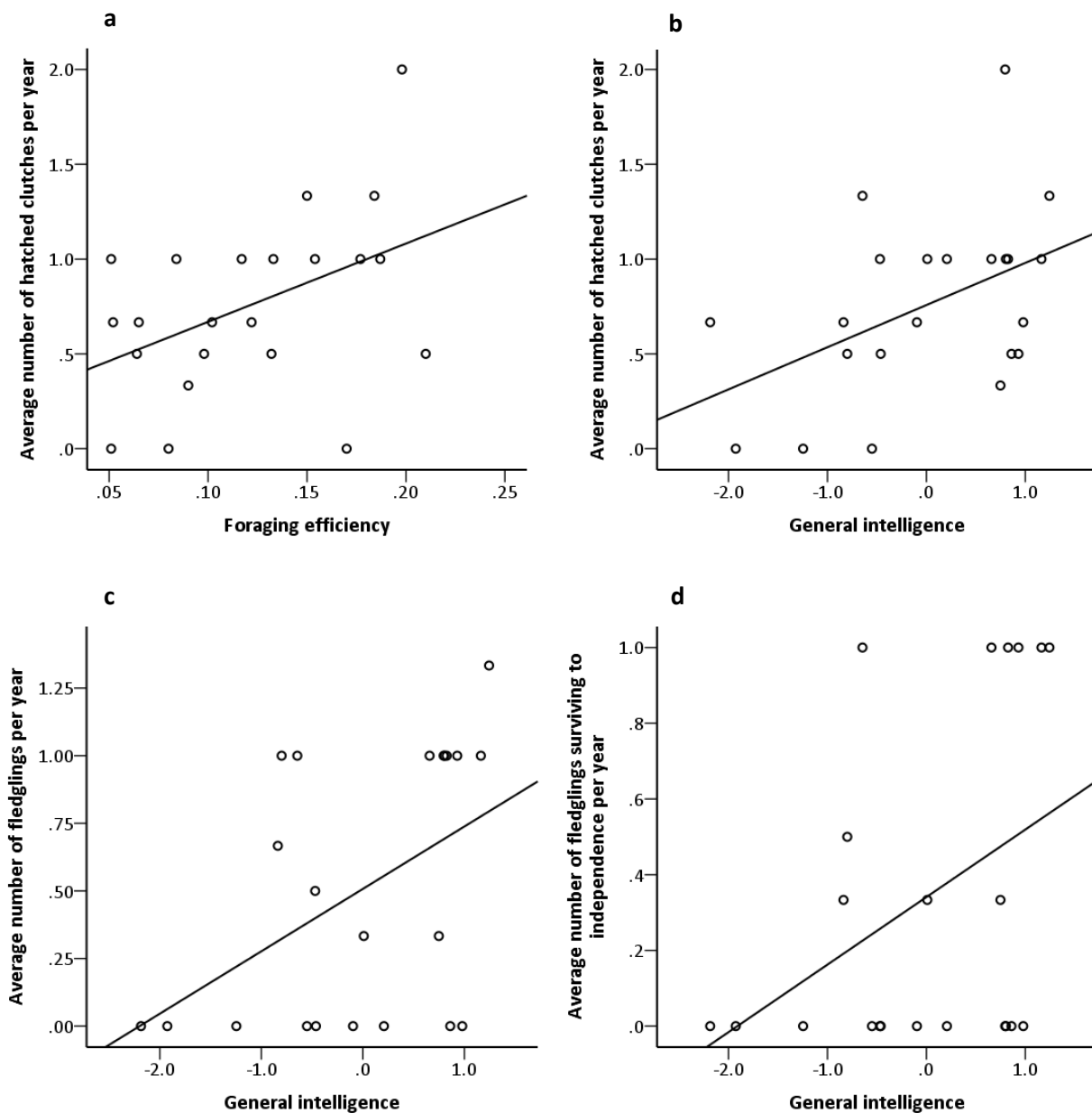
Lower or negative PC1 values indicated that individuals performed better across the battery of cognitive tasks; therefore, for the sake of clarity, we reversed the PC1 values for Figures 4.2b-d, to demonstrate the positive relationship between general intelligence and indicators of fitness.

#### 4.4 Results

**Performance across different cognitive tasks.** We found positive correlations in performance between all four cognitive tasks (5 out of 6 of these correlations were significant, Table S4.1). A principal components analysis revealed that there was only one principal component with an eigenvalue over one (PC1 eigenvalue=2.803), and all four tasks loaded positively onto this principal component (Table S4.2). PC1 accounted for 70.074% of total variance in task performance, providing strong evidence for a general cognitive factor, or general intelligence. Consequently, PC1 was used as an explanatory term representing general intelligence in the subsequent analyses investigating factors affecting measures of fitness (*sensu* Isden *et al.*<sup>23</sup>).

**Factors affecting measures of fitness.** The average number of hatched clutches per female per year ranged from 0-2 (mean  $\pm$  SD=0.758  $\pm$  0.479, N=22), and model selection revealed that the best predictors for the average number of hatched clutches per female per year were general intelligence and foraging efficiency (Table S4.3), whereby both more efficient foragers and individuals with a higher general intelligence produced a greater number of hatched clutches (Figures 4.2a-b). The average number of nestlings fledged per female per year ranged from 0-1.33 (mean  $\pm$  SD=0.508  $\pm$  0.489, N=22), and the best predictor for the average number of nestlings that fledged per female per year was general intelligence (Table S4.4), whereby individuals with a higher general intelligence

produced more fledglings (Figure 4.2c). The average number of fledglings surviving to independence per female per year ranged from 0-1 (mean  $\pm$  SD=0.341  $\pm$  0.438). General intelligence was the best predictor for the average number of fledglings surviving to independence per female per year (Table S4.5), whereby individuals with a higher general intelligence produced more offspring that survived until independence (Figure 4.2d). Interestingly, group size was not a significant predictor for any measures of reproductive success (Tables S4.3-4.5).



**Figure 4.2** The relationship between (a) foraging efficiency and the average number of hatched clutches per female per year, (b) general intelligence and the average number of hatched clutches per female per year, (c) general intelligence and the average number of fledglings per female per year, and (d) general intelligence and the average number of fledglings surviving to independence per female per year. N = 22 individuals.

**Relationship between general intelligence and behavioural traits.** In order to help tease apart the mechanisms underlying the relationships between i) general intelligence and indicators of fitness, and ii) foraging efficiency and indicators of fitness, we explored their relationship with several behavioural and morphological traits related to offspring survival. Foraging efficiency and general intelligence did not significantly correlate ( $r=0.06$ ,  $P=0.791$ ,  $N=22$ ), and foraging efficiency did not significantly correlate with chick body mass ( $r=-0.123$ ,  $P=0.651$ ,  $N=16$ ). General intelligence did not significantly correlate with provisioning rate ( $r=0.076$ ,  $P=0.789$ ,  $N=15$ ), and general intelligence did not significantly correlate with chick body mass ( $r=0.353$ ,  $P=0.237$ ,  $N=13$ ).

#### **Relationship between measures of reproductive success**

The number of hatched clutches per year and the number of fledglings per year was significantly positively correlated ( $r=0.618$ ,  $P=0.002$ ,  $N=23$ ), as was the number of fledglings per year and the number of fledglings surviving to independence per year ( $r=0.772$ ,  $P<0.01$ ,  $N=23$ ). The number of hatched clutches per year and the number of fledglings surviving to independence per year was positively correlated, but the relationship was not significant ( $r=0.318$ ,  $P=0.149$ ,  $N=23$ ).

#### **4.5 Discussion**

Our results provide the first evidence for a positive relationship between general intelligence and female reproductive success, and the first evidence of a selective benefit for high levels of general intelligence in a wild population of nonhuman animals. Individual performance across all four tasks in the cognitive test battery was positively correlated, allowing a general cognitive factor, general intelligence, to be used as a measure of cognitive performance. We found a positive relationship between general intelligence and three indicators of female fitness; the average number of clutches hatched per year, the average number of fledglings produced per year, and the average number of

fledglings surviving to independence per year. Importantly (given the findings from chapters two and three), this relationship was independent of group size.

It may be that the positive relationship between general intelligence and fitness arises because there is a nutritional benefit for offspring being sired by, or receiving parental care from females with a greater general intelligence. However, there is no relationship between general intelligence and foraging efficiency, and foraging efficiency was not a significant predictor for either the number of fledglings produced, or the number of fledglings surviving to independence per year. Moreover, there is no relationship between female general intelligence and fledgling provisioning rate. In addition, females with higher general intelligence do not produce heavier chicks. If general intelligence is heritable in magpies, as is the case in other nonhuman animals<sup>44-47</sup>, then the offspring of females with greater general intelligence might benefit due to the potential survival benefits associated with this trait. This is supported by an analysis of brain size in 236 avian species, whereby larger-brained individuals survived better in the wild compared to smaller brained individuals<sup>48</sup>. However, further work is needed to determine the mechanisms underlying any potential relationship between general intelligence and survivorship. An alternative, untested hypothesis is that females with higher general intelligence are better at defending their young, through avoiding inter and intra specific conflict. It is worth noting that all measures of reproductive success were positively correlated, therefore the mechanisms underpinning the relationship between general intelligence and the different measures of reproductive success may be closely linked.

Foraging efficiency was also a significant predictor of the average number of clutches hatched per year, but not for the two other indicators of fitness measured. The mechanisms underlying the relationship between foraging efficiency and the average number of clutches hatched per year are unclear; firstly we found no relationship between foraging efficiency and general intelligence, suggesting that females with higher general intelligence do not produce more successful clutches because they are more efficient foragers. Secondly, foraging efficiency did not correlate with chick

body mass, which tends to be a good predictor of fledgling survival in birds<sup>49–51</sup>, suggesting that foraging efficiency of the parent is not important in the early stages of fledglings lives. However, foraging efficiency was the strongest predictor for the average number of breeding attempts made by females per year (Table S4.6). This suggests that being a more efficient forager may afford individuals more time to both breed and re-clutch following breeding failure. It is also possible that more efficient foragers produce more hatched clutches as it allows individuals to spend more time at the nest. Chick mortality in magpie nests is very high, and there are known to be multiple predators capable of preying on chicks in the nest, including other bird species and reptiles<sup>52–54</sup>. Magpies actively defend nests, including “swooping” humans<sup>33,52–55</sup>; it is therefore possible more efficient foraging allows magpies to spend more time defending nestlings and eggs from potential threats.

We have shown for the first time, using a battery of psychologically grounded tests, that general intelligence predicts female fitness in a wild population of animals. We have demonstrated that the Australian magpie meets two of the three assumptions necessary for natural selection to act on general intelligence; variation and differential success, and a selective benefit of greater cognitive ability. Evidence for a selective benefit of greater general intelligence is of particular interest because it gives insight into how human intelligence, and cognition in general, may have evolved.

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#### 4.7 Supplementary materials

**Table S4.1** Spearman rank correlation matrix of cognitive performance between all four tasks in the cognitive test battery.

		Behavioural inhibition	Associative learning	Reversal learning
Associative learning	rs	0.360		
	P	0.1		
	N	22		
Reversal learning	rs	0.537	0.573	
	P	0.01	0.005	
	N	22	22	
Spatial memory	rs	0.590	0.679	0.655
	P	0.004	0.001	0.001
	N	22	22	22

**Table S4.2** Results of the principal components analysis for female magpies that completed all four tasks in the cognitive test battery. All tasks loaded positively onto the one principal component extracted with an eigenvalue >1. N=22 individuals.

Task	PC1
Behavioural inhibition	0.662
Associative learning	0.851
Reversal learning	0.902
Spatial memory	0.910
Eigenvalue	2.803
% of total variance explained	70.074

**Table S4.3** Full model set (top) and top model set (bottom) of candidate terms affecting the average number of hatched clutches per female per year. The top set includes models within 2 AICc values of the best model. N=22 individuals.

Term	AICc	$\Delta$ AICc
General intelligence + Foraging efficiency	31.693	0
General intelligence	33.532	1.839
Foraging efficiency	34.1	2.407
General intelligence*Group size	35.411	3.718
Basic	36.038	4.345
Group size	37.95	6.257
Body mass*Group size	38.072	6.379
Sex ratio*Group size	39.05	7.357
Body mass*Sex ratio	39.055	7.362
Body mass	39.057	7.364
Sex ratio	39.057	7.364

Parameter	Estimate	Standard error	Confidence intervals	p value	$w_i$
General intelligence	-0.2164	0.0835	-0.3939, -0.0389	0.02	0.58
Foraging efficiency	3.6838	1.5089	0.5332, 6.8345	0.024	0.42

1although within two AICc of the top model, not included in top model set as the confidence intervals intersected zero or explained less variation than the basic model.

**Table S4.4** Full model set (top) and top model set (bottom) of candidate terms affecting the average number of fledglings produced per female per year. The top set includes models within 2 AICc values of the best model. N=22 individuals.

Term	AICc	ΔAICc
General intelligence	34.773	0
Body mass + General Intelligence <sub>1</sub>	35.881	1.108
General intelligence*Group size <sub>1</sub>	36.722	1.949
Body mass <sub>1</sub>	36.723	1.95
Basic	37.288	2.515
Body mass*Group size	37.388	2.615
Group size	38.049	3.276
Foraging efficiency	38.164	3.391
Body mass*Sex ratio	39.715	4.942
Sex ratio*Group size	39.732	4.959
Sex ratio	39.799	5.026

Parameter	Estimate	Standard error	Confidence intervals	P value
General intelligence	-0.2307	0.0919	-0.4215, -0.04	0.02

<sub>1</sub>although within two AICc of the top model, not included in top model set as the confidence intervals intersected zero.

**Table S4.5** Full model set (top) and top model set (bottom) of candidate terms affecting the average number of fledglings surviving to independence per female per year. The top set includes models within 2 AICc values of the best model. N=22 individuals.

Term	AICc	ΔAICC
General intelligence	31.435	0
Body mass <sub>1</sub>	31.566	0.131
General intelligence + Foraging efficiency <sub>1</sub>	31.889	0.454
General intelligence*Group size <sub>1</sub>	32.049	0.614
General intelligence + Body mass <sub>1</sub>	32.176	0.741
Basic	32.408	0.973
Body mass*Group size <sub>1</sub>	32.584	1.149
Foraging efficiency <sub>1</sub>	32.605	1.17
Body mass*Sex ratio <sub>1</sub>	32.849	1.414
Sex ratio*Group size <sub>1</sub>	32.868	1.433
Sex ratio <sub>1</sub>	33.066	1.631
Group size <sub>1</sub>	33.327	1.892

Parameter	Estimate	Standard error	Confidence intervals	p value	w <sub>i</sub>
General intelligence	-0.1784	0.0853	-0.3551, -0.0016	0.048	0.62
Basic	0.3409	0.0912	0.1518, 0.5301	0.001	0.38

although within two AICc of the top model, not included in top model set as the confidence intervals intersected zero or explained less variation than the basic model.

**Table S4.6** Full model set (top) and top model set (bottom) of candidate terms affecting the average number of breeding attempts per female per year. The top set includes models within 2 AICc values of the best model. N=22 individuals.

Term	AICc	ΔAICC
Foraging efficiency	36.695	0
Basic	41.252	4.557
Body mass*Sex ratio	43.111	6.416
General intelligence*Group size	43.129	6.434
Sex ratio*Group size	43.159	6.464
Sex ratio	43.215	6.52
General intelligence	43.278	6.583
Body mass	44.232	7.537
Group size	44.268	7.573
Body mass*Group size	44.271	7.576

Parameter	Estimate	Standard error	Confidence intervals
Foraging efficiency	5.5499	1.8346	1.7219, 9.3779





## CHAPTER FIVE

### Larger group sizes facilitate the emergence and spread of innovative behaviour in a group-living bird



*Submitted to scientific reports for publication*



## 5.1 Abstract

The benefits of group living have traditionally been attributed to risk dilution or the efficient exploitation of resources, but individuals in social groups may also benefit from access to valuable information. Larger groups may therefore be predicted to solve novel problems faster than smaller groups. Additionally, it is unclear whether larger group sizes facilitate the subsequent spread of innovations through animal groups, as has been proposed for human societies. We presented a novel foraging task to 16 groups of wild, cooperatively breeding Australian magpies, ranging in size from 2-11 individuals. We found a non-linear decline in the time taken for the innovative behaviour to emerge with increasing group size, and social information use facilitated the transmission of novel behaviour. This led to the establishment of group-level traditions, with information spreading more quickly in larger groups. This study provides the first evidence for a nonlinear relationship between group size and the emergence of innovation, and its subsequent cultural transmission, in a wild population of animals, highlighting important advantages of living in large social groups.

## 5.2 Introduction

The benefits of group living have been studied extensively for decades<sup>1</sup>, and are often attributed to processes that help animals exploit resources more efficiently (e.g. social foraging;<sup>2,3</sup>), or reduce risks from threats such as predators<sup>4</sup>. More recently, a growing body of evidence is lending support to the hypothesis that larger group sizes may also facilitate the emergence of innovative solutions to novel problems<sup>5-7</sup>.

Much of the evidence supporting a positive relationship between group size and problem-solving performance comes from studies on humans<sup>8,9</sup>. Evidence of this relationship in nonhuman animals is limited to a handful of studies, and has produced equivocal results (reviewed in Griffin and Guez<sup>10</sup>). Some studies report positive effects of group size<sup>6,7,11,12</sup>, whereas others report negative effects<sup>13,14</sup> or no effect<sup>15,16</sup>.

A number of potential factors may generate a positive relationship between group size and the emergence of behavioural innovations. For instance, the presence of more group members may reduce neophobia and the need to invest in anti-predator vigilance, facilitating the exploitation of novel foraging resources<sup>10,17</sup> (but see Stowe *et al.*<sup>18</sup>). Alternatively, studies of captive house sparrows (*Passer domesticus*<sup>7</sup>) and wild parid flocks (*Parus major*<sup>6</sup>) have argued in favour of the “skill pool” or “pool of competence” hypotheses, whereby group size effects on innovation are driven by greater phenotypic diversity within larger groups<sup>19,20</sup>.

Larger groups are likely to have greater variation of individuals in terms of age, dominance rank, motor skills and neophobia, all of which have been found to influence innovative behaviour<sup>16,21-23</sup>. Critically, arguments based on phenotypic diversity would predict a non-linear relationship between group size and innovation: that is, the speed or probability of solving a task does not simply increase as a linear function of the number of individuals present, but rather the combination of phenotypes in large groups yields a disproportionate effect of group size on the emergence of innovative

behaviour. However, the evidence for “pool of competence” effects in wild animal groups is limited to a single study<sup>6</sup> and it remains unclear whether the benefits of large group size result directly from increased phenotypic diversity<sup>10</sup>.

In contrast to studies reporting positive associations between group size and innovation, Griffin *et al.*<sup>14</sup> and Overington *et al.*<sup>13</sup> found that larger group sizes inhibits innovative behaviour through risk off-setting. Captive Carib grackles, *Quiscalus lugubris*, were slower to produce innovative solutions to a novel foraging task when in the presence of conspecifics<sup>13</sup>. Similarly, the innovative propensity of wild-caught Indian mynahs, *Acridotheres tristis*, was greater when alone than in the presence of five conspecifics, or in pairs<sup>14</sup>. In addition, group size failed to explain the likelihood of wild meerkats, *Suricata suricatta*, interacting with or solving foraging tasks<sup>15,16</sup>. Likewise, solitary ravens (*Corvus corax*) were more likely to approach novel objects compared to dyads and groups<sup>18</sup>. Thus, although large groups may provide some benefits, increased levels of competition, scrounging and aggression, could also reduce opportunities for innovation as group size increases<sup>13</sup>.

If the effect of group size on the emergence of innovative behaviour is poorly understood, the effect of group size on the subsequent dissemination of novel information has received even less attention, particularly so in wild animal populations. Once an innovative behaviour has emerged, naïve group members may learn it from experienced conspecifics. Evidence for social learning is well-documented across a wide range of taxa, in both captive and wild animals (for a comprehensive review see Hoppitt and Laland<sup>24</sup>). However, the potential effect of group size on the rate at which novel information spreads through a group is unclear, despite being of crucial importance to our understanding of how novel behaviours spread and become established as local traditions. Evidence from studies on humans suggests that innovations are transmitted more rapidly and effectively in larger groups<sup>25,26</sup>, and the opportunity to learn from multiple individuals and combine knowledge from multiple sources has been argued to facilitate cumulative cultural evolution<sup>26–29</sup>. Consequently,

we predict that novel information will spread more rapidly in larger social groups of non-human animals.

In this study, we examined the relationship between group size and the emergence and subsequent spread of innovative behaviour in a wild animal population. The study was conducted on a colour-ringed and habituated population of wild Australian magpies (Western Australian subspecies *Cracticus tibicen dorsalis*; hereafter referred to as ‘magpies’), a large (250-400g) cooperatively breeding passerine. Magpies live in territorial groups ranging from 3-15 adults, in which multiple individuals of both sexes contribute to the rearing of offspring<sup>30-33</sup>. Unlike other subspecies of Australian magpie, sex can be determined visually in Western Australian magpies as they are sexually dichromatic. We presented a novel foraging task to magpie groups of differing sizes, whereby a food reward could be accessed by pushing a self-shutting sliding door either left or right (Figure 5.1). To determine the role of group size in the natural emergence and spread of innovative behaviour, we did not train specific individuals to act as “demonstrators”, unlike other similar experiments<sup>34-37</sup>. We predicted that (i) innovations would arise more rapidly in larger groups, and (ii) that innovative behaviour would spread more rapidly in larger groups.

### 5.3 Methods

**Study site & population.** The study took place in the urban grassland areas of Guildford, Western Australia, from July to December 2014. The study population consists of 16 groups, ranging in size from two to 11 individuals (excluding fledglings). The study population is habituated to human presence, allowing detailed behavioural observations (<2m) and the presentation of novel foraging tasks. In 11 out of the 16 groups, the majority of individuals are ringed, allowing individual identification. The remaining 5 groups are either partially ringed, or contain no ringed individuals. All 16 groups were included in analyses investigating the emergence of innovative behaviour, as individual identification was not necessary when recording the initial emergence of innovation at the group level. However, unringed individuals were excluded from further analyses investigating the

spread and social transmission of innovative behaviour because individual identity could not be confirmed between experimental trials.

**Novel foraging task.** To investigate the emergence of innovative behaviour, we presented 16 groups with a novel foraging task, similar to that used on other bird species previously<sup>35</sup>. The task consisted of a transparent plastic box containing grated mozzarella cheese as a food reward (Figure 5.1). The reward could be obtained by pushing a self-shutting sliding door either left or right. Elastic bands caused the door to re-set to the central (closed) position immediately after being released, thus preventing others from scrounging. To avoid devices being monopolised by a single dominant individual, we presented two identical devices to each of the 16 groups. Devices were only presented when all members of the group were present within 20m, and were placed 2m apart, in the middle of an area where the group was foraging. Each device contained sufficient food such that it did not become depleted during trials. All experimental trials were carried out as close to sunrise as possible (between 4:30am and 7:00am according to season) to control for satiation and motivation to access food. Experimental trials were recorded using a *Sony Handycam* (model HDR-XR260VE), and transcribed via video analysis using a *Cybertracker* program on an *Asus Google Nexus 7* tablet. For each ringed individual, behaviour was transcribed separately for each experimental trial at each group. All activity around the device was recorded, including time spent oriented towards the device, whether the bird made contact with the device, whether it obtained food, and if so, what direction it pushed the door, and any aggressive interactions between individuals. Since neophobia may play an important role in the emergence of innovative behaviour, we also recorded each individual's latency to approach the device after coming within 5m of it. In addition, the behaviour of birds observing other individuals interacting with the device (whether they solved it or not, what direction they pushed the door) was also recorded. This was determined by recording individual direction of gaze: following Samson and Manser<sup>38</sup>, observers were quantified as being attentive to solvers if they were within 10m of the solver, their body was oriented towards the solver, they had an uninterrupted line of sight, and they were not engaging in any other activities at that time.

Experimental trials were terminated after 15 minutes, or when any group member left the trial (i.e. when an individual that had been interacting with the task moved more than 20m away from either of the two devices). Each group was presented with the devices until every individual in the group had learned to access food, up to a maximum of 7 trials, with 24hrs between each presentation (the number of trials ranged from 1-7, mean  $\pm$ SE = 3.1 $\pm$ 0.49). To determine if reduction in the need for anti-predator vigilance may be the cause of a possible relationship between group size and the emergence of innovative behaviour, we monitored anti-predator behaviour (mobbing of predators, alarm calling, sentinel duty), but no such behaviour was observed during any experimental trial. In addition, behavioural focal follows were collected at the study site during the experimental period (20-minute behavioural activity focals which are carried out on all individuals multiple times per week, for further details of focal follows see Edwards *et al.* <sup>32</sup>), and the frequency of antipredator behaviour recorded was very low (mean  $\pm$  SE = 0.067  $\pm$  0.018 anti-predator events per 20 minute behavioural focal). Australian magpies are a large passerine with few natural predators; it is therefore unsurprising there were no antipredator behaviours observed during experimental trials.



**Figure 5.1** Novel foraging task. Food rewards could be extracted by pushing the self-shutting sliding door either left or right.



## **Statistical analyses.**

**Effect of group size on the emergence and spread of innovations.** To determine whether innovative behaviour emerges more rapidly in larger groups, we compared models fitting a linear versus a non-linear, asymptotic regression between group size and the time taken for innovative behaviour to emerge (i.e. time until the task was first solved within each group, measured in seconds). Secondly, we used a Cox proportional hazards regression model to investigate the effect of group size on the time taken for innovative behaviour to spread after initial emergence. The response term used was the time taken for each individual to learn the innovative behaviour after initial emergence within the group (measured in seconds), and explanatory terms were group size and the number of innovators in the group (multiple innovators are possible in a group if individuals solved the task without having observed any other individual attempt the task).

The initial innovators were removed from the analysis to ensure that we were only examining the spread rather than the initial emergence of innovation. We did not include age in the analyses as we do not know the exact fledge date of the majority of adults in the study population, and there were too few juveniles and fledglings tested (N=7) to include age as a categorical term.

**Social transmission of door opening preferences.** To examine whether magpies show any consistent side biases between pushing left or right on the device, we ran a binomial test on the initial innovators in each group. Only initial innovators were used in this analysis to control for social information use, which may influence the direction pushed for subsequent solvers.

To determine whether social information use influenced the direction in which birds pushed the door, we ran a GLMM to determine if observers were more likely to push the door in the same direction as the individual they had previously observed. The response term used was the direction pushed by the solver (binary response term, right=1, left=0), explanatory terms were the direction

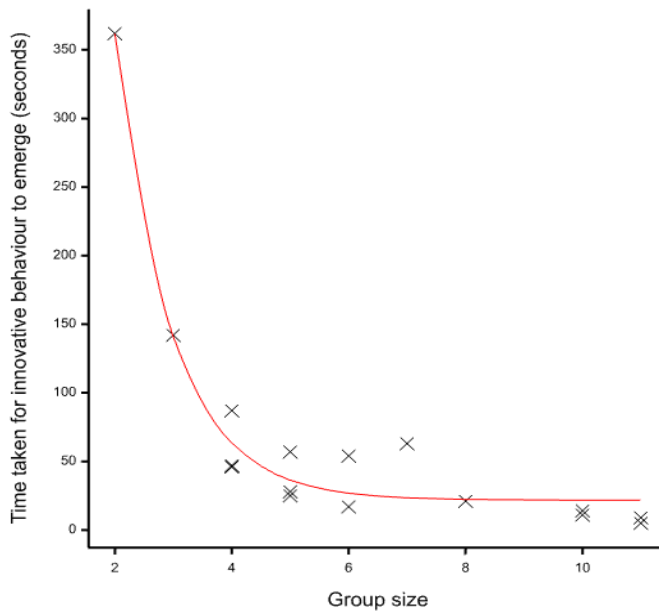
pushed by the last individual they observed, sex, age and group size. Group identity was included as a random term.

Finally, to determine whether the direction pushed by the initial innovator in each group influenced the direction of subsequent solutions by individuals in the group, we ran a binomial GLMM with a logit link function. Excluding solves by the initial innovator, for each individual we fitted the number of solves pushed to the right as the numerator and the total number of solves as the binomial denominator. The direction pushed by the initial innovator, group size and the number of innovators in each group were included as explanatory terms, and group ID as a random term. All analyses were conducted using IBM SPSS Statistics software (version 22).

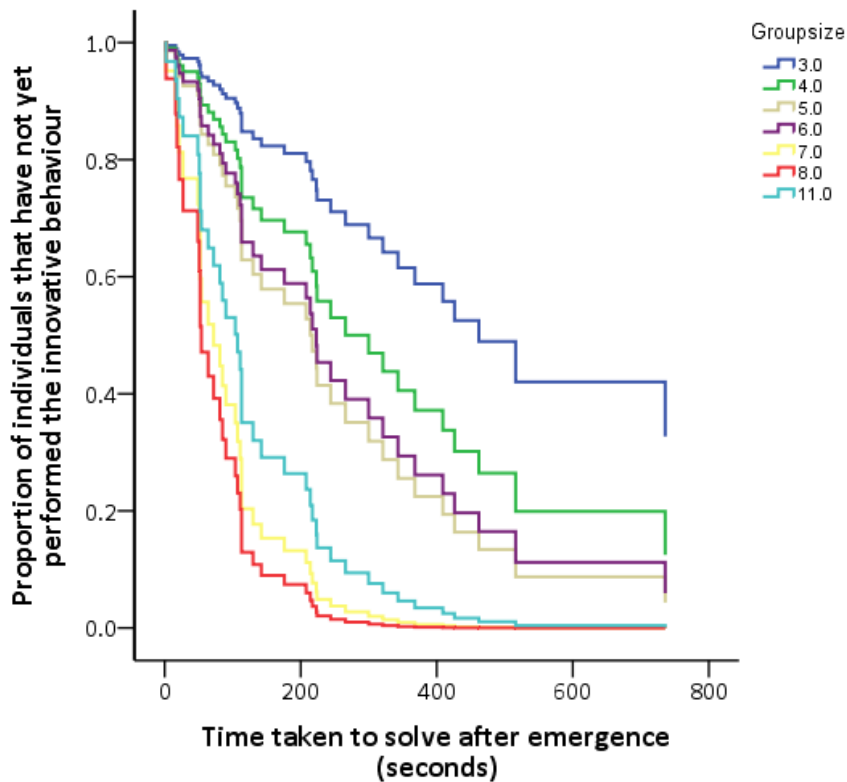
#### **5.4 Results**

**Does innovative behaviour emerge more rapidly in larger groups?** We recorded a total of 938 attempts to gain access to the food reward, including pecking and pushing the door, by 57 ringed individuals. Of these 57 birds, 53 were successful in accessing food (rate of success = 92.9%). Of these 53, 22 were never seen to observe other birds solving, and so were classed as innovators (the number of innovators per group ranged from 1-3, mean  $\pm$  SE =  $2 \pm 0.26$ , and group size positively correlated with the number of innovators per group;  $r_s = 0.648$ ,  $P = 0.043$ ,  $N=10$ ). At the group level, there was a non-linear decline in the time taken for the innovative behaviour to emerge with increasing group size (Figure 5.2). An asymptotic regression showed a much closer fit to the data ( $r = 0.95$ ,  $P < 0.001$ ) compared to a linear regression ( $r = 0.35$ ,  $P = 0.01$ ).

**Does innovative behaviour spread more rapidly in larger groups?** Following the initial innovation events, there was a significant effect of group size on the spread of innovative behaviour (Table S5.1, Figure 5.3). Innovative behaviour spread more quickly in larger group sizes, and larger group sizes were more likely to reach saturation (100% of group members learning the innovative behaviour).



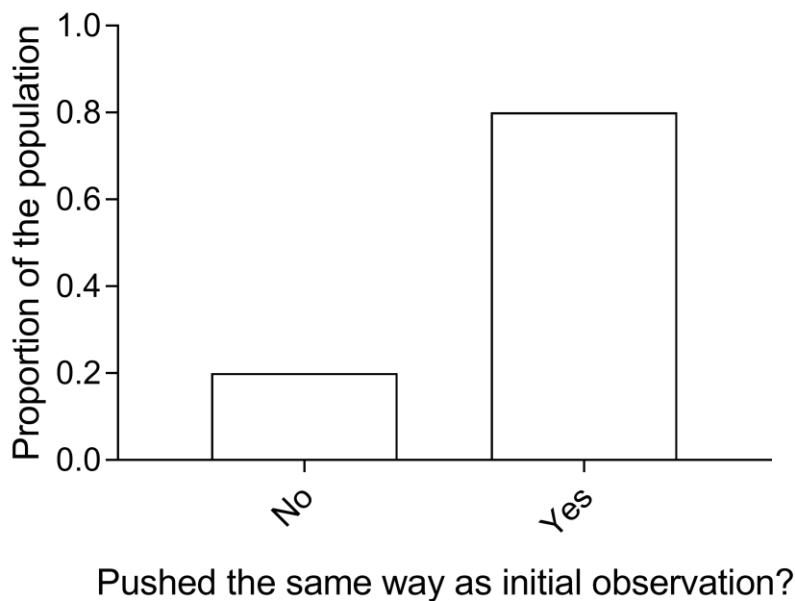
**Figure 5.2** The time taken for innovative behaviour to emerge in relation to group size ( $r=0.95$ ,  $P<0.001$ ,  $N=16$ ).



**Figure 5.3** Survival curves showing the effect of group size on the spread and establishment (100% of group members learning) of innovative behaviour within groups.

### Does social information use play a role in the spread and establishment of innovative behaviour?

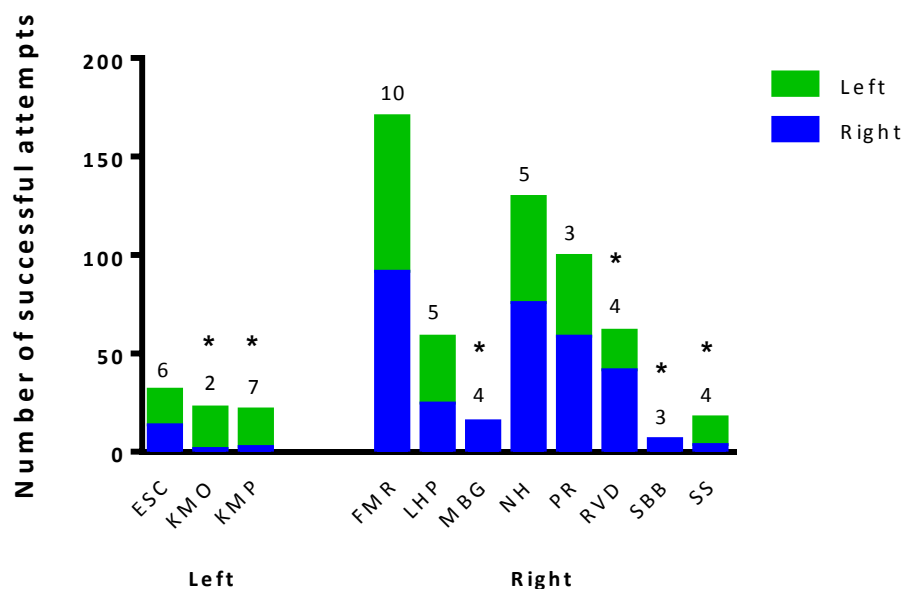
Of the entire population, 54% of birds ( $N = 31$ ) solved the task after observing another individual successfully solve the task, 39% of birds ( $N = 22$ ) solved the task having not observed any individuals interact with the task, and 7% of birds ( $N=4$ ) failed to solve the task. When the innovative behaviour first emerged in groups, innovators were no more likely to push left ( $N=3$  individual innovators) or right ( $N = 8$ ), suggesting there was no intrinsic, population-level side bias (binomial test,  $P= 0.227$ ,  $N = 11$ ). However, individuals who solved the task after observing a successful attempt were significantly more likely to push the door in the same direction as the last solver they observed, rather than the alternative direction (binomial test,  $P = 0.004$ , Figure 5.4, Table S5.2). Furthermore, the direction pushed by the initial innovator within the group predicted the proportion of left and right solves by subsequent solvers within the group (Figure 5.5, Table S5.3).



**Figure 5.4** The likelihood of an individual pushing the door in the same direction as the individual it initially observed ( $N=30$  individuals).

## 5.5 Discussion

Positive relationships between group size and the emergence of innovative behaviour have been suggested as a possible benefit of living in larger group sizes. In accordance with this prediction, we found a strong asymptotic effect of group size on the time to solve the task, with individuals in larger groups solving an innovative foraging task faster than those in smaller groups. To our knowledge, only two other studies have reported positive effects of group size on the emergence of innovative behaviours in the context of novel foraging tasks (Liker and Bókonyi<sup>7</sup> and Morand-Ferron and Quinn<sup>6</sup>; although see the literature on collective decision-making, e.g. Sumpter<sup>12</sup>). Our findings thus add to the body of evidence that group size effects may play a critical role in driving behavioural innovations in wild populations.



### Direction pushed by initial innovator

**Figure 5.5** The total number of successful attempts using each solution (either pushing left or right on the novel foraging task) in each group, in relation to the direction pushed by the initial innovator within groups. In 10 of the 11 groups solves were biased towards the side pushed by the initial innovator, in 6 of the 11 groups these biases were significant (indicated by \*, binomial tests:  $p < 0.05$ ). Numbers above bars indicate group size minus the initial innovators.

In previous research, positive relationships between group size and the emergence of innovative behaviour reported have been postulated to be the result of larger groups having more individuals with a greater range of traits at their disposal, enabling them to solve novel problems more rapidly<sup>6,19</sup>. This is known as the “skill pool” or “pool of competence” hypothesis<sup>19</sup>. However, it remains possible that an exponential relationship between group size and time taken to innovate could be generated by statistical probability, without the need to invoke a “skill-pool” or “pool of competence” explanation<sup>10</sup>. If, for instance all individuals have an equal, set probability of solving a task at a given time step, then the decrease in time taken to for an individual to innovate scales exponentially with group size (Hoppitt *et al.*<sup>39</sup> make similar arguments concerning the use of sigmoidal curves as diagnostics of social learning). Therefore, whilst our current results appear consistent with the predictions of the pool of competence hypothesis, it is not possible to conclude whether this relationship emerged due to a skill-pool effect, or due to simple statistical probability. To address whether increased phenotypic diversity per se facilitates the speed or likelihood of innovation, the best approach may be to compare the emergence of innovative behaviour between groups of the same size with different compositions of individuals in terms of age, sex, dominance status or personality. Nevertheless, regardless of the precise mechanism underpinning the effect, our findings still indicate that the rapid emergence of solutions to novel problems may be a substantial benefit of living in large groups.

Explanations other than the “pool of competence” hypothesis have been suggested for the observed relationships between group size and the emergence of innovative behaviour. For instance, positive relationships could be the result of an antipredator vigilance effect in larger groups, allowing more time for exploration and innovative behaviour<sup>10</sup>. During the course of our study we recorded no antipredator behaviour (mobbing of predators, alarm calling, sentinel duty), suggesting that antipredator effects are unlikely to account for the relationship between group size and the emergence of innovative behaviour observed in Australian magpies. Likewise, Liker and Bókony<sup>7</sup> found no evidence of antipredator vigilance having an effect on the rate of success on innovative problem

solving tasks. Conversely, there is also evidence to suggest that larger group sizes can inhibit innovative behaviours<sup>13,14</sup>. This may be due to risk negotiation<sup>13,14</sup>, such as avoiding costly encounters. However, in our study the frequency of aggressive and submissive interactions between individuals at the experimental device had no effect on the time taken for individuals to learn the innovative behaviour, suggesting that in the Australian magpie at least, levels of aggression do not influence the emergence of innovative behaviour.

The rapid emergence of innovative behaviour in large groups will only be of benefit to other group members if they can learn from the initial innovator. We found that innovative behaviour spread more rapidly in larger groups, suggesting larger group sizes promote not only the initial emergence of innovations, but also the subsequent transmission among group members. Theoretical and empirical research suggests that increasing population size played a critical role in the accumulation of cultural knowledge in human societies<sup>28</sup>. Our results suggest that this may also be the case in group-living nonhuman animals. The positive relationship between group size and the number of innovators within a group suggests multiple innovation events may facilitate the faster spread of innovative behaviour. Information may spread particularly rapidly in larger groups due to the greater frequency of social interactions<sup>25</sup>, but of course transmission rates will also be influenced by the particular structure of social groups<sup>40</sup>. Investigating the interplay between social group size and network structure in social transmission dynamics in natural animal populations is therefore an important priority for future research.

Our experiment also shows that social learning can lead to the establishment of group-level traditions. In a study of wild great tits (*P. major*), using a similar foraging device to ours, Aplin et al.<sup>35</sup> found that sub-populations exhibited strong conformity to the door-opening technique (pushing left or right) modelled by experimentally trained demonstrators. Similarly, in a study on wild common marmosets (*Callithrix jacchus*), Gunhold et al.<sup>37</sup> found groups showed a strong preference to an extractive foraging technique modelled by a trained demonstrator. Furthermore, Gunhold et al.<sup>37</sup>

demonstrated that group level traditions can arise in the absence of a trained demonstrator.

Likewise, we found that group-level preferences were predicted by the technique used by the initial innovator within the group. Much like Gunhold *et al.*<sup>37</sup>, our findings show traditional preferences can arise within groups under natural circumstances, even in the absence of trained demonstrators.

In conclusion, our study provides strong evidence for a positive relationship between group size and innovation in wild animals. Furthermore, our findings show that, as suggested by studies of human cultural transmission<sup>25–28</sup>, novel information spreads more rapidly in larger groups. Moreover, the initial preferences of innovators appear to be transmitted through groups by social learning, leading to the establishment of local traditions. Together, our results provide a rare link between the emergence, spread and establishment of novel information in a social animal in their natural environment.

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## 5.7 Supplementary materials

**Table S5.1** Survival models for the diffusion of innovative behaviour. Statistically significant terms in bold.

Variable	B	SE	P
<b>Group size</b>	<b>0.184</b>	<b>0.071</b>	<b>0.01</b>
Number of innovators	0.364	0.194	0.075

**Table S5.2** GLMM model investigating factors affecting the direction first pushed by observers at the device, including the full model set (top) and top set (bottom). The top set includes models within 2 AICc values of the best model. Group identity was included as a random term. N=30 individuals.

Model	AICc	ΔAICc
Direction first observed	34.526	0
Basic	40.43	5.904
Group size	42.973	8.447
Age	43.099	8.573
Sex	45.953	11.427

Parameter	Estimate	Standard error	Confidence interval	P value
Direction first observed	-0.46	0.146	-0.759, -0.162	0.004

**Table S5.3** GLMM model investigating whether the direction pushed by the initial innovator in the group influenced the direction pushed by subsequent solvers in the group, including the full model set (top) and the top model set (bottom). The top set includes models within 2 AICc values of the best model. Group identity was included as a random term. N=40 individuals.

Term	QICc	$\Delta$ QICc
Direction pushed by innovator	3263.004	0
Number of innovators	3904.735	641.731
Group size	4023.566	760.562
Basic	4054.225	791.221

Estimate	Standard error	Confidence intervals	P value
-1.422	0.573	-2.545, -0.298	0.013



## CHAPTER SIX

### Discussion







## 6.1 Introduction

In this thesis I adopted an intraspecific approach to investigate the causes and consequences of individual variation in cognitive ability. With the use of a uniquely tractable study system, my findings have shed light on how sociality may play a crucial role in the development and evolution of cognition in the wild.

Typically, theories for the evolution of cognition are grouped into two categories. Firstly, environmental hypotheses theorise that cognition evolved due to the cognitive demands associated with ecological factors such as patchy resource availability, habitat complexity and seasonality<sup>1-5</sup>. Secondly, hypotheses focusing on the social environment predict that cognition evolved as a consequence of living in complex social systems<sup>6-9</sup>. Evidence from comparative studies, primarily on primates, have lent support to both groups of hypotheses<sup>7,10-12</sup>. However, an intraspecific approach to the study of cognition has recently been advocated<sup>13-16</sup>. Not only does an intraspecific approach minimise the potential ecological and phylogenetic confounds associated with interspecific comparisons, but a focus on individual differences in cognition, often neglected in comparative studies, may reveal crucial insights into cognitive evolution by linking individual variation to fitness<sup>14</sup>. Critically, studies adopting this approach in wild populations of animals are rare.

## 6.2 Main findings

The results from Chapter 2 provide compelling evidence for general intelligence, whereby individual performance across four different tasks was positively correlated, and a general cognitive factor (commonly called general intelligence) accounted for over 64% of total variance in task performance. Furthermore, repeatability of performance within cognitive tasks was high, indicating our measures of cognitive performance reflect true variation in cognitive traits, rather than noise due to confounding variables. Critically, a robust link between group size and general intelligence was found. There was no relationship between foraging efficiency or body mass and cognitive performance, indicating a nutritional benefit of living in larger groups does not drive the observed

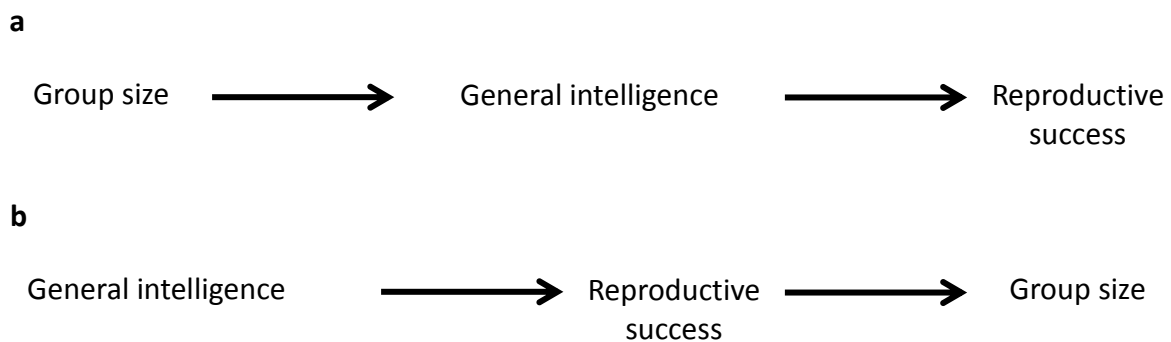
relationship between group size and general intelligence, suggesting sociality may have a causal effect on cognitive development. The results from Chapter 2 therefore support a social theory of intellect, complementing evidence from interspecific comparisons<sup>7,12,17</sup> and intraspecific studies on captive populations<sup>10,18</sup>. However, without being able to carry out experimental manipulations, it is not possible to provide clear evidence for a causal effect of social group size on cognition. If general intelligence is heritable, and individuals with greater cognitive abilities have greater reproductive success (as has been demonstrated in some laboratory studies<sup>19</sup>), then it is possible that individuals with greater general intelligence may form larger groups containing individuals with greater general intelligence. However, the high rates of extra group paternity present in Australian magpies<sup>20</sup> suggest this is unlikely, as extensive gene flow is likely to preclude genetic differentiation between groups.

To further examine whether variation in group size may be linked to cognitive development, a longitudinal study on fledglings was carried out (Chapter 3), measuring cognitive performance at 100, 200, and 300 days post-fledging. Individual performance was significantly positively correlated across all four tasks at 200 and 300 days post-fledging, providing further evidence for general intelligence in the Australian magpie. There was a positive relationship between group size and general intelligence in magpie fledglings, but this emerged only after 100 days post-fledging. A lack of a relationship between body mass and cognitive development suggests the positive relationship between group size and general intelligence in fledglings does not occur because of a nutritional effect of living in larger groups. In addition, a lack of a correlation between offspring and mother cognitive performance suggests cognitive development in fledglings is not mediated by heritable variation alone, providing further support for an influence of sociality on cognitive development. This is particularly interesting because the social intelligence hypothesis is traditionally portrayed as an evolutionary hypothesis. In common with previous studies on cichlids<sup>18</sup> and captive macaque groups<sup>10</sup>, our results indicate group size has a causal effect on cognitive development, indicating the social environment may play a significant role in the development of general intelligence.

The consequences of individual variation in cognitive ability are poorly understood. Typically studies investigating the relationship between cognition and fitness have used measures of problem-solving performance as a proxy for cognitive ability<sup>21,22</sup>, limiting the conclusions that can be drawn because the cognitive processes underlying problem-solving are unclear<sup>14</sup>. Furthermore, the majority of studies investigating the relationship between cognition and fitness have been carried out on captive populations of animals (e.g. Boogert *et al.*<sup>23</sup>). It is critical that studies on wild populations of animals are carried out, as the selective pressures are likely to be substantially different from laboratory conditions<sup>14</sup>. Such studies are likely to provide important insights, complementing experimental manipulations on captive populations. Using psychometric tests, a positive relationship between general intelligence and three indicators of female fitness was found, providing the first evidence for a selective benefit for high levels of general intelligence in a wild population of animals (Chapter 4). Together with the results from Chapters 2 and 3, these findings demonstrate how sociality may mediate the evolution of cognition (Figure 6.1a). However, it is worth noting that the positive relationship between general intelligence and indicators of fitness suggests the direction of causality in the relationship between group size and general intelligence could indeed be larger groups forming as a result of individuals with greater general intelligence producing more offspring (Figure 6.1b). Although this may prove to be the mechanism by which larger groups form, the high rates of extra group paternity, and the lack of a correlation between offspring and mother general intelligence, still indicates that group size has a causal effect on cognitive development.

It has been postulated that a potential consequence of individual variation in cognition is that it may result in benefits associated with solving novel problems at the group level<sup>24-26</sup>. Given the positive relationship between group size and general intelligence, I wanted to investigate whether there was a positive relationship between group size and the emergence of innovative behaviour in Australian magpies. There was a non-linear decline in the time taken for the innovative behaviour to emerge with increasing group size (Chapter 5). The 'pool of competence' hypothesis predicts that disproportionate relationships between group size and the emergence of innovative behaviour arise

because larger groups contain more individuals with a wider variety of traits<sup>24</sup>. Although a non-linear relationship between group size and the emergence of innovative behaviour was identified, it is not possible to conclude whether this occurred due to a “skill-pool” effect or due to statistical probability with increasing group size. Nevertheless, it is apparent that a considerable benefit of living in larger groups is the ability to solve novel problems more quickly. Furthermore, the emergence of innovative behaviour led to the establishment of local traditions. This provides a rare link between the emergence, spread and establishment of an innovative behaviour.



**Figure 6.1** Potential causal pathways between group size, general intelligence and fitness; **(a)** group size has a causal effect on the development of general intelligence, which in turn affects reproductive success, **(b)** general intelligence has a causal effect on reproductive success, which in turn affects group size.

### 6.3 Talking points arising from this thesis

#### General intelligence

Psychometric tests were originally designed to measure intelligence in humans<sup>27</sup>. Individual performance across psychometric tests is usually correlated in humans, and a general cognitive factor, commonly called general intelligence (*g*), typically accounts for around 30% of the total variance in test performance, and sometimes up to 50%<sup>28,29</sup>. Furthermore, there is evidence of positive associations between general intelligence and various indicators of fitness such as mental and physical health, and longevity<sup>30</sup>. However, studies looking for the presence of something akin to general intelligence in nonhuman animals have produced equivocal results. Evidence of general

intelligence has been documented in a wide range of taxa including honeybees<sup>31</sup>, birds<sup>32,33</sup>, primates<sup>34,35</sup>, and rodents<sup>36</sup>. However, no evidence of general intelligence was found in studies on satin bowerbirds<sup>37</sup>, zenaida doves<sup>38</sup> (*Zenaida aurita*) or song sparrows<sup>23</sup>. In Chapters 2 and 3 compelling evidence for general intelligence was found in both adults and fledglings. A general cognitive factor accounted for over 64% of total variance in task performance in adult magpies and fledglings 200 days old, and over 80% in fledglings 300 days old. These measures of general intelligence are far higher than anything reported previously. Furthermore, individual-level repeatability of performance in all tasks was high, indicating the measures of cognitive performance reflect true, consistent cognitive differences among individuals, rather than noise due to confounding variables.

It is apparent that evidence for the presence of general intelligence in nonhuman animals is ambiguous; a possible reason for this is the variable nature of the test batteries used. Not only are the number of tests used in cognitive batteries variable; some use as little as two<sup>38</sup>, whilst some upwards of 10<sup>35</sup>, but there is also a large discrepancy in the cognitive traits being quantified<sup>15</sup>. Together, this variation in experimental design may contribute to the variation in measures of general intelligence reported. This might also explain why measures of general intelligence were so high for Australian magpies, as the cognitive test battery was largely limited to associative tasks; if associative learning plays a role as a key mechanism underlying performance in all the tasks used, this may help to explain the high levels of correlation. In order to address our lack of understanding surrounding the prevalence of general intelligence, future attempts at investigating the presence of general intelligence should endeavour to quantify a wide range of traits spanning a wide range of cognitive domains, including physical and social cognition<sup>15</sup>. If possible, multiple test batteries should be carried out to ensure cognitive traits are reliably quantified. Furthermore, ideally the same test batteries should be used on different species so as to make meaningful comparisons.

### **Benefits of living in larger groups: pool of competence effect?**

It has been postulated that a potential benefit of living in large groups is that solutions to problems will arise more quickly<sup>24–26,39</sup>. In line with this prediction, a nonlinear decline in the time taken for innovative behaviour to emerge with increasing group sizes was found (Chapter 5). The “pool of competence hypothesis” predicts a disproportionate relationship between group size and the emergence of innovative behaviour, and critically, that this occurs due to a greater phenotypic diversity in larger groups. However, it is possible that a disproportionate relationship between group size and the emergence of innovative behaviour could emerge through statistical probability, without the need to invoke a “pool of competence” effect; indeed Griffin and Guez<sup>39</sup> argue that increased group size will *always* lead to higher probabilities of solving due to statistical probability. If all individuals have an equal, set probability of solving a task at a given time step, then the decrease in time taken for an individual to innovate scales exponentially with group size. Thus, although the results from Chapter 5 are in line with the predictions of the pool of competence hypothesis, it is not possible to conclude whether the observed relationship between the emergence of innovative behaviour and group size occurred due to a pool of competence effect or due to statistical probability.

Two recent studies on house sparrows<sup>26</sup> and great and blue tits<sup>25</sup> have also reported positive associations between problem solving efficiency and group size. It is possible that a reduction in individual investment in antipredator behaviour in larger groups might drive this relationship: Liker and Bokony<sup>26</sup> found no evidence of this, although Morand-Ferron and Quinn<sup>25</sup> found solvers were more efficient near tree cover, suggesting an effect of predation risk. Neither study provides conclusive evidence that phenotypic diversity drives the relationship, although Morand Ferron and Quinn<sup>25</sup> did find that the presence of experienced individuals (individuals trained to solve the task in captivity) increased the probability of innovating in groups. Furthermore, using a simulation approach, Griffin and Guez<sup>39</sup> found that the addition of competent individuals to a group resulted in a positive relationship between group size and the emergence of innovative behaviour, supporting the theory that phenotypic diversity may drive the relationship between group size and the

emergence of innovative behaviour. Griffin and Guez's<sup>39</sup> simulation also found the sharing of antipredator vigilance contributed to a positive relationship between group size and the emergence of innovative behaviour. Together these findings hint at the dual role group diversity and antipredator vigilance may play in the emergence of innovative behaviour, although my findings suggest antipredator vigilance does not play a role in the emergence of innovative behaviour in Australian magpies. Crucially, further work is needed to explicitly quantify phenotypic diversity within groups, and its relationship with innovative behaviour.

### **Benefits of living in larger groups: cognitive consequences of group size**

The results from Chapters 2 and 3 suggest a social theory of intellect may help to account for variation in cognitive performance in Australian magpies; however causality in the relationship between group size and general intelligence cannot be unequivocally determined from my results. The most promising way of addressing this issue may be to carry out a cross fostering experiment on fledglings between small and large groups to examine the relative importance of the social environment versus heritable variation in cognition on cognitive development.

Despite being unable to definitively claim causality, the results from Chapters 2 and 3 indicate group size may have a causal effect on cognitive development. However it remains to be tested what aspects of larger group sizes promote cognitive development. The social intelligence hypothesis suggests maintaining and coordinating multiple relationships is likely to be a selective pressure present in larger social groups that is cognitively demanding<sup>6,7</sup>. Remembering individual relationships, monitoring third party relationships, and learning from and reacting strategically to the behaviour of conspecifics are likely to be cognitively demanding features posed by the presence of multiple relationships<sup>40-42</sup>. In accordance with this prediction social network size positively correlates with brain size in humans<sup>43</sup> and captive macaques<sup>10</sup>. Future research should focus on the relationship between social network size, group size and cognitive performance in wild populations of animals. Determining this relationship is crucial as it will allow us to determine if

individuals in larger groups form more relationships. Furthermore, investigating the effect of network structure, and who interacts with whom and at what frequency, will be crucial in determining the importance of specific relationships and their consequences in terms of cognitive development. In addition, quantifying social network size in fledglings at regular time intervals, and exploring its relationship with cognitive development might prove to be a powerful approach to determine the impact of sociality on cognitive development. Furthermore, assessing the causes of variation in social network size and cognitive performance *within* groups may help determine what factors of group size promote cognitive development.

### **Fitness consequences of cognitive ability**

Chapter 4 found a link between general intelligence and reproductive success, suggesting that selection may act upon variation in general intelligence. However, exactly why females with greater general intelligence have greater reproductive success remains unclear. It was possible to rule out that females with greater general intelligence produce more offspring because they provision their offspring with more food. However, it is possible that females with greater general intelligence provide offspring with higher quality food; this possibility should be addressed in future studies. The hypothesis that females with greater general intelligence produce more offspring because they are better at protecting their offspring remains untested. Threats may come from predators or other magpies; protecting offspring may therefore require the flexible navigation of both the social and ecological environment. Experimental manipulations of predation pressure, and threats from natal and non-natal magpies (potentially from playback experiments), may help elucidate what mechanisms underpin the positive relationship between general intelligence and reproductive success.

### **6.4 Conclusion**



In conclusion, the results gained from Chapters 2, 3 and 4 demonstrate how group size plays a pivotal role in the development of individual variation in cognitive ability, and the resulting fitness benefits associated with higher levels of cognition. Not only does this suggest how sociality may mediate the evolution of intelligence, but in conjunction with the findings from Chapter 5, also the emergence and social transmission of novel behaviours. Future work needs to be carried out on a wider range of taxa to determine how widespread these patterns are in wild populations of animals. Once this is achieved, a more complete framework for the evolution of intelligence can begin to emerge.

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