The causes and consequences of individual differences in cognitive performances in relation to the social environment in pheasants

Submitted by Ellis Jessica Grace Langley to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Psychology in June 2018.

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

Signature:

Dedicated to Nanny Mills

A truly wonderful woman

i. Abstract

Identifying the causes and consequences of intra-specific variation in cognitive abilities is fundamental to our understanding of the evolution of cognition. The social environment and cognitive abilities appear inextricably linked, yet evidence for how the social environment affects cognitive performances and further, how cognitive performances influence the social environment, has seldom been explored. Using the pheasant, *Phasianus colchicus*, I explore the relationships between individual variation in cognitive performances in relation to broad and fine-scale structure of the social environment and endeavour to separate cause and consequence.

I demonstrate a positive causal effect of the broad-scale social environment on cognitive performances by observing increases in the accuracy of spatial discrimination performances when individuals are in larger groups (Chapter Two and Chapter Four). I show that the positive effects of larger group size occur over a relatively short period (less than one week), suggesting that cognitive performances are flexible in response to the social environment and I suggest four potential mechanisms.

I show that while males are part of a social hierarchy, spatial discrimination performances are related to this fine-scale social structure and higher-ranking males outperform lower ranking males (Chapter Three). When attempting to determine cause and consequence, I found that spatial learning performances early in life did not predict adult cognitive performances on the same task or predict their adult social rank (Chapter Four). Hence, my results do not support that social rank is a consequence of

spatial learning abilities in male pheasants. The relationship between spatial learning performances and social rank was found in adult males that had their social rank artificially elevated, suggesting that cognitive performances were not simply the result of the current social environment but remain closely related to past agonistic relationships. I did not find a relationship between early life aggression with performances on either a spatial or a non-spatial task in females or males (Chapter Five). This highlights the importance of investigating early life relationships and suggests that the relationship between spatial learning and aggression in adult males may become associated over time as a consequence of further spatial learning experiences, and, or, aggressive interactions.

I then demonstrate a consequence of individual variation in cognitive abilities and show that adult foraging associations in the wild disassort by early life cognitive performances (Chapter Six). Individuals with good inhibitory control performance and poor visual discrimination performances were more central in social networks. I propose that differences in cognitive abilities manifest in foraging strategy and influence the resulting social structure. The implications of this predictable social structure remain to be explored.

Finally, I discuss these results and how they contribute to our understanding of how the social environment causes individual differences in cognitive performances, as well as how variation in cognitive performances may shape the social environment. I suggest the potential implications of these findings and ideas for future work.

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iv. Acknowledgements

This PhD would not have been possible without the help and support from multiple people. First, I would like to thank the CRAB group. I feel extremely lucky to be part of such a supportive and nurturing research group. Rob and Sam, even when you were really busy you found time to help with a problem or talk through ideas, your enthusiasm was contagious. A special thanks to Sam for proof reading and sharing your expertise...your jokes are ok sometimes too. Tim and Andy, thanks for the fun statistics chats and insightful feedback on presentations and general life advice. Tim, I am especially grateful for your comments and the effort you put in to my upgrade submission. You are always willing to help and are so knowledgeable. Mike, your interest and knowledge has been invaluable, huge thanks. Lucy, Sylvia and Chloe, I’m grateful to have met you three at Winter ASAB and without meeting you, I might not even be here. I’ve valued your presence in the office and for sharing complaints, laughs and being the go-to people in the office that know pretty much everything. Lauren, a special thank you for the reference, being reliable when I had a last-minute plea for help(!), and of course the interesting chats over coffee. Where are you going next? I may accidentally follow you there too.

I adored working at North Wyke, such a peaceful place with friendly and accommodating staff. Lovely Lizzy, I will especially miss our chats. I am gutted that my time there had to come to an end.

This PhD is not without the blood, sweat and tears of the PEC group. There have been many great research assistants over the years, Rachel, Sara, Kenzie, Molly, Heather,

Joe, Camille, Elena, thank you for all your help and hard work. Huge thanks to the core members of the team: Pip, Christine, Mark and Jayden it has been very enjoyable working with each of you. Thank you for comments on presentations, manuscripts, discussions and being supportive, but most importantly, thank you for being a good bunch. Thinking of fun times we have had at the farm makes my face beam. Pip, for all your truths (or your lies), you are a true gem. Christine, for always being so helpful and knowing how to make me laugh. Jaydo, the chats about coffee and music, times in the trench and your nuggets of wisdom. Mark, for your work ethic and always offering to help, but most importantly thank you for bringing *Pop Maaaster*, and of course Gary, into our lives.

Joah, this PhD would not have been possible without your supervision and guidance. Thank you for the entertaining stories, your knowledge, enthusiasm, the endless ideas, your neologisms, teaching me that everything can be fixed with a cable tie and giving me [virtually] free-reign over what I did during my PhD. I am extremely grateful that you selected me for a PhD and I am happy to have been part of this awesome project. I look forward to pheasant-collaborations in the future.

Friends at home, who I miss dearly. Even though I’ve not been able to give our friendships the attention they deserve, you always take an interest and are so encouraging. Dave, Carly, Phill, Luke, Laura, Emily and Kirsty, I am lucky that you have been a part of this in one way or another. Jahcub, thank you for listening, it’s been great having you around.

A massive thank you to my family. Janey, I have really valued your support (as well as your excel skills). Nan and Grandad B and Nan and Grandad L, it has not been easy living so far away but I'm so grateful for our long talks on the phone and your continued support and interest in what I'm doing. It means so much, where would I have been without your knowledge that "it'll be alright in the end". Sure enough, it was always alright in the end. Steve, for your curiosity in my work, being understanding when I'm busy, your encouragement and mostly for you and Iris being my support network in Devon. Aidan and Jess, your fascination in what I do makes me excited by it all over again and a special thank you for your help with data collection, which unfortunately didn't make the cut for the thesis, but it will see the light of day, I promise!

Clearly, I wouldn't have achieved any of this without Mum and Dad. You are my inspiration, your constant care and backing to succeed in something that interests me is the motivation for everything I do. I am fully aware of how lucky I am to have you both. You are undoubtedly a big reason why this PhD was possible.

Finally, Jon. The list of things to thank you for is endless… but to name a few, help with data collection, R coding (especially the nice figures), long discussions, proof reading, the jokes, listening to my complaints, the pep talks, being patient, but most importantly, thank you for the wonderful dinners. I definitely couldn't have done it without you.

v. Declaration

This thesis contains five data chapters, each of which is written as a manuscript for publication and is therefore intended to stand alone. Consequently, some information may be redundant or repeated. While the candidate made substantial contributions to the manuscripts and is fully responsible for the work presented in this thesis, where the first person (‘I’) in the manuscripts is used, the plural ‘we’ is inferred to reflect contributions from co-authors and, or research assistants. Contributions by co-authors are detailed for each chapter below. Dr Joah Madden was involved in the design and conception of all chapters and provided comments on drafts of all chapters. All data used in this thesis were collected during the PhD period.

Chapter Two: Individuals in larger groups are more successful on spatial discrimination tasks

Ellis J.G. Langley, Jayden O. van Horik, Mark A. Whiteside, Joah R. Madden

The candidate designed the experiment and collected a significant proportion of the data. The candidate analysed the data and wrote the manuscript. All authors and three anonymous reviewers provided feedback on drafts of the manuscript. The paper was submitted to the *Journal of Animal Behaviour* in August 2017 and accepted in March 2018 after minor revisions.

Chapter Three: Group social rank is associated with performance on a spatial learning task

Ellis J. G. Langley, Jayden O. van Horik, Mark A. Whiteside and Joah R. Madden

Jayden van Horik designed and carried out the spatial learning task. The candidate conceived the idea for the manuscript. The candidate, co-authors and research assistants, Philippa Laker and Rachel Peden collected behavioural data. The candidate analysed the data and wrote the manuscript. All authors and three anonymous reviewers provided feedback on drafts of the manuscript. The paper was submitted to the *Biology Letters* in August 2017 and it was rejected. It was subsequently submitted to *Royal Society Open Science* in September 2017 and accepted in January 2018 after minor revisions.

Chapter Four: The relationship between social rank and spatial learning*:* Cause or consequence?

Ellis J.G. Langley, Jayden O. van Horik, Mark A. Whiteside, Christine E. Beardsworth, Joah R. Madden

The candidate designed the experiment, collected a significant proportion of cognitive data and collected behavioural data with co-authors and a research assistant, Kenzie Bess. The candidate analysed the data and wrote the manuscript. All authors and three anonymous reviewers provided feedback on early drafts of the manuscript. It was submitted to *PeerJ* in February 2018 and is due to re-submitted in June 2018 following major revisions.

Chapter Five: Individual differences in learning performances during early life on spatial and non-spatial tasks are unrelated to aggression, sex or body condition

Ellis JG Langley, Jayden O van Horik, Philippa R Laker, Christine E Beardsworth, Lucy A. Capstick, Mark A Whiteside & Joah R Madden

The candidate designed the experiment and collected all aspects of the data along with Philippa Laker, Lucy Capstick and Jayden van Horik. The candidate analysed the data and wrote the manuscript. Mark Whiteside and Christine Beardsworth provided feedback on a draft of the manuscript.

Chapter Six: Disassortative mixing by cognitive performances in wild pheasants

Ellis J.G. Langley, Jayden O. van Horik, Mark A. Whiteside, Christine E. Beardsworth, Michael Weiss, Joah R. Madden

Cognitive performance data were collected by Jayden van Horik and research assistants: Aidan Hulatt, Seb Bekker and James Foley. The candidate conceived the manuscript, processed a significant amount of the data along with the co-authors and research assistants: Aidan Hulatt, Kenzie Bess and Alicia Wiltshire. The candidate analysed the data with assistance from Michael Weiss. The candidate wrote the manuscript. Sam Ellis and Michael Weiss provided comments on the manuscript.

vi. Co-authored papers

2016

Whiteside, M. A., **Langley, E. J. G.**, & Madden, J. R. (2016). Males and females differentially adjust vigilance levels as group size increases: effect on optimal group size. *Animal Behaviour*, *118*, 11–18. http://doi.org/10.1016/j.anbehav.2016.04.025

The candidate collected 25% of the data, conducted all analyses except for the modelling aspect, drew 50% of the figures and commented on the manuscript.

2017

Meier, C., Pant, S. R., van Horik, J. O., Laker, P. R., **Langley, E. J. G.,** Whiteside, M. A., Madden, J. R. (2017). A novel continuous inhibitory-control task: variation in individual performance by young pheasants (*Phasianus colchicus*). *Animal Cognition*, *20*(6), 1–13. http://doi.org/10.1007/s10071-017-1120-8

The candidate collected 20% of the data and commented on the manuscript.

van Horik, J. O., **Langley, E. J. G.**, Whiteside, M. A., & Madden, J. R. (2017). Differential participation in cognitive tests is driven by personality, sex, body condition and experience. *Behavioural Processes*, 1–9. http://doi.org/10.1016/j.beproc.2016.07.001

The candidate assisted in conceptualising the paper, carried out the majority of the analyses and commented on the manuscript.

Whiteside, M. A., Horik, J. O. Van, **Langley, E. J. G.**, Beardsworth, C. E., Laker, P. R., & Madden, J. R. (2017). Differences in social preference between the sexes during ontogeny drive segregation in a precocial species. *Behavioral Ecology and Sociobiology*, *71*(103). http://doi.org/10.1007/s00265-017-2332-2

The candidate assisted in data collection and commented on the manuscript.

2018

van Horik, J. O., **Langley, E. J. G.**, Whiteside, M. A., Laker, P. R., Beardsworth, C. E., & Madden, J. R. (2018). Do detour tasks provide accurate assays of inhibitory control? *Proceedings of the Royal Society B: Biological Sciences*, *285*(1875). http://doi.org/10.1098/rspb.2018.0150

The candidate collected 25% of the data, helped conceptualise the paper and commented on the manuscript.

Van Horik, J. O., **Langley, E. J. G.**, Whiteside, M. A., Laker, P. R., & Madden, J. R. (2018). Intra-individual variation in performance on novel variants of similar tasks influences single factor explanations of general cognitive processes. Royal Society Open Science, 5(7). http://doi.org/10.1098/rsos.171919

The candidate collected much of the data, helped conceptualise the paper and commented on the manuscript.

Whiteside, M. A., van Horik, J. O., **Langley, E. J. G.**, Beardsworth, C. E., Capstick, L. A., & Madden, J. R. (2018). Patterns of association at feeder stations for pheasants released into the wild: sexual segregation by space and time. Ibis. http://doi.org/10.1111/ibi.12632

The candidate collected and processed much of the data and commented on the manuscript.

Wascher, C. A. F., Kulahci, I. G., **Langley, E. J. G.**, & Shaw, R. C. (2018). How does cognition shape social relationships? *Philosophical Transactions of the Royal Society B*, 373: 20170293. http://doi.org/10.1098/rstb.2017.0293

The candidate contributed ideas for structuring the manuscript, wrote multiple sections and commented on the manuscript.

Cauchoix, M., Chow, P. K. Y., van Horik, J. O., Atance, C. M., Barbeau, E. J., Barragan-Jason, G., Bize, P., Boussard, A., Buechel, S. D., Cabirol, A., Cauchard, L., Claidière, N., Dalesman, S., Devaud, J. M., Didic, M., Doligez, B., Fagot, J., Fichtel, C., Henke-von der Malsburg, J., Hermer, E., Huber, L., Huebner, F., Kappeler, P. M., Klein, S., Langbein, J., **Langley, E. J. G.**, Lea, S. E. G., Lihoreau, M., Lovlie, H., Matzel, L. D., Nakagawa, S., Nawroth, C., Oesterwind, S., Sauce, B., Smith, E. A., Sorato, E., Tebbich, S., Wallis, L. J., Whiteside, M. A., Wilkinson, A., Chaine, A. S., Morand-Ferron, J. (2018). The repeatability of cognitive performance: a meta-analysis. *Philosophical Transactions of the Royal Society* B 373: 20170281. http://doi.org/10.1098/rstb.2017.0281

The candidate contributed data for the meta-analysis and commented on the manuscript.

Madden, J., **Langley, E.J.G.**, Whiteside, M., Beardsworth, C., & van Horik, J. (2018). The quick are the dead: Pheasants that are slow to reverse a learned association survive for longer in the wild. *Philosophical Transactions of the Royal Society B*, 373: 20170297. http://doi.org/10.1098/rstb.2017.0297

The candidate carried out the initial analyses and commented on the manuscript.

Chapter One: The causes and consequences of individual differences in cognitive abilities in relation to the social environment

1.1 General Introduction

The social environment is considered a key component in the evolution of cognitive abilities. The social environment imposes significant cognitive demands on animals, requiring individuals to monitor and maintain multiple relationships, adopt flexible behaviour and recognise suitable partners for critical behaviours such as foraging, mating or competition (Byrne & Whiten, 1988; Dunbar, 1998; Humphrey, 1976; Jolly, 1966; Seyfarth & Cheney, 2002). Hence, species with more complex social environments are reported to outperform species with less complex social environments on cognitive tasks. For example, social complexity may be defined in terms of quantity and lemur species that live in larger groups outperform sister taxa that live in smaller groups on a social cognition task (MacLean et al., 2013). Social complexity may also be defined in terms of quality and avian species with long-term pair bonds have a larger relative brain size than non-pair bonded species (Emery et al. 2007), but see a comprehensive meta-analysis that reports no relationship between mating system and brain size in birds (Sayol et al., 2016). Social complexity may also be defined by the group dynamics. Primates living in fission-fusion societies outperform primates living in more cohesive and stable groups on cognitive flexibility tasks (Amici et al. 2008). However, quantifying both social complexity and cognitive performance is not trivial and this can hamper our understanding of the relationships when comparing across species. Furthermore, there is homogeneity in the choice of study species, with the focus being on ‘intelligent’, relatively large brained species such as primates and corvids and an emphasis on tasks that purportedly represent more ‘advanced’ cognition such as tool use (apes, Mulcahy et al. 2005) or theory of mind (apes, Herrmann et al. 2010). Test paradigms that permit comparisons of cognitive performances across species are also difficult and subject to criticism

(Chittka, Rossiter, Skorupski, & Fernando, 2012; Healy & Rowe, 2007; Thornton & Lukas, 2012).

An alternative to such species comparisons is to consider differences within species, both in individual social environments and individual cognitive performances. The causes and consequences of intra-specific variation in cognitive abilities have been advocated as a more fruitful approach to investigate the evolution of cognitive abilities (Thornton & Lukas, 2012). Recognising the intra-specific variation removes confounding factors associated with inter-specific comparisons. Within species, we know that social structure and cognitive performances are highly variable, and both have potential fitness implications. For instance, whitetail damselfish, *Dascyllus aruanus,* that were given the opportunity to learn the visual or olfactory stimuli from local predators survived longer than naïve individuals (Ferrari et al. 2014), and dolphins, *Tursiops sp.,* more central in their social network survive for longer (Stanton & Mann, 2012). Despite the potential importance of both cognitive abilities and the social environment, how individuals vary in their social relationships and cognitive abilities concurrently and how one factor shapes the expression of the other, has seldom been investigated. The aim of this thesis is to explore the causes and consequences of individual differences in cognitive performances in relation to the social environment using the pheasant, *Phasianus colchicus,* as a model system. In the following literature review I define the social environment (**Section 1.2.**) in terms of broad-scale (**Section 1.2.1.1**) and fine-scale structures and briefly describe tools used to study two forms of fine-scale social structure that I have utilised, namely social rank (**Section 1.2.1.2.**) and social network structure (**Section 1.2.1.3.**). I then discuss animal cognition from a behavioural ecological perspective (**Section 1.3.**) and describe general cognitive abilities: associative learning (**Section 1.3.1.**), spatial learning (**Section 1.3.2.)** and executive control (**Section 1.3.3.**). I review recent methods used to study cognitive abilities, specifically problem solving and what this may or may not tell us about cognition (**Section 1.3.4.**). I briefly address some of the difficulties researchers face when attempting to measure individual variation in cognitive abilities (**Section 1.3.5.**) and review recent opinions on whether the most meaningful assays of cognitive ability are in the wild or in captivity (**Section 1.3.6.**). The next section explores the evidence that social structures impact on individual variation in cognitive performances (**Section 1.4.**), in terms of the broad-scale social structure, i.e. group size (**Section 1.4.1.**), and the fine-scale social environment, specifically social rank (**Section 1.4.2.**) and throughout these sections I discuss the potential mechanisms behind the relationship between social structures and cognition. I then explore this relationship from the other direction and review the limited evidence that cognitive abilities may shape the social environment (**Section 1.5.**), specifically social rank (**Section 1.5.1.**) and assortative or disassortative group mixing and social centrality (**Section 1.5.2.**). Finally, I introduce my study system the pheasant, *Phasianus colchicus*, (**Section 1.6.**) and discuss how this species is a novel and suitable system to address questions regarding the social causes and consequences of individual differences in cognition.

1.2 The social environment

1.2.1 Defining the broad and fine scale social environment

The social environment encompasses all of the conspecifics and heterospecifics that a focal individual has direct or indirect interactions or associations with, and these interactions or associations are termed relationships. Relationships can be agonistic and involve aggressive and submissive interactions and such relationships are characteristic of social hierarchies (Drews, 1993). Alternatively, relationships may be affiliative and include behaviours such as grooming (e.g. rhesus macaques, *Macaca mulatta* Brent et al., 2013) or allopreening (e.g. jackdaws, *Corvus monedula,* de Kort, Emery, & Clayton, 2006). In some species there is limited evidence of direct affiliative interactions but affiliations may be inferred from individuals showing non-random associations and preferred foraging (great tits, *Parus major,* Aplin et al. 2013) or resting (greylag geese, *Anser anser,* Frigerio et al. 2001) partners. I define 'complexity' of the social environment using two terms. First, the social environment can be defined by its *broad-scale* structure, which is simply the number of possible relationships, e.g. group size. Second, the social environment can be defined by its *fine-scale* structure, which refers to specific relationships between dyads in relation to group or population level patterns, e.g. social rank, social centrality or assortative and disassortative mixing in social networks. The social environment is critical in determining an individual's fitness (e.g. Ellis et al., 2017; Hougen & Iii, 2011; Noe, 2001; Oh & Badyaev, 2010), hence reliably quantifying fine-scale social structures is key to our understanding of their evolution. Below I describe the broad-scale social environment and then discuss tools to quantify two forms of fine-scale social structure.

1.2.1.1 Broad-scale social structure; group size

Group living is associated with costs and benefits to the individual (Krause & Ruxton, 2002) that could play a role in the relationship between cognitive performance and the social environment. Costs of large group sizes include increased competition for food that could act as a stressor (Milinski & Parker, 1991) and conspicuousness of the group to predators (Krause & Ruxton, 2002). Furthermore, larger group sizes are said to impose a cognitive demand due to the greater cognitive processing and responses needed to maintain group cohesion (Dunbar 1998). However, a benefit of living in a large group is the reduction in individual vigilance levels (Beauchamp, 2015; Elgar, 1989; Roberts, 1995) and increase in time spent foraging (Krause & Ruxton, 2002). Quantifying group size in the wild is likely to be dependent on the species. For example, in elks, *Cervus elaphus*, group size was defined as a group of elks with the nearest neighbour distance within 100m (Childress & Lung, 2003). Whereas in badgers, *Meles meles*, group size was determined as the number of individuals caught or observed at a particular sett within a season (Macdonald, Newman, Morecroft, & Johnson, 2001). While the overall size of the group that an individual is part of is an important structural aspect of the social environment, within groups there are different forms of fine-scale social structure that may also relate to critical behaviours.

1.2.1.2 Fine-scale social structure; social hierarchies and tools for their inference

The formation of social hierarchies is characteristic of social species (Chase, 1982; Landau, 1951) and is defined as the hierarchy that arises from dyads in groups (Drews, 1993). Social hierarchies are an example of agonistic social structure. A social hierarchy is deemed perfectly linear when higher ranked individuals dominate all individuals of lower rank and dominance relations between every triad is ‘transitive’: when individual A dominates B and B dominates C, then A also dominates C (Chase, 1982; De Vries, 1998). Traditional methods of hierarchy inference include matrix based methods in which interaction matrices of wins and losses are reorganised to reduce the interactions above the matrix diagonal; i.e. the order deviates least from a linear rank order (IS&I, De Vries 1998), or for which values of success (i.e. the amount of ‘wins’ during agonistic interactions) are calculated for each individual and individuals are ranked accordingly (David's scores (DS), Gammell et al. 2003). However, it is argued that these methods are unreliable when considering relatively sparse and dynamic interaction data (Neumann et al., 2011). The Elo-rating method (Albers & de Vries, 2001; Neumann et al., 2011) deals with such circumstances. The Elo-rating method was developed for the rating of chess players (Elo, 1978) and therefore copes well with hierarchies in which not all individuals interact; a situation prevalent in nature. Individuals begin with the same rating and after each dyadic contest, ratings are updated and the winner gains points, whereas the loser loses points. The number of points gained or lost is dependent on whether the outcome was ‘expected’. If the individual that is expected to lose, actually wins the interaction, the loser gains more points because the outcome was unexpected (Elo 1978). This method is also useful because it allows for the tracking of dynamic hierarchies and there is no minimum number of individuals needed (as in matrix-based methods). In situations whereby dynamic changes in hierarchy structure are not of interest and a single social rank measure is required for each individual, an extension of this method has been proposed, termed ‘Randomized Elo-rating’ (Sánchez-Tójar, Schroeder, & Farine, 2017). This method involves generating random datasets and from these the repeatability of Elo-ratings and uncertainty estimates for the inferred hierarchy can be calculated (Sánchez-Tójar et al., 2017). This allows one to deduce confidence in the final inferred hierarchy. The most appropriate hierarchy inference method will depend on the questions of interest (i.e. dynamic changes in social rank or a single social rank measure).

1.2.1.3 Fine-scale social structure; social network analysis

Social network theory has revolutionised the way in which we study the social environment (Croft, James, & Krause, 2008). Social network analysis allows the quantification of types of relationship that vary in number, strength and direction and therefore consider heterogeneity of individuals in their network position (Wey, Blumstein, Shen, & Jordán, 2008). Individuals (nodes) are connected by the relationship (edges) between two individuals. Constructing social networks allows one to quantify network metrics, such as degree: the number of edges, and strength: weight of edges. In addition to considering social relationships at the individual-level, social network analysis allows one to explore overall patterns in individual preferences, leading to group mixing and the resulting social structure. Generally, there is a tendency for individuals to associate or interact with individuals similar to themselves, i.e. homophily (Newman, 2003). These predictable assortative social network structures are related to positive fitness implications (feral horses, *Equus sp.* Cameron, Setsaas, & Linklater, 2009; Trinidadian guppies, *Poecilia reticulata*, Croft, Krause, & Darden, 2009a; bottlenose dolphins, *Tursiops sp*. Frère et al., 2010; theoretical study, Fu, Nowak, Christakis, & Fowler, 2012). Disassortative mixing, i.e. heterophily, has been reported less frequently but too, could have potential fitness implications (e.g. through frequency-dependent selection, theoretical study, Dall et al. 2004). Overall, social structure has implications for information transmission (Paridae, Aplin et al. 2012), disease transmission (Tasmanian devil, *Sarcophilus harrisii,* Hamede et al. 2009) and the spread of novel behaviour (great tits, Aplin et al. 2014). Thus, social network analysis allows us to make a link between individual level behaviour and population-level patterns (Croft 2008).

1.2.2 Concluding comments

Considering both the broad and fine-scale structures of the social environment will allow us to fully examine the factors associated with cognitive performances. The number of relationships an individual has, and the types of relationship are both important elements that form an individual's social environment. With the development of useful tools such as the Elo-rating method (Elo, 1978; Neumann et al., 2011) and social network analysis (Krause, Croft, & James, 2007; Wey et al., 2008), we can endeavour to reliably quantify agonistic and affiliative relationships, both at the individual level, but also in relation to overall group patterns and thus better understand their evolution. Consequently, we can examine how these details of the social environment relate to individual variation in cognition.

1.3 Animal cognition

Animal cognition encompasses the mechanisms that underpin how animals perceive, encode, store and respond to stimuli in their environment (Shettleworth, 2010). These mechanisms are governed by neuronal processes (Reuven Dukas, 2004) that are energetically expensive (Aiello & Wheeler, 2009; Ames, 2000; Reuven Dukas, 1999). General cognitive abilities such as learning, memory and executive function include these cognitive mechanisms and are manifested in critical behaviours, such as foraging (bumblebees, *Bombus terrestris*, Raine and Chittka 2008), mate attraction, mate finding, mate choice (Dukas & Ratcliffe, 2009; Madden, Isden, & Dingle, 2011) and navigation of the environment (Jones, Braithwaite, & Healy, 2003), hence animal cognition has potential implications for reproduction and survival (Boogert, Anderson, Peters, Searcy, & Nowicki, 2011; Maille et al., 2016; Shohet & Watt, 2009; Smith, Philips, & Reichard, 2015). Below I describe three cognitive abilities critical to animal behaviour; associative learning, spatial learning and inhibitory control and how they are measured in behavioural ecology research.

1.3.1 Associative learning

Associative learning can be measured when a behavioural response becomes associated with a particular stimulus; for example, learning that a colour is paired with a food reward. The change in behavioural responses may arise through operant conditioning (also known as instrumental conditioning), whereby reinforcement (S+) or in some cases, punishment (S-) increases or decreases the likelihood that the behaviour will occur in the future (Skinner, 1938). When an animal is reinforced for performing a different response to each of two or more stimuli, this is also referred to as discrimination learning (Shettleworth, 2010). Associative learning processes underpin a broad range of contexts and various cue types (Heyes, 2012). For example, individuals may be tested on their ability to discriminate between olfactory cues. In bank voles, *Myodes glareolus*, individuals were presented with two fruit juice odours in a Y-maze, one of which was associated with the reward of returning to the home cage (S+) and the other was associated with a blocked exit (S-) (Mazza, Eccard, Zaccaroni, Jacob, & Dammhahn, 2018). Alternatively, individuals may be tested on their ability to discriminate between auditory cues. In black-capped chickadees, individuals were assessed on their ability to associate a C or B note with either a food reward (S+) or the houselights being turned off (S-) (Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2014). Likewise, learning ability may be measured through individuals' ability to discriminate between visual cues. Predominantly in avian subjects, individuals are presented with foraging grids consisting of differently coloured or decorated wells which either contain food rewards (S+) or, are empty or blocked (S-) (Australian magpies, Ashton, Ridley, Edwards, & Thornton, 2018; black-capped chickadees, Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy 2014; song sparrows, Boogert, Anderson, Peters, Searcy, & Nowicki, 2011; spotted bowerbirds, Isden, Panayi, Dingle, & Madden, 2013; Katsnelson, Motro, Feldman, & Lotem, 2011; Lucon-Xiccato & Bisazza, 2014; Australian magpies, Mirville, Kelley, & Ridley, 2016; New Zealand robins, Shaw, Boogert, Clayton, & Burns, 2015).

Learning performances may be quantified in various ways, such as, the number of trials taken to reach a learning criterion (Guillette et al. 2014; Boogert et al. 2011), the percentage of correct choices by the end of testing (Katsnelson et al., 2011), or predicted values generated from learning curves (Wolf & Chittka, 2016). Performances on associative learning tasks is accompanied by brain activation in the hippocampus (mammals, Gould, Beylin, Tanapat, Reeves, & Shors, 1999; Myhrer & Johannesen, 1995; but see Colombo, Cawley, & Broadbent, 1997 for no relation in birds), pre-frontal cortex (mammals, Passingham, Toni, & Rushworth, 2000), and the hyperstriatum in birds (pigeons, Parker & Delius, 1980).

1.3.2 Spatial learning

As well as learning to discriminate between rewarded and unrewarded (or negatively rewarded) cues (olfactory, auditory or visual), individuals may be tested on their ability to learn the position and relationships between cues in space, and this ability is referred to as spatial learning (Gaulin & Hoffman, 1988). In ‘true’ spatial learning, subjects are said to form a dynamic spatial map, i.e. a neural representation of the external environment that is not dependent on forming as association between an external cue and the rewarded location (O'Keefe & Nadal, 1978). For the purposes of this thesis, I will not distinguish between the mechanisms used to learn spatial tasks, but I refer to testing paradigms commonly used in behavioural ecology. Assays of spatial learning and memory ability are measured using foraging grids which contain food in hidden locations (western scrub-jays, *Aphelocoma californica*, Pravosudov et al. 2005; zebra finches, *Taeniopygia guttata*, Sanford and Clayton 2008; song sparrows, *Melospiza melodia*, Sewall et al. 2013; New Zealand robins, *Petroica longipes*, Shaw et al. 2015), or maze tasks, which require individuals to navigate a maze in search of food reward (rat, *Rattus norvegicus*, Juraska et al. 1984; Spritzer et al. 2011; red-footed tortoise, *Geochelone carbonaria*, Mueller-Paul et al. 2012; pheasant, Whiteside et al. 2016b). Spatial learning ability on these tasks is typically quantified by the number of errors (incorrect locations searched) prior to reaching the reward. Performances on these tasks are associated with brain activation in the hippocampus (foraging grid: western scrub jays, Pravosudov et al. 2005; maze: pigeons, *Columbia livia,* Colombo et al. 1997; mice, Luine 2015). While learning to discriminate between rewarded and unrewarded (or negatively rewarded) cues, as well as the relationships between them in space, the ability to adjust these learned responses is also deemed critical for individuals in dynamic environments.

1.3.3 Executive control

Executive control allows individuals to respond flexibly to stimuli in their environment and inhibitory control forms part of this, which is the ability to inhibit a prepotent response. Inhibitory control is deemed important in changing social environments whereby individual's may be frequently required to inhibit behaviour that could result in negative consequences from conspecifics (Amici, Aureli, & Call, 2008; Aureli et al., 2008). For example, it may allow individuals to behave appropriately towards conspecifics, by enabling them to inhibit aggression (pigtail macaques, *Macaca nemestrina,* Strayer 1976) or refrain from stealing food (Brockman & Barnard, 1979). A commonly used paradigm to assay inhibitory control is the detour reach task, in which individuals are presented with a reward behind a transparent barrier and the subject is required to inhibit the impulse to reach for the reward, resulting in hitting the barrier, and to detour around the barrier (primates, Diamond 1990, Vlamings et al. 2010; zebra finch, Boogert et al. 2011; New Zealand robin, Shaw et al. 2015; corvids, Kabadayi et al. 2016; pheasant, van Horik et al. 2018; see for review, Kabadayi et al. 2018). Measures of inhibitory control include the number of attempts to incorrectly access the food reward (hitting the barrier) and time to reach the reward. Performances on inhibitory control tasks show brain activation in the prefrontal cortex in mammals (Ghahremani, Monterosso, Jentsch, Bilder, & Poldrack, 2010; Miller, 2001) and the nidopallium caudolaterale in birds (Rose & Colombo, 2005), a region analogous to the mammalian prefrontal cortex. Some authors have questioned the interpretation of performances on the detour reach task (van Horik et al., 2018). For instance, there was no intra-individual consistency across multiple tasks purported to assess inhibitory control in dogs (Brucks, Marshall-Pescini, Wallis, Huber, & Range, 2017) and inhibitory control performances were found related to body condition in North Island robins (Shaw, 2017). Furthermore, in pheasants, prior experience of transparent materials enhanced their subsequent performances on detour reach tasks (van Horik et al. 2018). While detour reach tasks are commonly used to assess inhibitory control (see references above), this highlights that caution should be given to non-cognitive factors, such as motivation to acquire food and previous experience with transparent objects.

1.3.4 What about problem solving?

One approach to studying individual differences in cognitive abilities has focused on *problem-solving* performances (Benson-Amram & Holekamp, 2012; Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2012; Cole & Quinn, 2012; Cole, Cram, & Quinn, 2011; Seibt & Wickler, 2006; Thornton & Samson, 2012; Zandberg, Quinn, Naguib, & van Oers, 2017). Some authors deem problem-solving to be a general cognitive ability (Roth & Dicke, 2005) and problem-solving tasks are often deployed to investigate innovation (Lefebvre, Reader, & Sol, 2004). These tasks typically use single-solution problems and are presented to individuals once or twice. It is not clear from many of these studies which cognitive processes are being measured because the underlying psychological mechanisms are not described or targeted (Isden et al., 2013; Thornton, Isden, & Madden, 2014; Thornton & Lukas, 2012). Furthermore, performance on these problem-solving tasks may be explained by non-cognitive factors, such as persistence and motivation (carib grackles, *Quiscalus lugubris*, Overington et al. 2011; meerkats, *Suricata suricatta,* Thornton and Samson 2012; theoretical, Guez and Griffin 2016; pheasants, van Horik and Madden 2016). Hence, problem solving performances may not be an adequate or informative measure of cognitive ability.

Instead of a problem-solving approach, tasks aimed at testing specific, predefined cognitive domains in which individuals are presented with choices that require the reliance on distinct cognitive abilities may be a more informative approach to studying cognition (song sparrows, *Melospiza melodia*, Boogert et al. 2011; spotted bowerbirds, *Ptilonorhynchus maculatus*, Isden et al. 2013; New Zealand robin, *Petroica longipes*, Shaw et al. 2015; Australian magpie, *Cracticus tibicen dorsalis*, Ashton et al. 2018). Furthermore, repeated presentations of a task allow one to quantify the level at which these performances differ from chance and hence, performances are not as sensitive to variation in non-cognitive factors such as motivation and persistence as the 'single trial' problem solving tasks (Thornton & Lukas, 2012).

1.3.5 Difficulties with measuring cognition

In addition to motivation and persistence that may affect our assays of cognitive abilities, cognitive performances are confounded by a multitude of factors, including hunger, previous experiences, salience of cues (Rowe & Healy, 2014; van Horik et al., 2018), neophobia (Sabine Tebbich, Stankewitz, & Teschke, 2012), stress (de Kloet, Oitzl, & Joels, 1999; Mendl, 1999) and duration between testing trials (honeybees, *Apis mellifera*, Menzel et al. 2001). Thus, quantifying individual variation in cognitive abilities is not trivial. These factors also make it difficult to distinguish whether individual variation in cognitive abilities is consistent and can therefore be selected for. A recent meta-analysis suggests that temporal and contextual repeatability in individual cognitive performances is low and is dependent on the species, type of task and cognitive performance measure (Cauchoix et al., 2018). Evidently, it is important to consider the non-cognitive factors that affect the measurement of cognitive abilities.

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1.3.6 Captive versus wild studies

There is much debate about whether cognitive abilities should be assayed in the field or in captivity (Pritchard, Hurly, Tello-Ramos, & Healy, 2016; Thornton et al., 2014; Thornton & Lukas, 2012). When using individuals bred in captivity, experimenters can control which stimuli individuals are exposed to during development, thus standardising the effect that previous experiences may have (Rowe & Healy 2014). However, individuals that have been bred in captivity have not been faced with the same ecological challenges and experiences as their wild counterparts (Pritchard et al., 2016), hence testing wild individuals in their natural habitat may be more informative. Nevertheless, testing cognition in the wild is problematic. First, it may lead to a bias in test subjects. For example, territorial individuals are easier to target (spotted bowerbirds, *Ptilonorhynchus maculatus*, Isden et al. 2013; New Zealand robin, Shaw et al. 2015) as they are consistent in their location and highly motivated to interact with task apparatus in their territory. Although performances between territorial individuals will be comparable, it does not allow us to explore the full range of cognitive performances that may exist in a population as non-territory holders are not assessed. Further, it is not always possible to standardise confounding factors like hunger (Rowe & Healy 2014) and inter-trial intervals (Menzel et al. 2001) described above.

A further criticism of testing wild individuals of unknown developmental history is that we do not have information on their previous experiences (Rowe and Healy 2014). Some of these problems can be overcome by incorporating the initial bias in statistical analyses, and if the explanatory variable of interest still explains a significant amount of variation then we can be confident that these factors contribute to individual variation in cognitive performances, in spite of previous experiences.

An alternative approach may be to test wild animals held temporarily in captivity. Although the housing of wild animals may be stress-inducing, over time these levels of stress may eventually return to baseline (see Pravosudov 2003) and reliable and realistic assays of cognitive performance can be collected. In great tits, *Parus major*, variation in learning curve performances on a serial-reversal task assayed in wild and captive individuals were found to be repeatable (Cauchoix, Hermer, Chaine, & Morand-Ferron, 2017). This suggests that testing wild animals in captivity may be representative of ‘natural’ behaviour and may be a profitable approach to measuring individual variation in cognition.

1.3.7 Concluding comments

Ideally, a study system in which individuals readily learn, are amendable to various test paradigms and their early life experiences can be standardised, will prove fruitful in quantifying individual differences in cognitive abilities while controlling for developmental history (Nowicki et al. 2002) and different experiences (Rowe and Healy 2014). Furthermore, a system in which there is the opportunity to release individuals in to the wild, whereby their behaviour can be shaped by ecological challenges and natural behaviour can be investigated in relation to early life cognitive performances. Finally, a system in which individuals can be held temporarily in captivity and are motivated to engage in cognitive testing as adults would allow us to detect changes or differences in cognitive performances since early life and the associated social factors.

1.4 Social environment as the cause of individual differences in cognitive performances

While individual variation in cognitive ability can be attributed to multiple factors (genetic: Plomin and Spinath 2002, Croston et al. 2015; environmental: Girvan and Braithwaite 2000, Evans et al. 2016; ontogenetic factors, birds, Nowicki et al. 2002), evidence that the social environment influences cognitive performances is mounting. Both broad-scale and fine-scale social structures may be a cause of individual variation in cognitive performances which may arise though various mechanisms.

1.4.1 Broad-scale social structure; Group size

How variation in group sizes contributes to individual variation in cognitive performances has seldom been explored. One study on free-ranging Australian magpie, *Cracticus tibicen dorsalis,* reveals that stable group size was found to be associated with a general intelligence factor (*g*), with individuals from larger groups outperforming individuals from smaller groups on a battery of four cognitive tasks (Ashton et al. 2018). Below I discuss the potential mechanisms underlying this relationship.

1.4.1.1 Group size, perception and attention

This higher level of performance from individuals living in larger groups may be related to less time spent being vigilant. Less time spent being vigilant allows individuals to invest more time in perception while foraging and interacting with conspecifics. When perception and attention are interrupted, random choices may be made (Guilford & Dawkins, 1987), indicating that these abilities precede learning. Ashton et al. (2018) explain that anti-predatory vigilance behaviour was not observed during interactions with the tasks. Instead, the authors suggest that living in larger groups presented cognitive stimulation and facilitated cognitive development because the relationship between cognitive performance and group size became ‘stronger’ with age. However, it is difficult to distinguish genetic from social factors; Australian magpies live in stable family groups throughout life and experimental studies are needed to decouple these effects.

1.4.1.2 Group size, cognitive stimulation and development

Experimental evidence suggests that when individuals are reared in isolation they suffer severe impairments in cognitive performances (reversal learning in rats, *Rattus norvegicus*, but not acquisition learning or spatial memory, Schrijver, Pallier, Brown, & Würbel, 2004; spatial learning in rats, Holson, 1986; Juraska, Henderson, & Muller, 1984; discrimination learning in rhesus macaques, *Macaca mulatta*, Harlow, Harry, Dodsworth, & Harlow, Margaret, 1965). Cognitive stimulation from inanimate objects and social interactions (Rosenzweig, Bennett, Hebert, & Morimoto, 1978) causes behavioural (Hebb, 1949) and neurological changes (mammals, see van Praag et al., 2000 for review). Individuals are particularly susceptible to cognitive stimulation effects early in life. Early in life, neurological structures are still forming and are affected by interactions with the environment (mammals, Knudsen, 2004; songbirds, Stephen Nowicki, Peters, & Podos, 1998). These isolation rearing studies compared the cognitive performances of isolated individuals to that of group reared individuals. We therefore do not know the effect of different group sizes (i.e. group size that varied on a continuous scale) on cognitive performances and if this is a linear relationship. The only experimental evidence of the effect of different group sizes on cognition, has focused on neural structures and this has produced mixed evidence. When captive rhesus macaques were housed in different group sizes for three months, those living in larger groups had increases in grey matter and increased activity in frontal and temporal cortex compared to individuals housed in smaller groups (Sallet et al., 2011). In mountain chickadees, *Poecile gambeh,* social group size or composition did not have an effect on neurogenesis (Fox, Roth, LaDage, & Pravosudov, 2010). However, neural substrates and cognitive performances are not always positively related. For example, macaques are better at task switching than humans, yet have a relatively smaller pre-frontal cortex than humans (Stoet & Snyder, 2009). Whether group size causes variation in cognitive performances and, or, whether these mechanisms affect adults, after individuals have surpassed critical periods, remains to be tested.

1.4.2 Fine-scale social structure; Social hierarchies

In addition to the relationship between the broad-scale social environment and individual cognitive performances, associations have also been made between cognitive performances and fine-scale social structures, in terms of social hierarchies. There is reproductive skew in favour of higher ranking individuals (Clutton-Brock, Albon, & Guinness, 1984; Ellis, 1995; Wilson, 1975), and an individual’s position in a social hierarchy governs many factors that may contribute to the relationship between social rank and cognitive performances, such as the receipt of information due to being more centrally located in social networks (black-capped chickadees, *Poecile atricapillus*, Jones et al. 2017), learning opportunities (Kummer and Goodall 1985; Chalmeau and Gallo 1993), resource distribution (Popp & DeVore, 1979; Wilson, 1975) and stress (Abbott et al., 2003; Sapolsky, 2005). Evidence that dominance may facilitate better cognitive performances includes reports that dominant individuals outperform subordinate individuals on operant learning (starlings, *Sturnus vulgaris,* Boogert et al. 2006), observational learning (chickens, *Gallus gallus domesticus,* Nicol and Pope 1999), spatial learning (mice: Barnard and Luo 2002, Fitchett et al. 2005; meadow voles, *Microtus pennsylvanicus,* Spritzer et al. 2004) and spatial memory (mountain chickadees, *Poecile gambeli*, Pravosudov et al. 2003 but see Spritzer et al. 2004) tasks. In the following section I discuss the potential factors behind this positive relationship between social rank and cognitive performances and why in some cases we may observe the opposite relationship, i.e. subordinates outperform dominants.

1.4.2.1 Social hierarchies and the distribution of resources

Dominant individuals are often larger than subordinate individuals (red-winged blackbirds, Searcy 1979; red-deer, Clutton-Brock et al. 1982; carrion crows, Richner 1989), although not always (song sparrows, Arcese & Smith 1985), and in many cases more aggressive (Chase, Tovey, Spangler-Martin, & Manfredonia, 2002 but see; Francis, 1988), and physically outcompete subordinates for resources (Wilson, 1975; Popp and DeVore, 1979). In some species, social rank may be inherited (Japanese macaques, *Macaca fuscata,* Kawamura 1958). Access to resources may facilitate increased opportunity for learning for dominant individuals (chimpanzees, *Pan* *paniscus,* Kummer and Goodall 1985), and decrease opportunities for subordinate individuals (chimpanzees, Chalmeau and Gallo 1993).

In addition to altering learning opportunities, social rank directly alters nutrient intake. Dominant individuals are reported to be in better body condition than subordinate individuals (body size: rainbowfish, *Melanotaenia duboulayi*, Colléter and Brown 2011; common waxbill, *Estrilda astrild*, Funghi et al. 2014: body condition: Icelandic horses, *Equus caballus*, Vervaecke et al. 2007). Hence, the superior performances on cognitive tasks by dominant individuals may be because they can afford the costs of energetically expensive neural structures that underlie cognitive abilities (Dukas 1999; Ames 2000; *The expensive tissue hypothesis,* Aiello and Wheeler 2009). However, there are mixed findings for the association between body condition and cognitive performances. Body condition is associated with superior performance on the detour reach task in New Zealand robins (Shaw, 2017), but there was no relationship reported between body condition and colour discrimination performances in Zenaida doves, *Zenaida aurita* (Boogert, Monceau, & Lefebvre, 2010).

1.4.2.2 Social rank and 'playing dumb'

Dominants and subordinates may not differ in their learning ability, but their expression of this ability is dependent on their social rank and the social partners present while completing a cognitive task. In rhesus macaques, *Macaca mulatta,* subordinate individuals solved a previously learned foraging task but only when dominant individuals were not present (Drea & Wallen, 1999).

1.4.2.3 Social rank and stress

Social rank may not just alter opportunities and imperatives for learning, it may influence underlying psychological mechanisms that in turn shape cognitive performance. Stress is known to alter the expression of cognitive abilities (de Kloet et al., 1999; Mendl, 1999). Whether stress is at detrimental levels in dominant or subordinate individuals is likely to be dependent on the overall social structure of a species and how the social rank is maintained (primate review, Sapolsky 2005). In species that have unstable social ranks and which typically maintain rank through direct aggressive encounters, such as male rhesus macaques, *Macaca mulatta,* being dominant may be extremely stressful (Sapolsky 2005). The *stress of domination* hypothesis requires that higher ranking individuals have more aggressive contests and suffer from increased stress as a result (review, Creel 2001; male bison, *Bison bison*, Mooring et al. 2006). This may explain why in crab-eating macaques, *Macaca fascicularis,* dominants were found to make more errors before reaching a learning criterion than subordinate individuals on a visual discrimination and reversal tasks (Bunnell, Gore, & Perkins, 1980). The authors report a decrease in social rank was associated with a decrease in the number of errors made. However, this study was correlational; a third variable that determined social rank and learning performance, such as parasite load could have impeded individuals from achieving high social rank (red jungle fowl, *Gallus gallus*, Zuk et al. 1998) and hindered cognitive performance (bumblebees, *Bombus impatiens,* Gegear, Otterstatter, & Thomson, 2005). Thus, it is not clear that the social environment was driving this relationship.

There is evidence for a direct effect of aggressive interactions on memory performances of the aggressor. Dominant crabs, *Chasmagnathus granulatus*, had impaired memory performances of a dangerous context signal compared with subordinates (Kaczer, Pedetta, & Maldonado, 2007). This difference between dominants and subordinates in the duration of memory retention was only apparent after a dominance encounter and not before, suggesting that the differences between individuals of different social rank was as a direct consequence of this social interaction.

In some forms of social hierarchy, harassment and little control over social situations may lead to subordinates suffering from greater levels of physiological stress, termed the *stress of subordination* hypothesis (Abbott et al., 2003; Blanchard, Sakai, McEwen, Weiss, & Blanchard, 1993). In mice, levels of basal corticosterone were higher in subordinate mice compared with dominant mice and this was accompanied by poorer performances by subordinates on learning tasks (Francia et al. 2006). In mountain chickadees, there were no differences between corticosterone levels of dominants and subordinates, but subordinates had lower levels of cell proliferation, accompanied by poorer spatial memory (Pravosudov et al. 2003). It is difficult however, to determine causality in these correlational studies because learning was not assessed when the same individuals occupied different social ranks. Only one study to date has observed impairment in subordinates' learning ability as a direct result of social rank. Mice were housed singularly and had their spatial learning ability assessed, and were then housed in pairs and a dominance relationship was established before having their spatial learning ability re-assessed (Barnard & Luo, 2002). Differences in learning performances between individuals of different social rank were only apparent after paired housing, and the authors suggest this difference was mediated through aggression, as there was a positive relationship between post-pair learning and number of agonistic interactions initiated. When this relationship was explored in reverse and learning performances were assayed once social rank was established and again when social pressures involved with rank were removed, by housing mice individually, impairments in subordinates' spatial learning ability were found to persist (Fitchett et al., 2005). These differences between dominant and subordinate individuals were found to persist long after the social environment had changed, and individuals were no longer experiencing social pressure from dominants, i.e. housed individually again. This suggests that the effects of negative social interactions are long lasting, or that the effects of social isolation may have also contributed to poor performances.

1.4.2.4 The absence of a relationship is also informative

The absence of a relationship between cognitive performance and social rank is also informative. In mountain chickadees, *Poecile gambeli*, performances on a spatial learning task were related to social rank, whereas, performances on a non-spatial version of the task were not (Pravosudov et al., 2003). This may suggest that the ability to distinguish between spatial cues specifically is related to high social rank in this food-caching species, but learning performances more generally are less important. In the eastern water skink, *Eulamprus quoyii*, dominant individuals outperformed subordinates in an associative learning task but there were no social rank differences on the reversal of the task (Kar, Whiting, & Noble, 2017). This may suggest that behavioural flexibility is not important to dominance, compared with general learning processes. Exploring these individual differences can help to elucidate the mechanisms underlying the relationships between cognitive abilities and social rank.

1.4.2.5 Ecological relevance of hierarchy measures

The methods of hierarchy inference used in previous research may be unreliable and not representative of the relationship between social rank and cognitive performances in the real world. The relationship between cognitive abilities and social rank has been explored in terms of dyads (mice: Barnard and Luo 2002, Fitchett et al. 2005; meadow voles, Spritzer et al. 2004; mountain chickadees, Pravosudov et al. 2003) or small groups (chickens, Nicol and Pope 1999; starlings, Boogert et al. 2006). However, in nature, social hierarchies typically consist of multiple individuals. Furthermore, there are other behavioural processes besides the interactions between dyads that lead to the overall social hierarchy. For instance, bystanders affect the resulting social structure (Chase, 1982). Hence, we do not fully understand how the relationships between cognitive abilities and social rank manifest in a more ecologically relevant social environment.

1.4.3 Concluding comments

It is evident that both the broad and fine scale social environments govern various mechanisms that impact on the development and expression of cognitive abilities. There is correlative evidence for the relationship between group size and a general cognitive ability factor in a single study (Ashton et al. 2018), however, no studies exist that identify group size as the causal factor (Figure 1.1), thus experimental manipulations are required. There is correlative and causal evidence for an effect of agonistic relationships on cognitive performances but our ignorance of these relationships relative to more realistic fine-scale social structures impedes our understanding of how cognitive performances may manifest in the real-world social environment. Additionally, our knowledge of how these relationships form and develop is limited (Thornton & Lukas, 2012) and the field would benefit from investigations at various stages of life.

1.5 Social environment as the consequence of individual differences in cognition

There is likely a complex interplay between the social environment and cognition. Whilst the social environment may shape an individual’s cognitive performance, it is equally likely that the social environment may be shaped by individual variation in cognitive abilities. Cognitive abilities may play a role in determining partner choice and how individuals respond to social partners. Evidence that individual variation in perception, attention, learning, memory and inhibitory control affects social relationships is limited (Wascher, Kulahci, Langley, & Shaw, 2018). In the following section I review evidence that individual variation in cognitive abilities may affect two forms of fine-scale social structure. First, I discuss how cognitive abilities may influence social hierarchies through their influence on agonistic interactions. Second, I review evidence that cognitive abilities may influence assortative or disassortative group mixing through their influence on individual relationships.

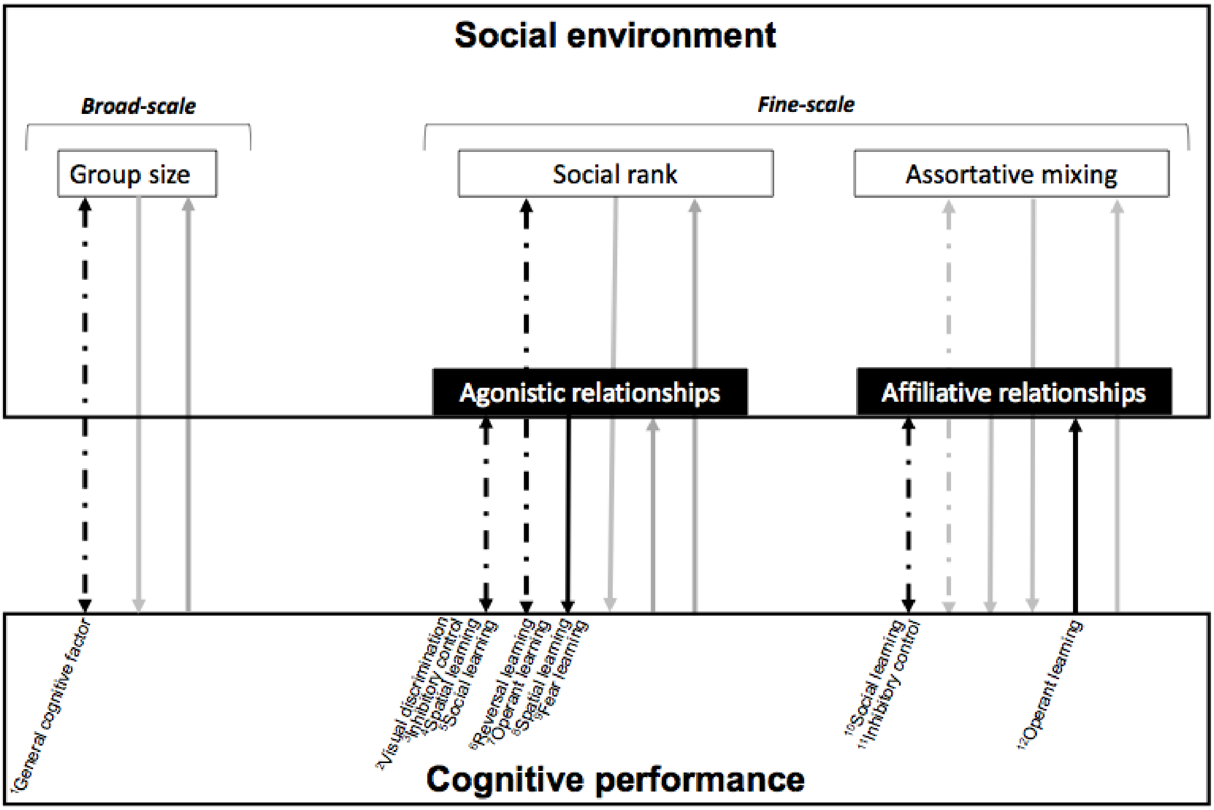

Figure 1.1: Relationships between individual differences in cognitive performances and the social environment. Dashed, double headed arrows represent evidence of a relationship whereby causality was not determined. Single headed arrows indicate the direction of causality in the relationship. Black arrows represent existing evidence, grey arrows represent no existing evidence. Agonistic relationships indicate investigations into aggressive interactions between dyads. Social rank represents the overall patterns of these agonistic interactions and includes investigations with groups containing >4 individuals in which social rank was inferred. Affiliative relationships indicate affiliative interactions or non-random associations. Assortative mixing indicates social network structure by these affiliative relationships. For clarity, the diagram does not contain research with non-significant relationships. Figure references are detailed in the appendix.

1.5.1 Fine-scale social structure; Social hierarchies

The *prior attributes* hypothesis suggests that linearity of a social hierarchy may be predicted by linearity for other traits (Chase, 1974; Chase, Tovey, Spangler-Martin, & Manfredonia, 2002). This hypothesis was focused on physical attributes and social hierarchies are found to be structured according to age (African elephant, *Loxodonta Africana*, Hollister-Smith et al. 2007; mountain goat, *Oreamnos americanus*, Côté 2000), body size (Gambel’s quail, *Callipepla gambelii*, Hagelin 2002; alpine ibex, *Capra ibex*, Bergeron et al. 2010), weaponry (pheasants, Mateos 1998), and even consistent behavioural attributes (e.g. exploration of a novel environment in mountain chickadees, *Poecile gambeli*, Fox et al. 2009). If variation in cognitive abilities aid individuals in attaining high social rank (Humphrey’s 1976; Bryne and Whiten 1988; Seyfarth and Cheney 2002), we may find that cognitive performances predict social rank. However, it is not trivial to tease these factors apart because agonistic interactions directly impact on cognitive performances (Barnard & Luo, 2002; Kaczer et al., 2007). As yet, whether cognitive ability influences contest outcomes or the resulting social rank has not been formally tested (Chichinadze, Chichinadze, Gachechiladze, Lazarashvili, & Nikolaishvili, 2014).

1.5.1.1 Cognitive abilities that may influence social rank

Evidence that individual variation in cognitive abilities may shape social hierarchies either by affecting partner choices for contests or affecting the outcome of agonistic interactions is lacking (see Reichert and Quinn 2017 for review). There is some evidence suggesting how variation in cognitive abilities may play a role. Perception and attention abilities are likely to enable individuals to attend to conspecifics and make accurate assessments of their fighting ability (Arnott & Elwood, 2009). The gathering of this information prior to contest could reduce costs of engaging in an interaction. For example, in American lobsters, *Homarus americanus,* levels of aggression remained elevated when urine cues of prior opponents were blocked and this contrasted with controls in which the urine cues were available and contests were much shorter in duration (Kaplan, Lowrance, Basil, & Atema, 1993). This indicates how attention and perception abilities could shape the interactions that ensue.

Observational or social learning allows individuals to learn about conspecifics by observing them, and permits the gathering of information while reducing time (Galef & Giraldeau, 2001), energy, and potential injury costs from direct social interactions (Johnstone, 2001). In fighting fish, *Betta splendens,* males monitor conspecifics' interactions to guide their future interactions with those they have observed (Oliveira, McGregor, & Latruffe, 1998). This may involve simple associative processes that enables individuals to respond appropriately to a competitor. In hermit crabs, *Pagurus longicarpus*, individuals are able to associate the odour of a social partner with the size of their shell and they readily relearn this association when the social partner switches to a larger shell (Gherardi, Tricarico, & Atema, 2005). This flexibility in learning may also prove useful in changing social environments.

Inhibitory control is likely to prove useful in agonistic contexts. Specifically, the ability to withhold aggressive tendencies from more dominant or highly aggressive conspecifics may avoid costs arising from negative interactions. Subordinate individuals often outperform dominants on tasks involving inhibitory control abilities, such as reversal learning tasks (pigtail macaques, *Macaca nemestrina*, Strayer 1976).

However, whether individual variation in this ability precedes the formation of social rank or is a result of social rank, is unknown.

As well as assisting prior to and during an agonistic interaction, cognitive abilities may also indirectly influence social rank. In territorial species, spatial learning ability may allow individuals to learn and remember rewarding or non-rewarding locations of competitors, mates and food resources (Stamps & Krishnan, 1999). Hence, this information will firstly enable individuals to behave most appropriately. Intruders avoid territories in which they have previously received aggression (Stamps, 1994) thus reduce costly aggressive interactions (Neat, Taylor, & Huntingford, 1998). Second, if individuals preferentially visit rewarding locations then they are able to invest in energy needed for aggressive interactions (Hsu, Earley, & Wolf, 2006). Spatial learning ability consequently, may influence social rank but as yet there is no empirical evidence to support this idea.

1.5.2 Fine scale structure; Group mixing

Assortative or disassortative group mixing may be a consequence of individual characteristics. We observe social structures assorted by kinship (meerkats, *Suricatta suricata,* Madden et al. 2012), age (baboon, *Papio ursinus*, Carter et al. 2015), sex (Tasmanian devil, *Sarcophilus harrisii*, Hamede et al. 2009; pheasants, *Phasianus colchicus,* Whiteside et al. 2018), body size (chub, Krause 1994; golden shiner *Notemigonus crysoleucas*, and banded killifish *Fundulus diaphanous*, Krause et al. 1996; Hoare et al. 2000) and even consistent behavioural traits (boldness in female Trinidadian guppies, *Peocilia reticulate*, Croft et al. 2009; exploration in male great tits, *Parus major,* Aplin et al. 2013; boldness in baboons, Carter et al. 2015; socialibility and boldness in chimpanzees, *Pan paniscus,* Massen and Koski 2014). Alternatively, social structures may disassort based on individual variation. Disassortment by sex is seen in monogamous species in which mated pairs are observed together (passerines, Farine 2014). Disassortative mixing by consistent behavioural type is seen in large aggregations of barnacle geese, *Branta leucopsis,* and this disassortment is suggested to reflect producer-scrounger dynamics in foraging strategy (Kurvers et al., 2010). As yet, whether fine-scale social structures are also an emergent property of individual variation in cognitive abilities is relatively unexplored.

1.5.2.1 Cognitive abilities that may influence group mixing

In addition to the examples described above, in which cognitive abilities may aid individuals in partner choices for agonistic relationships, cognitive abilities may indirectly influence affiliative and associative relationships and the resulting social structure by increasing an individual's 'attractiveness' to conspecifics. For instance, the ability to refrain from negative behaviour, such as inhibiting the impulse to steal food, will likely result in individuals being preferred foraging partners. In carrion crows, *Corvus corone corone,* for example, individuals that exhibited superior levels of performance on a self-control task ('A not B' task) received a greater number of affiliative and aggressive interactions (Wascher, 2015). Thus, individuals with good inhibitory control abilities are attractive to non-aggressive and aggressive partners alike. However, the study on crows was correlational, and it is possible that these high rates of social interaction, facilitated an individual's ability to exert inhibitory control.

Learning, locating and remembering profitable resources may also make an individual an ‘attractive’ social partner, thus influencing the relationships that are formed. Recent evidence suggests that ringtailed lemurs, *Lemur catta,* that are observed successfully acquiring food in an operant foraging task, became more central in their social network as a consequence (Kulahci, Ghazanfar, & Rubenstein, 2018b). It is possible that observers were associating the successful individuals with food and hence increased their associations with this individual as a consequence of local enhancement. Kulahci et al. (2018) suggest that this affiliation was not a consequence of the observer scrounging food, because only a single food reward was available to the solver. Hence, the mechanisms for this relationship between successful foraging and resulting social structure are unclear.

Individual learning performances have also been linked to foraging strategies which in turn go on to shape fine-scale group structures. *Producer-scrounger* theory explains the foraging strategy that individuals’ may adopt when foraging in a group, whereby some individuals behave as ‘scrounger’ individuals that exploit resources provided by ‘producer’ individuals (Barnard & Sibly, 1981; Caraco & Giraldea, 1991; Vickery, Giraldeau, Templeton, & Donald, 1991). It has been suggested that individuals that are inefficient learners more readily adopt the scrounger foraging strategy (Katsnelson et al., 2011). This relationship between learning and foraging strategy has been shown in wild sub-populations of great tits, *Parus major,* in which stable frequencies of producer and scrounger were identified and those slow to learn a social foraging task were more likely to adopt the scrounger role (Aplin & Morand-Ferron, 2017). The scrounger individuals also had a greater number and strength of social connections. However, these data on learning performances, foraging strategy and social dynamics were collected simultaneously, hence it is difficult to determine the driving factor in these relationships.

In captive house sparrows, *Passer domesticus,* individuals were tested on a visual association task early in life and there was a positive relationship between task performances and the tendency to forage as a ‘producer’ in an aviary after fledging (Katsnelson et al., 2011). This study demonstrates that foraging strategy does not necessarily drive variation in learning abilities. Katsnelson et al. (2011) describe that this relationship could emerge through two non-exclusive mechanisms. First, individuals that have an innate or acquired advantage in learning ability, learn to prefer producing. Second, learning ability and foraging tendency are initially associated via a shared (genetic or non-genetic) mechanism. If this link between learning ability and social foraging strategy is a general phenomenon, it could have potential implications for the role that cognitive abilities play in foraging associations and the resulting social structure.

1.5.3 Concluding comments

Due to the difficulties with separating cause and consequence in the link between cognitive abilities and the social environment, there is a lack of empirical evidence that individual differences in cognition can influence dyadic social relationships (Wascher et al., accepted), let alone the more complex, emergent broad and fine scale structures of the social environment (Figure 1.1). Individual variation in cognitive abilities and social relationships are likely to influence each other. For example, spatial learning ability may influence an individual’s movement throughout their physical environment and thus, affect their social interactions. Thus, cognitive performance influences the social environment. Social interactions will determine whether an individual has rewarding, unrewarding or negative experiences and consequently, may influence what an individual learns. Thus, the social environment influences spatial learning performance. While this bi-directional relationship is likely for various types of cognition and social structure, being able to distinguish between cause and consequence will aid our understanding of how one factor may shape the evolution of the other.

1.6 Study system; the pheasant

The pheasant offers an unusual opportunity to explore questions regarding individual variation in cognitive performances in relation to the social environment. Individual pheasants vary in their propensity to learn (Madden, Langley, Whiteside, Beardsworth, & van Horik, 2018; van Horik, Langley, Whiteside, Laker, & Madden, 2018) and behave flexibly (Madden, Langley, Whiteside, Beardsworth, & van Horik, 2018; Meier et al., 2017; van Horik et al., 2018). Furthermore, individuals vary in their social preferences (Whiteside et al., 2018; Whiteside et al., 2017) and immediate social environments (Whiteside et al., 2016). By understanding whether the variation in social and cognitive phenotypes is associated may elucidate how these relationships arise and are maintained. Thus, we can further our understanding of how and why general cognitive abilities have evolved. Below I describe the natural history of the pheasant and their suitability as a study system.

1.6.1 Natural history of the pheasant

In the UK, between 25 – 50 million pheasants are artificially reared and released into the wild each year for game sporting purposes (see Madden, Hall, & Whiteside, 2018 for review). It is estimated that 45% of released pheasants are shot, 42% die from natural, non-shooting causes such as predation (predominantly foxes and birds of prey, Brittas, Marcström, Kenward, & Karlbom, 1992; Kenward, Hall, Walls, & Hodder, 2001) and disease, and 13% are still alive before the end of the shooting season in February (Tuner 2007 reviewed in Madden et al., 2018).

In the wild, pheasants exhibit a varied and complex social life. Generally, pheasants forage in open landscapes (Bertram 1978).They are omnivorous and forage on insects, grass, seeds and galls (Whiteside, Sage, & Madden, 2015) and populations show some reliance on artificial wheat feeders (Draycott, 2002; Whiteside et al., 2015). During the winter, pheasants exhibit sexual segregation; females forage in groups and males generally avoid other males (Whiteside et al., 2018).

In the spring following hatching, pheasants become sexually mature (Cramp, 1998). Adults are sexually dimorphic, with males 40% larger than females and males possessing elaborate secondary sexual traits such as brightly coloured plumage, ear tufts, red wattle, spurs and long tails. Male pheasants defend a territory and, or females on a territory (Ridley and Hill 1987). Territory acquisition begins as early as October (Whiteside et al., 2018) and males acquire territories, usually at the edges of woodland or shrubby vegetation (Lachlan and Bray 1976) and do so through direct agonistic interactions with other males (Mateos & Carranza, 1997). Agonistic interactions take the form of chases, threats and even direct contact with spurs, used as weapons. Males advertise territory ownership through displays. Displays include crowing, a loud ‘kok-kok’ noise (Robertson, 1997), and lateral displays, whereby a male flattens the wing closest to the observer so that the tips of the primaries touch the ground, the head is held low with erected ear tufts, wattles swollen, body feathers fluffed out and tail spread, sometimes the wing is vibrated to produce an audible sound (Mateos & Carranza, 1999). The lateral display functions to deter competitors and advertise their quality to potential mates (Mateos & Carranza, 1999). Males that do not acquire a territory are subordinate to territory holders and behave as satellite males, hence dominant territory holders have smaller home ranges than satellite males (dominant males: 0.42ha and satellite males: 0.57ha, Grahn et al. 1993). There is high reproductive skew in favour of territory holders and up to 50% of males may not obtain a territory (Cramp & Simmons, 1980; Ridley & Hill, 1987). Subordinate males achieve copulations with females through harassment and force (Ridley & Hill 1987).

Females may choose to join a male’s harem based on secondary sexual traits. Females have been shown to prefer males with longer spurs (Göransson, von Schantz, Fröberg, Helgee, & Wittzell, 1990; von Schantz et al., 1989), longer ear tufts and longer tails, but there is no evidence of female choice for wattle size or brightness of plumage (Mateos & Carranza, 1995). Females have also been shown to prefer dominant males (Ridley & Hill 1987). Females are also attracted by male courtship feeding behaviour (Mateos & Carranza, 1999), sometimes referred to as ‘tidbitting’ in which a male picks up and drops food repeatedly while making a soft contact call (Hill and Robertson 1998; Cramp and Simmons 1980). Females respond to tidbitting by joining the male and consuming the food. Although males provide no parental care

(Taber 1949), it is suggested that the harem holding male provides protection from harassing males, occupy favoured habitats (Robertson 1997), and, or provide levels of vigilance that allows females to invest more time in foraging (Whiteside, Langley, & Madden, 2016). Harem formation occurs towards the end of winter, through to the breeding period. Harem sizes have been found to vary from a single female to eight females (Hill and Robertson 1988), with a harem size of a single male and 2.7 females for optimal predator detection (Whiteside et al., 2016).

The breeding season begins in March and persists throughout April. Purportedly, harems remain relatively stable during this period (Hill & Robertson, 1988; Ridley & Hill, 1987), although females have been reported as nesting outside of the territory of the harem holding male (Hill and Robertson 1988). Once females begin producing eggs they lay an egg almost daily until a clutch of approximately 12 eggs is laid, females then incubate for nearly 23 days before the eggs hatch simultaneously. Females provide uniparental care (Cramp, 1998) whereby mothers defend the nest from predators and chicks remain close to their mothers to learn foraging skills (Robertson, 1997). Chicks feed predominantly on insects and this high protein diet is necessary for growth and survival (Robertson, 1997). Chick survival in the wild is low and this is suspected to be a result of modern farming practices (see Robertson, 1997).

1.6.2 Suitability of the pheasant as a study system

Pheasants offer three distinct advantages for studies of the relationship between cognitive performances and the social environment. First, we can examine cognitive performances and social relationships during early life in captivity; when environmental and spatial conditions are identical and where only the social environment differs (aggression among conspecifics). Pheasants are a precocial species and can be reared without parents. Pheasants are galliformes, the same taxonomic order as chickens, for which cognitive tests are well developed (Marino, 2017). Each year we rear ~200 pheasants, identifiable by numbered wing tags, and assay their cognitive performance individually on a range of cognitive tasks (Meier et al., 2017; van Horik et al., 2018; van Horik, Langley, Whiteside, & Madden, 2016; van Horik & Madden, 2016).

Second, the pheasant system allows us to investigate how these cognitive performances relate to social structures in their natural environment. During the summer we release the pheasants at North Wyke Farm, Devon (50°77'N, 3°90'W). The site covers 250Ha containing grassland, lowland deciduous woodland, fen meadow and 40 artificial wheat feeders. The site is not subject to predator control or game shooting. On release we place the birds into an open-topped release-pen ~2500m^2 situated near to the centre of the farm. The release-pen is surrounded by an electric fence to exclude terrestrial predators but is exposed to the threat of aerial predation. Pheasants can disperse from this pen at will. At each of the artificial feeders we have motion activated cameras that enable us to monitor who associates with whom. During some years we also installed radio frequency identification (RFID) antennae at feeders and birds were fit with RFID tags on their tarsus. Thus, we are able to follow individuals in the wild and investigate the relationship between their natural social environment and early life cognitive performance.

Third, we can re-test individuals' cognitive performances when adult, observe their social environments in fine detail and manipulate their social environment to observe the associated effects on cognitive performances. During spring of each year, we capture adult pheasants prior to their breeding season and house them in captivity. During this period, we are able to observe direct aggressive interactions between males, something that would not be feasible in the wild. Furthermore, we can manipulate their social environment to see how this affects cognitive performances. While housed in captivity we collect the eggs for artificial incubation to begin the process again.

1.7 Conclusions and research questions

There are large gaps in our knowledge surrounding the relationship between individual variation in cognitive performance and the social environment. Critically, there have been few attempts to distinguish between social causes and consequences of individual differences in cognitive performances. Furthermore, we have little understanding of how these factors so pertinent to an individual's fitness manifest over an individual's life and are so entwined. In five experimental chapters I will investigate the causes and consequences of individual differences of cognitive performances in relation to the social environment.

In **Chapter 2** I investigated whether the broad-scale social environment causes individual variation in cognitive performances of captive adult female pheasants by manipulating group size and measuring discrimination performances on two similar yet distinct associative spatial learning tasks. Species that live in larger group sizes outperform species that live in smaller groups on cognitive flexibility (Amici et al., 2008) and social cognition tasks (MacLean et al., 2013). Within species, larger group are more likely to solve novel problems than smaller groups (Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011). Comparably, at the individual level, cognitive abilities are found impaired in adults that were reared in isolation (Schrijver, Pallier, Brown, & Würbel, 2004; Holson, 1986; Juraska, Henderson, & Muller, 1984; Harlow, Harry, Dodsworth, & Harlow, Margaret, 1965) and a study of wild Australian magpies showed that stable group size correlates positively with a general intelligence factor *(g)* (Ashton et al. 2018). Currently, evidence for the positive relationship between group size and cognitive performances is correlational (Ashton et al. 2018) and does not explore cognitive performances in relation to group size on a continuous scale (i.e. not isolation versus group studies as described above). In this chapter, I examine the direct, short term effects that group size has on cognitive performances. In line with the general patterns that we see in inter and intra-specific studies, I predicted that individuals in larger groups would outperform those in smaller groups on the learning tasks.

I then explore the fine-scale social environment and investigate the relationship between male social rank and spatial discrimination performances in an escape type task in **Chapter 3.** In the wild, male pheasants occupy different home range sizes depending on their social rank, therefore I expected that a task involving spatial cues would be likely to capture social rank-related differences between males in their cognitive performances. Previous studies investigating social rank and cognitive performance have focused on ranking dyads as either dominant or subordinate. Rarely in nature are individuals simply dominant or subordinate as they have many relationships, hence we explored this relationship while males were in a large group, giving a more realistic insight into how this relationship may manifest in nature. In agreement with what is reported in dyads, in which dominants outperform subordinates on cognitive tasks, I predicted a positive linear relationship between cognitive performances and social rank.

To determine cause and consequence in the relationship between social rank and cognitive performance, in **Chapter 4** I investigate whether variation in learning ability may cause social rank position, or instead it is the current social environment that causes variation in cognitive performance. I investigated this in a number of ways; first by looking at whether chick performance on a spatial discrimination task predicted future adult performance on the same task, as well as whether their chick performance predicted adult social rank. This may be taken as evidence for the prior attributes hypothesis that outlines how individual differences predict the structure of social hierarchies (Chase et al. 2002). Second, I re-tested adult males on the same task while living in a housing treatment designed to manipulate their social rank; all males were provided with harems and uncontested territories. I assessed whether their most recent recording of social rank has any predictive power in explaining variation in learning performances. Previous studies have been mainly correlative, and few have investigated cognitive performances before and after exposure to social interactions. I predicted that cognitive performances would not be consistent across an individual's life due to cognitive development and varying spatial experiences which may inform cognitive performances. I also predicted that early life cognitive performances therefore would not predict social rank. I predicted that with the removal of social pressures and by providing males with a near equivalent social environment (that only differed in the number of females), variation in cognitive performances would not be predicted by their most recent recording of adult social rank.

To gain a broader understanding of cognitive abilities, it is necessary to explore the relationships between individual variation in cognitive abilities and other behavioural attributes at various stages in life. In **Chapter 5** I further explore the relationship between aggression and individual differences in cognitive performances during early life in pheasant chicks. The majority of research focuses on the positive relationship between aggression and spatial learning in adult males. This provoked multiple questions: are the same relationships observable in early life, are they observable in females and is this relationship also relevant to the learning of non-spatial cues? The data presented in this chapter are from chick performances on a spatial and non-spatial task. If there is a relationship between aggression and spatial learning during early life, before individuals have the opportunity and experiences of winning contests and securing a territory, it may suggest that this cognitive-behavioural phenotype is present prior to extensive experiences and may exist via a shared mechanism, e.g. genetic, hormonal or maternal effects, rather than being a consequence of social interactions. I predicted that this relationship may be sex-dependent and would not be apparent in females. Similarly, I predicted that the relationships between cognitive performances and aggressive behaviour in adult animals is due to cognitive development and experiences throughout life and therefore, cognitive performances and aggression would be unrelated during early life in pheasant chicks.

Finally, in **Chapter 6** I investigate whether early life cognitive performances predict adult social network structure in the wild as evidence that cognitive abilities may indeed shape social structure. Social structures may have potential fitness implications (Croft et al., 2009a), hence understanding how cognitive abilities shape social structure can better inform us of how selection may operate on cognitive abilities. There is contrasting evidence for the direction of the relationship between learning ability and social centrality (Kulachi et al. 2018; Aplin & Morand-Ferron 2017), but because this chapter focused on *individual* learning ability (as in Kulachi et al. 2018), I predicted that individuals with superior learning performances would be more centrally located in the social network. Similarly, I predicted that individuals with good inhibitory control would be more centrally located in the social network (as in Wascher 2015). How individual variation in cognitive abilities influences overall mixing in social structures has not directly been addressed and therefore I made no predictions about whether individuals would assort or disassort by cognitive performances.

1.7.1 Conclusion

This thesis is a first attempt at separating cause and consequence of individual variation in cognitive performances in relation to the social environment. By exploring multiple cognitive abilities and both broad and fine-scale social structures, I have endeavoured to begin building the complex picture of the bi-directional relationship between cognitive performances and the social environment. This thesis highlights the importance of considering the social environment when quantifying individual differences in cognitive abilities, as well as how particular cognitive performances may affect the social environment and thus, influence how selection may act upon them. Distinguishing between cause and consequence will increase our understanding of why and how these factors are interlinked and which factor is more pertinent in shaping the relationship. Thus, we can better understand their evolution.

1.8 Appendix

Figure 1.1 references

[1] Ashton et al. 2018

[2] Kitaysky et al. 2003

[3] Wascher 2015

[4] Pravosudov et al. 2003; Spritzer et al. 2004; Fitchett et al. 2005; Francia et al. 2006

[5] Nicol & Pope 1999

[6] Bunnell, Gore & Perkins 1980

[7] Boogert et al. 2006

[8] Barnard & Luo 2002

[9] Kaczer et al. 2006

[10] Aplin & Morand-Ferron 2017

[11] Wascher 2015

[12] Kulachi et al. 2018

Chapter Two: Individuals in larger groups are more successful on discrimination learning tasks

2.1 Abstract

To understand how natural selection may act on cognitive processes, it is necessary to reliably determine inter-individual variation in cognitive abilities. However, an individual’s performance in a cognitive test may be influenced by their social environment. The social environment explains variation between species in cognitive performances; with species that live in larger groups purportedly demonstrating more advanced cognitive abilities. It also explains variation in cognitive performances within species; with larger groups more likely to solve novel problems compared with smaller groups. Surprisingly, there is no experimental evidence for an effect of group size on individual variation in cognitive performances. Using a within-subjects design we assayed individual learning performance of adult female pheasants (n = 17), *Phasianus colchicus*, whilst housed in groups of three and five. Individuals experienced the group sizes in a different order, but were presented with two spatial discrimination tasks, each with a distinct cue set, in a fixed order. We found that across both tasks individuals housed in the large groups had higher levels of success than individuals housed in the small groups. Individuals had higher levels of success on their second task, compared with their first task, irrespective of group size. We suggest that the expression of individual learning performance is responsive to the current social environment but the mechanisms underpinning this relationship require further investigation. Our study demonstrates that it is import to account for an individual’s social environment when attempting to characterise cognitive capacities. It also demonstrates the flexibility of an individual’s cognitive performance depending on their social context.

2.2 Introduction

A compelling and relatively recent approach to understanding the evolution of cognition is to determine the causes and consequences of individual differences in cognitive performance (Thornton & Lukas, 2012). The social environment may be one cause of individual variation in cognitive performance as this governs individuals' access to resources (Wilson, 1975), the stress they experience (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008), and their predation risk (Pulliam, 1973). Although living in a social group can bring benefits, it may also impose a cognitive demand in terms of monitoring and maintaining social relationships and recognising suitable partners for specific behaviours such as foraging or cooperation; Social Intelligence Hypotheses (SIH) detail how brain size and cognitive abilities have evolved in response to these social challenges (Byrne & Whiten, 1988; Call, 2001; Cheney, Seyfarth, & Smuts, 1986; Dunbar, 1998; Humphrey, 1976; Seyfarth & Cheney, 2002; Taborsky & Oliveira, 2012). Group size is often used to quantify the social environment. Larger groups will likely have greater fluctuations in group-composition, as subgroups develop and dissipate and/or there are changes in individual motivations and social status. To cope with this unpredictability, species that live in larger groups are reported as having greater levels of behavioural flexibility (corvids, Bond, Kamil, & Balda, 2007; primates, Amici, Aureli, & Call, 2008) and are more competent on social cognition tasks (lemurs, MacLean et al., 2013), relative to sister taxa that live in smaller groups. In contrast to our knowledge of how sociality relates to cognition across species, little is known about how the social environment affects individual cognitive performances within species.

Within a species, larger groups are more likely than smaller groups to solve novel problems (great tits, *Parus major* and blue tits, *Cyanistes caeruleus*, Morand-Ferron & Quinn, 2011; house sparrows, *Passer domesticus*, Liker & Bókony, 2009). This may simply be because a greater number of individuals were attempting to solve a problem, and/or there was a greater likelihood that larger groups contained individuals with the required skills to solve a problem (Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011). Alternatively, different rates of problem solving between group sizes could be related to the costs and benefits of group living. Reduced predation risk in larger groups may allow individuals to invest more time (less vigilance, Beauchamp, 2015; Elgar, 1989; Roberts, 1995) and therefore energy in acquiring and processing novel information. It could also be that increased competition, associated with larger group sizes, causes individuals to adopt alternative behavioural strategies, such as innovation, to acquire necessary resources (Reader & Laland, 2002; Thornton & Samson, 2012).

Despite demonstrable relationships between the social environment and cognitive performances at the species and group level, the effect of the social environment on individual cognitive performance has seldom been explored. Individuals reared in isolation have lower levels of neurogenesis (prairie voles, *Microtus ochrogaster,* Fowler, Liu, Ouimet, & Wang, 2002; mice, Branchi et al., 2006; zebra finches, *Taeniopygia guttata*, Adar, Lotem, & Barnea, 2008; Pravosudov & Omanska, 2005) and are reported to have impaired learning performance in later life (reversal learning in rats, *Rattus norvegicus*, but not acquisition learning or spatial memory, Schrijver, Pallier, Brown, & Würbel, 2004; spatial learning in rats, Holson, 1986; Juraska, Henderson, & Muller, 1984; discrimination learning in rhesus macaques, *Macaca* *mulatta*, Harlow, Harry, Dodsworth, & Harlow, Margaret, 1965), compared with individuals reared socially (but see for no effect: associative learning in chickens, *Gallus gallus domesticus,* Goerlich, Nätt, Elfwing, Macdonald, & Jensen, 2012 and spatial learning in skink, *Egernia striolata*, Riley, Noble, Byrne, & Whiting, 2016). These studies highlight the effects of social stimulation on neural development and function, during which time however, there may be other ontogenetic factors to consider (Hall, 1998). Outside of critical developmental periods, the social environment may still cause structural changes to the brain (van Praag, Kempermann, & Gage, 2000); young rhesus macaques housed in larger groups were found to have increased grey matter compared with those housed in smaller groups, after approximately four months (Sallet et al., 2011). Although such studies demonstrate that an individual’s historical social environment may have effects on neural development and cognitive performance, they cannot reveal whether an individual’s current social environment influences their cognitive performance. Evidence for this would suggest that the expression of cognitive abilities is subtly adjusted in response to changing social circumstances. Such flexibility would have important implications both for the interpretation of inter-individual differences in cognitive performance, and for understanding how natural selection may act on such differences depending on the social environment an individual inhabits.

One recent study reveals that an individual’s current social group size is related to their general cognitive performance. In free-ranging Australian magpies, *Cracticus tibicen dorsalis* a correlation between cognitive performance, given as a composite score across a battery of four tasks, and group size was seen from early in life through to adulthood (Ashton et al., 2018). Ashton et al. (2018) suggest that the challenges of living in larger group promote cognitive development. However, it is difficult to separate genetic from social explanations for differences in cognitive performances – individual magpies typically live in one stable group so their flexibility in response to changing social environments is difficult to establish under natural conditions. Manipulations of the social environment are necessary to disentangle these factors.

We explored the effects of the current social environment on learning performance by manipulating the group size of wild-caught captive pheasants, *Phasianus colchicus,* and assessing their learning performances on two spatial discrimination learning tasks. In the wild, pheasants live in variable group sizes throughout the year; inhabiting large, same-sex groups from September to February with a gradual shift to single male, multiple female groups (harems) from March to July for breeding (Robertson, 1997; Whiteside et al., 2018). These harem sizes range from two (one male and one female) to 25 (Robertson, 1997), with an optimal group size of 3.7 for collective predator detection (Whiteside, Langley, & Madden, 2016). If the social environment affects cognitive performance, in a way synonymous with that seen across species and in isolated-rearing experiments, we predict that learning performance will be enhanced in larger groups, compared to smaller groups. Critically, by manipulating the group size of adult female birds, we were able to test causality of the relationship. We were unsure on the time it would take for the effects of group size to influence learning performance but due to a previous finding in which female pheasants adjusted their vigilance based on their group size after two days of habitation, we used the same methods as those in Whiteside et al. (2016).

2.3 Methods

2.3.1 Study site, subjects and housing

The study was conducted from March – June 2016 at North Wyke Rothamsted Research Farm, Devon (50^0 77’N, 3^0 9’W). We captured pheasants from the wild using baited funnel traps and housed Individuals in one of ten identical pens (4m x 8m), in visual but not auditory isolation from each other. All pheasants had access to commercial wheat and water *ad libitum* and each pen contained elevated perches, branch shelters and two refuge areas (Figure 2.1).

Although all birds were caught from the wild, their origins differed. Of the 30 females included in this study, we had reared eight of the females in the previous year for the first 10 weeks of life. During this period they were subject to a battery of cognitive tasks, before being released into the wild (van Horik et al., 2016). The other 22 individuals were birds of unknown rearing history, however, it is likely that they were also reared in captivity, released into the wild and migrated to the site from neighbouring commercial shoots. All birds were ≥10 months old, indicated by their body size and the time of year. Individuals were identifiable by numbered patagial wing tags, either attached during rearing, or upon capture if they were not from our released birds.

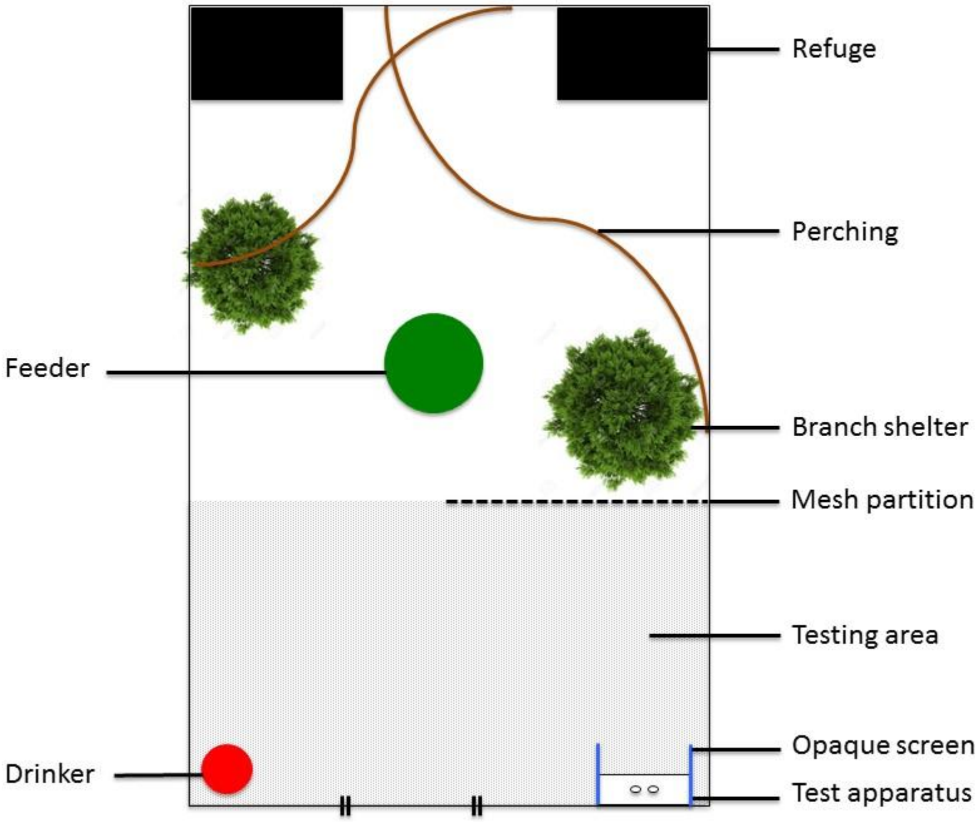

Figure 2.1: Aerial view of housing pen (4m x 8m). Mesh partition could be extended to cover width of the pen to allow testing of individuals without disturbance from conspecifics.

2.3.2 Group sizes

Captured birds were randomly assigned to a breeding group. Each group consisted of a single male with either two females (small group) or four females (large group). There were five replicates of each group size. While housed in these groups, birds were trained to the testing procedures. Training lasted three weeks (see *Cognitive test apparatus and training)*. The task was voluntary and consequently we had a different number of participating females from each group size. For small groups, we assayed the cognitive performance of four females, each from a separate pen. For large groups, we assayed the cognitive performance of 13 females from all five pens.

We switched all participating females to a pen with the alternate group size after they had completed testing on the first task. Each female was housed with at least one familiar female from their previous group. Because the majority of females that participated in the first task were from large groups, during the second training and testing period there were: seven pens containing small groups, each with a single participating female and one non-participating female; three pens containing large groups (4 females), two of these pens contained two participating females and two non-participating females, while the final large group pen contained four non-participating females. Individuals were left to habituate to their new group composition for three nights and two days before being tested on the second cognitive task. Four females in a large group came from two pens. The thirteen females now in a small group size came from seven pens.

2.3.3 Cognitive test apparatus and training

The test apparatus (38cm x 14cm x 4cm), located in the testing area of the pen (Fig. 1), was situated between two opaque screens so that the apparatus could only be approached and viewed by a bird ‘front-on’ and prevented conspecifics viewing the box while the focal bird was being tested. Situated on the top of the test apparatus were two identical circular wells (diameter 2.8cm), 1.2cm apart, both concealed by a layer of opaque crepe paper. One of the wells contained a mealworm food reward (correct) and the other was blocked with a wooden bung (incorrect).

We trained individuals to voluntarily approach the test apparatus when a visual cue (black and white swirl pattern) was displayed on the wall of the pen accompanied by the experimenter tapping and scratching the apparatus to attract a bird. The experimenter was located behind a screen and not visible to the focal individual while they were interacting with the apparatus. Females that reliably interacted with the apparatus were trained to peck ‘open’ the crepe paper that covered the wells. Habituation to our presence, the test apparatus and the procedures is a time-consuming process with wild birds. To ‘speed up’ this process we reduced handling by only moving the birds upon capture from the wild and for the change in group size, thus improving their likelihood to participate. Participating individuals were given equal exposure to the apparatus during training.

2.3.4 Cognitive testing

Individuals were tested on two distinct spatial tasks that differed only in the positions of the wells. The two tasks exactly matched, in layout and affordances, those that we had presented to chicks in the previous year. For Task 1, the *top-bottom discrimination*, the wells were arranged vertically and the top well was rewarded. For Task 2, the *left-right discrimination,* the wells were arranged horizontally and the left well was rewarded. Testing began at 08:30am from Monday to Friday and we chose at random which pen to begin testing each day. The order in which individuals were tested was dictated by the birds’ motivation to interact with the apparatus. Testing only proceeded if an individual was alone at the apparatus, as we wanted to avoid any effects of social learning. The opaque screens helped to mitigate this but if another individual came within two metres of the focal individual while at the test apparatus, the visual cue and apparatus were removed and testing ceased. Testing was resumed once this individual was alone. On four occasions it proved difficult to test the focal individual of a large group because multiple individuals were motivated to participate at the same time. In these instances, we ushered the focal individual into the testing area of the pen and put up a temporary mesh partition that covered the width of the pen. This allowed the focal individual to be tested without being disturbed by conspecifics and individuals were allowed as much time as necessary to complete the task. Due to its rare occurrence we did not include this in analyses, however it did not affect the behaviour of the focal bird, as motivation to participate in the task remained high. It was not necessary to food deprive birds prior to testing as mealworms are a highly valued food reward that individuals were motivated to retrieve.

For each task, each individual received a single test session per day, consisting of 20 presentations of a pair of wells, over five days, producing 100 trials per task. Individuals' were only allowed to make one choice per pair of wells. When an individual chose the incorrect well first, indicated by pecking at the crepe paper of the well, the wells were removed and a new binary choice was revealed. When an individual chose correctly we allowed the focal individual to consume the food reward before revealing a new binary choice. Therefore, the costs of choosing incorrectly constituted pecking at a blocked well and not retrieving a mealworm reward for that trial. On day one of testing, we checked whether an individuals' first 20 trials revealed a pre-existing 'position bias' (Mackintosh, 1974) to a particular well. For Task 1, two females (both in a large group) had biases (>80%) for the top well (furthest from the bird), so these were tested with a rewarded bottom well later that day and for the remainder of testing.

For the remaining females, the top well was rewarded for the rest of testing and this remained consistent with our chick cognitive testing (as part of a separate experiment). For Task 2, a single female (within a small group) had a bias for the left well, therefore she was tested with a rewarded right well later that day and for the remainder of testing. The remaining females were tested with the left well rewarded for the rest of testing because this maintained consistency with our chick cognitive testing. All other birds showed no strong pre-existing biases (<75%) on either task. The first 20 trials that revealed a bias for three individuals were excluded from further analysis. On subsequent days, both biased and unbiased birds all received 20 trials per day. Task presentation was not counterbalanced and hence individuals received tasks in the same order.

2.3.5 Statistical analysis

All analyses were conducted in R v.3.1.1 (The R Core Team, 2015). We used the *lme4* package (Bates, Machler, Bolker, & Walker, 2014) to fit a generalized linear mixed model (GLMM) with a binomial error structure to assess whether learning performance (correct/incorrect) is explained by an individuals' group size. Mixed models cope relatively well with unbalanced designs (Zuur, Leno, Walker, Saveliev, & Smith, 2009). The model included 'Trial (11-100)', 'Group size (small/large)', 'Task (1. Top-bottom/2. Left-right)', 'Start performance (percentage correct of first 10 trials)' and 'Origin (known/unknown bird)' as explanatory factors. A two-way interaction between group size and trial was included to assess whether group sizes differed in their 'rate' of learning. We define rate of learning as the speed at which individuals increase their probability of making a correct choice with increasing trial number. A main effect of group size indicates a difference between the group sizes in the 'accuracy' of learning.

We define accuracy as overall performance by the end of the task, inclusive of performance on all trials. The trial variable consisted of trials 11-100 because the first 10 trials were removed and included in the 'start performance' explanatory variable. The start performance explanatory variable is the percentage of trials that were correct during the first 10 test trials and this controlled for differences in start performances between individuals, which we felt was important because we did not train to criterion and naturally individuals begin tasks at different levels of inherent preferences. We used the percentage of first 10 trials correct during testing because it allowed us to acquire an informative measure of initial bias to a particular well location, but it is also a low enough number of trials before allowing individuals time to learn the affordances of the task and avoided removing much data from the response variable. The inclusion of Task accounted for the difference in task type and whether it was the first or second task the individual had experienced, as individuals were presented with the two tasks in a fixed order. The inclusion of Origin accounted for whether we had reared the individual and they had previously experienced these cognitive tasks as a chick; seven individuals were reared by us (known), 10 individuals were not (unknown). On fitting the first model it failed to converge, therefore trial was standardised ($X – \mu / \sigma$) and this resolved the issue. The model estimates presented are from the model with standardised trial variable. We used a random intercept and random slopes model by nesting trial within bird as a random effect. This allowed individuals to vary in their rate of learning performance. The minimum adequate model was reached by backward stepwise removal of non-significant variables, determined using the 'drop1' function in the base package. To visualise the data we plotted curves drawn using a binary logistic regression model in ggplot2 package (Wickham, 2009) for each group size and each task. To test whether the order in which individuals experienced the group sizes influenced their improvement from the first to the second task in learning accuracy, we used a Wilcoxon Rank-Sum test to test for a difference between the two ‘sets’ of females, i.e. did females that experienced a small then large group make a greater/lesser improvement than females that experienced a large and then a small group. We noticed that the group sizes differed in their starting performances, therefore we conducted a *post-hoc* analysis to test for a difference between the group sizes. We did this for each task using a Wilcoxon Rank-Sum test due to the unbalanced sample sizes.

2.3.6 Ethical considerations

During capture, traps were checked at least three times a day. All captive bird husbandry adhered to the DEFRA Code of Practice (DEFRA, 2009). Birds were subject to minimal handling. Participation in cognitive tests was voluntary and experimenters were concealed from view of the birds, keeping stress to a minimum. Birds were held in captivity for three months, after which they were released back onto the site. All work was approved by the University of Exeter Psychology Ethics Committee and the work was conducted under Home Office licence number PPL 30/3204 to JRM.

2.4 Results

Individuals differed in the accuracy of their learning performances according to the size of the group they were tested in (GLMM: Group size, $X^2 = 10.475$, *df* = 1, $p < 0.002$), with individuals in larger groups performing with a higher probability of choosing correctly than individuals housed in smaller groups (Table 2.1, Figure 2.2, Figure 2.3). There was a significant effect of trial (GLMM: Trial, $X^2 = 50.138$, *df* = 1, $p < 0.001$), indicating learning (Table 2.1, Figure 2.2), but no interaction between trial and group size, indicating no difference between the group sizes in learning rate (GLMM: Trial*Group size, $X^2 = 0.267$, *df* = 1, $p = 0.605$). There was significant effect of task (GLMM: Task, $X^2 = 53.871$, *df* = 1, $p < 0.001$; Table 2.1, Figure 2.2), with higher levels of performance on Task 2 (left-right task), compared with Task 1 (top-bottom task) (Table 2.1, Figure 2.2). We controlled for variation in starting performances and found this was also a significant predictor of learning performance (GLMM: Start performance, $X^2 = 18.726$, *df* = 1, $p < 0.001$), with individuals that made more correct choices in their first 10 trials, having a higher level of performance for the remainder of the task. The birds' origin (known/unknown) was not related to their learning performance (GLMM: Origin, $X^2 = 0.741$, *df* = 1, $p = 0.389$). The inclusion of this variable also accounts for whether individuals had experienced these tasks as chicks.

Table 2.1: Minimum adequate model of a generalized linear mixed model (random slopes and random intercepts) on factors affecting learning performance (Correct: 1 yes / 0 no) on spatial discrimination tasks for females while housed in two different group sizes. The analysis included 17 individuals that performed 100 trials on each task. Model was fitted with log-link function.

Variable	Estimate*	Standard error	Confidence interval 95%		Odds Ratio
Intercept	0.234	0.141			
Group size					
Large	0.386	0.121	0.130	0.643	1.471
Task					
2. Left-right	0.888	0.124	0.625	1.151	2.430
Trial	0.797	0.050	0.691	0.903	2.219
Start performance	1.142	0.141	0.843	1.441	3.133

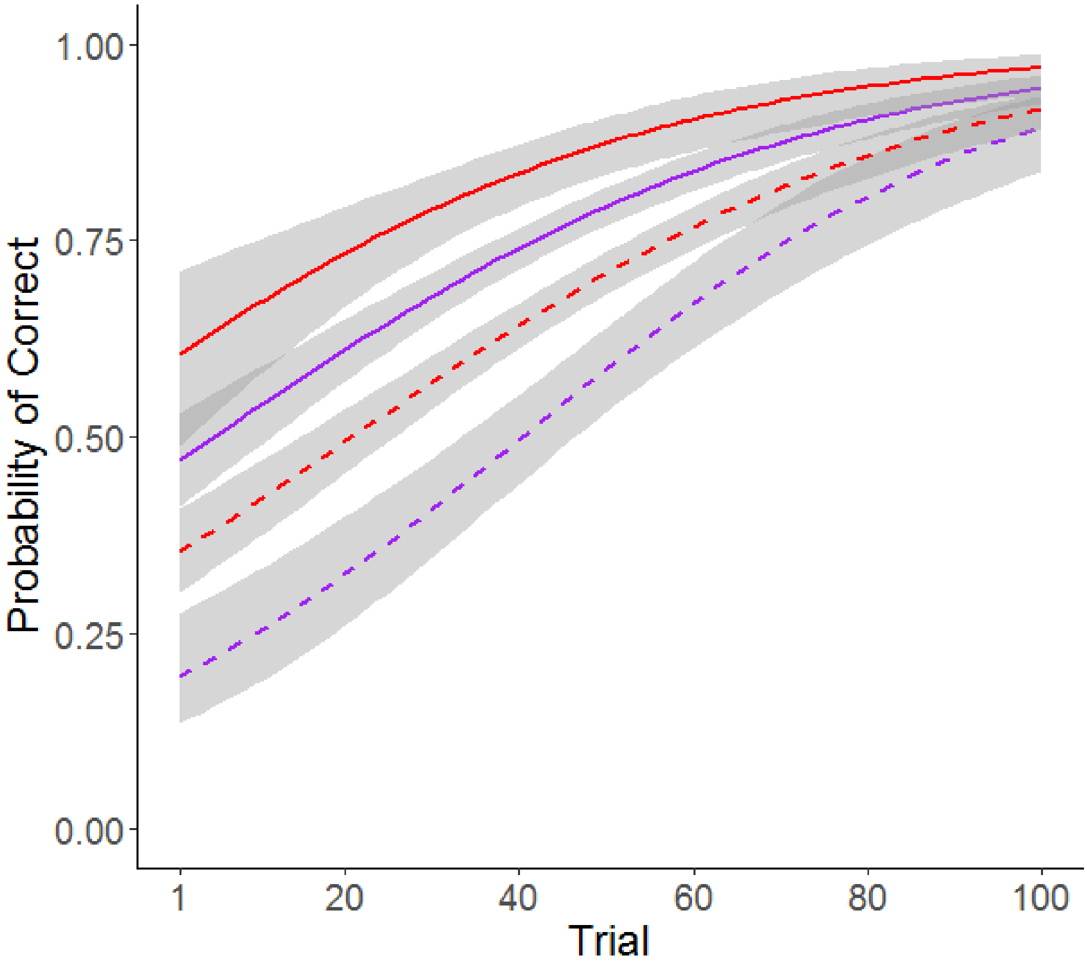

Figure 2.2: Predicted probability curves drawn using a binary logistic regression model (glm) on performance of females on Task 1 (dashed lines) and Task 2 (solid lines), when in small (purple) and large (red) groups. Grey shaded areas represent 95% Confidence Intervals (CI's).

Individuals that experienced the large group size second made a greater improvement in accuracy from the first to the second task than females that experienced the small group size second (Figure 2.3). However, the improvement in accuracy by individuals that experienced a small and then a large group was not significantly greater than the improvement made by females that experienced the large and then the small group (Wilcoxon Rank-Sum test: $W = 40.500$, $n = 17$, $p = 0.111$).

Post hoc tests revealed that the group sizes differed significantly in their starting performances and this was found for both task 1 (Wilcoxon Rank-Sum test: $W = 289$, $n = 17$, $p < 0.001$) and task 2 (Wilcoxon Rank-Sum test: $W = 289$, $n = 17$, $p < 0.001$).

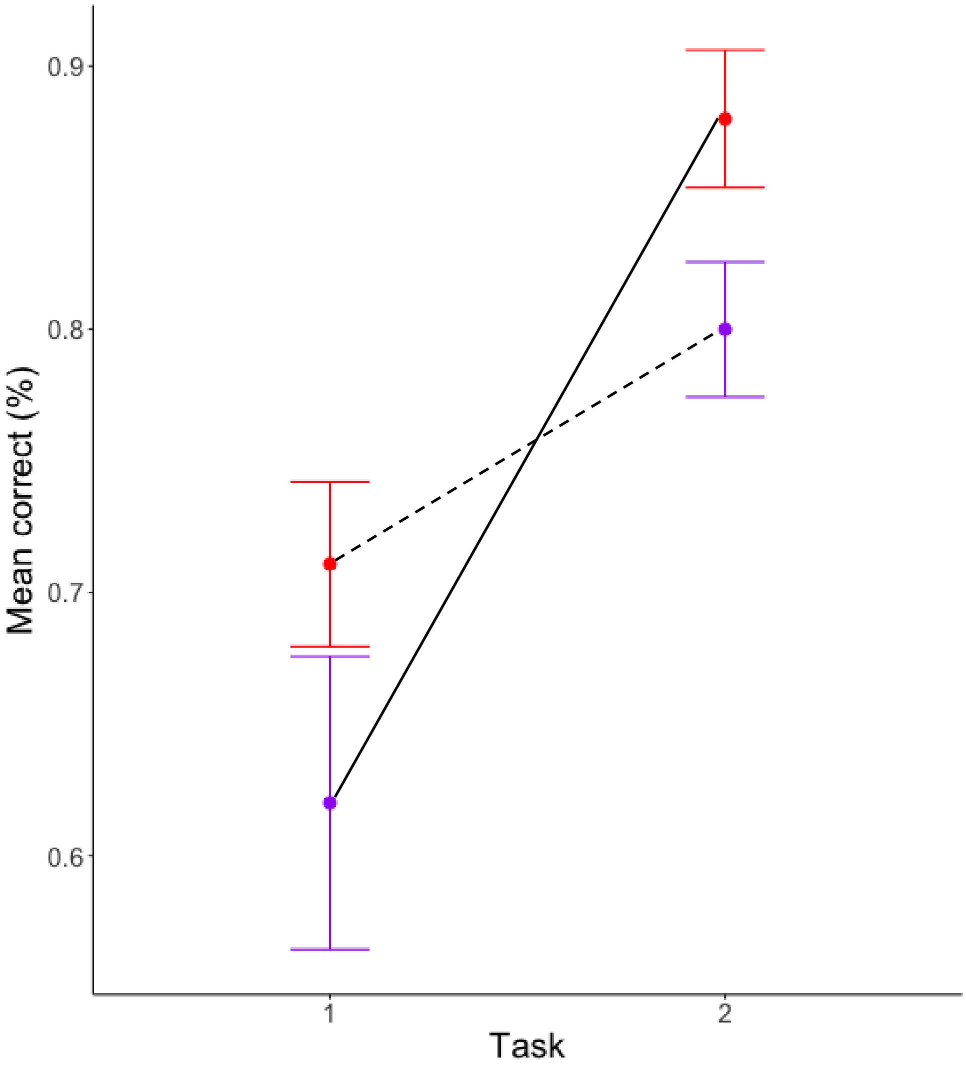

Figure 2.3: Mean percentage of correct choices made in 90 trials (after first 10 trials removed), by small (purple) and large (red) group sizes, within each spatial discrimination task. Black solid line represents improvement in task accuracy for females that went from a small to a large group. Black dashed line represents improvement in task accuracy for females that went from a large to a small group. Error bars indicate standard error of the mean.

2.5 Discussion

We provide the first evidence for a causal effect of the social environment, in terms of group size, on individual cognitive performance. Across two spatial discrimination tasks, individuals housed in large groups performed with higher accuracy, compared with individuals housed in small groups. This was independent of previous experience with the test apparatus during rearing, suggesting that known females did not remember this task from early life. Generally, individuals improved on the second task, relative to their performance on the first task, irrespective of group size. This improvement was not significantly greater for individuals that experienced the large group size second, compared with individuals that experienced the small group size second. By exposing the same individuals to two different social environments we demonstrate that not only is variation in the accuracy of learning performance predicted by an individual's group size, but also that learning performance is variable and responsive to short-term changes in the social environment.

Individuals housed in smaller groups were more biased towards the incorrect well in their starting performances, with a lower percentage of correct choices in the first 10 trials compared with those in larger groups. This was evident for both tasks. Individuals were randomly assigned to their initial group size and experienced both group sizes, therefore we suspect that these differences are not simply due to individual variation. We propose that the effect of group size on cognitive performances occurs in very early trials and because the group sizes did not differ in their rate of learning, individuals in both group sizes improved at a similar speed, but due to the initial poor performance of small groups, the overall accuracy of small groups remained lower than that of large groups by the end of the task. We controlled for this difference in starting biases statistically by including starting performance as an explanatory variable; even so, group size remained a significant predictor of learning performance.

Learning performance was also more accurate on the second task compared with the first task. Tasks were presented to individuals in the same order, so we are unable to determine whether learning performance increased during the second task due to generalised learning for the task affordances, or because of the different cues that were used; as perhaps pheasants are better able to distinguish between horizontally positioned cues compared with vertically positioned cues. We also highlight that individuals experienced their second group size for less time than their first group size because individuals were trained on the cognitive testing procedures while housed in their first group size. If the duration that individuals were housed within a group size influences cognitive performance, this suggests that a shorter duration in a particular group size may enhance learning accuracy and over time, these effects are reduced. However, our result is confounded by the different tasks used and so we are unable to tease these two factors apart. Irrespective of this, it does not alter our conclusion that larger groups outperform smaller groups on either learning task. We also considered individual improvement from the first to the second task and whether there was an effect of order in which the group sizes were experienced. Individuals that experienced the large group size second demonstrated a greater improvement in learning accuracy than females that experienced the small group size second. However, the order in which individuals experienced the group sizes did not significantly influence improvement in learning accuracy. We suspect that this non significance is related to low statistical power as a result of the small, unbalanced sample size. While the effects of different task affordances, duration within a group size and the order in which the group sizes are experienced are interesting questions for future research, it is not critical for understanding the relationship between group size and learning performance, as large groups performed more accurately overall.

Our results complement findings in Australian magpies, in which group size and a general intelligence factor are correlated (Ashton et al. 2018). Critically, we randomly allocated our pheasants to experimental groups and females were tested in both group sizes, thus demonstrating a direct effect of the social environment on individual variation in cognitive performances. We suggest four (non-exclusive) mechanisms to explain this relationship.

The group size related differences in learning performance might have been related to differences in the level of attention they could direct at the task. One benefit of group living is collective vigilance, which allows individuals to reduce their own vigilance, in favour of other behaviours that demand their attention (Beauchamp, 2015; Elgar, 1989; Roberts, 1995). We have previously demonstrated that female pheasants in large groups spend a lower proportion of their time being vigilant compared with females in small groups (Whiteside et al., 2016). Individuals had the opportunity to spend as much time as necessary at the apparatus to complete the task and although we did not record the duration of time spent interacting with the task each day, it is possible that individuals in large groups spent longer at the task apparatus due to less investment in vigilance and this benefitted their task performance. Individuals that take longer completing cognitive tasks, perform with higher accuracy (speed-accuracy trade-off, Chittka, Skorupski, & Raine, 2009; Trimmer et al., 2008). Additionally, individuals in the large group may not have only spent longer completing the task but they may have invested more 'quality' time, paying greater attention to the task due to fewer vigilance bouts. In pipefish, *Syngnathus typhle,* when predator threat was increased, male mate choice discrimination abilities were hindered (Berglund, 1993). It is suggested this was because less attention was paid to the mate choice task, thus resulting in random choices (Guilford & Dawkins, 1987). We speculate that female pheasants in the larger groups may have had fewer 'interruptions' for vigilance bouts and paid more attention to the learning task, thus facilitating their discrimination/learning abilities. Of course, large groups could also provide more sources of distraction involving social interactions between the members which could retard learning performances. The difference between individuals when housed in small and large groups in the overall time taken to complete the task, the number of vigilance 'bouts' and other social interruptions during engagement with the task, are interesting avenues to consider for future work.

Second, the differences in cognitive performance that we observed may reflect deliberate changes in foraging strategies, manifested in their test performance. Foraging strategies are plastic and readily respond to changes in the level of resources (Belmaker, Motro, Feldman, & Lotem, 2012; Morand-Ferron & Giraldeau, 2010). Group size affects the level of resources available and in a larger group it may be more rewarding to forage independently, i.e. be a 'producer' (Barnard & Sibly, 1981). Producers are predicted to have better individual learning performances because their behaviour is reliant on personal information rather than social information (S. Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Giraldeau, Valone, & Templeton, 2002). This has been demonstrated in house sparrows, *Passer domesticus*, whereby learning performance on a colour discrimination task was positively related to the tendency to forage as a producer while in a group (Katsnelson, Motro, Feldman, & Lotem, 2008). Although learning performance of the sparrows was measured prior to social interactions, Katsnelson et al. (2008) suggest that these two factors (learning performance and tendency to 'produce') may be associated through shared mechanisms. Therefore, when pheasants were housed in the large group, they may have adopted a 'producer' foraging strategy and by association, demonstrated higher levels of learning performance.

Third, an individual's learning performances may have differed between the group sizes due to differences in stress. In larger groups there is increased within-group competition for resources and this may act as a stressor (Milinski & Parker, 1991). Stress is known to affect performance on cognitive tasks, with a bell-shaped relationship between stress and success often reported (Yerkes-Dodson law) (Mendl, 1999). For example, chronic levels of corticosteroids have detrimental effects on performance on spatial learning tasks (kittiwakes, *Rissa tridactyla*, Kitaysky, Kitaiskaia, Piatt, & Wingfield, 2003), whereas, intermediate or short term levels of stress improve spatial memory performance (Belding's ground squirrels, *Spermophilus beldingi*, Mateo, 2014; rats, Luine, 1996). Although our pheasants had unlimited access to wheat, there may have been increased competition for favourable foraging patches whilst in the bigger group or other social stressors. Such moderate stress could have improved their learning performances.

Finally, individuals may have varied in their learning performances according to group size due to differences in the levels of social stimulation they experienced. Social stimulation, along with inanimate stimulation, are combined to form environmental enrichment (Rosenzweig, Bennett, Hebert, & Morimoto, 1978), which causes behavioural (Hebb, 1949) and neurological changes (at least in mammals see van Praag et al., 2000 for review). Neural mechanisms are associated with learning and memory (Greenough, 1976). We suggest that individuals experience greater social stimulation when housed in the large group due to having more individuals to interact with and this causes alterations to neural structures, which in turn has a positive effect on their individual learning performance. However, it is unknown whether brain plasticity in response to social stimulation can occur over the short period of time, as demonstrated in our study, whether similar neural changes that occur in mammals also occur in a birds, and how long the effects of such social enrichment may last (van Praag et al., 2000).

2.5.1 Conclusion

We show that the social environment affects the expression of learning ability, and this reveals a fine-scale, intra-individual flexibility in cognitive performance. This mirrors the correlative patterns we see between and within species, with those living in larger groups outperforming those in smaller groups. However, our manipulation demonstrates that such differences may not be just fixed strategies, inextricably linked to the mean group size that an individual will live in, but rather a more facultative rapid response to a changing social environment. The potential mechanisms underpinning the higher levels of performance for individuals in the larger group are likely related to benefits and costs of group living, divergences in foraging strategy and/or changes in brain plasticity following increased social interactions. If these processes are present in the wild and female pheasants are more efficient at learning the location of a rewarded stimulus when in a larger harem, compared with when in a smaller group, this could have important implications for the optimal harem size for female when she chooses which harem to join. We suggest that it is critical to consider an individual's current social environment when characterising causes of individual variation in cognitive performances, and that the effects of their social environment on their cognitive performance may be transitory and relatively fast acting.

Chapter Three: Group social rank is associated with performance on a spatial learning task

3.1 Abstract

Dominant individuals differ from subordinates in their performances on cognitive tasks across a suite of taxa. Previous studies often only consider dyadic relationships, rather than the more ecologically relevant social hierarchies or networks, hence failing to account for how dyadic relationships may be adjusted within larger social groups. We used a novel statistical method; Randomized Elo-ratings, to infer the social hierarchy of 18 male pheasants, *Phasianus colchicus,* while in a captive, mixed sex group with a linear hierarchy. We assayed individual learning performance of these males on a binary spatial discrimination task to investigate whether inter-individual variation in performance is associated with group social rank. Task performance improved with increasing trial number and was positively related to social rank, with higher ranking males showing greater levels of success. Motivation to participate in the task was not related to social rank or task performance, thus indicating that these rank-related differences are not a consequence of differences in motivation to complete the task. Our results provide important information about how variation in cognitive performance relates to an individual's social rank within a group. Whether the social environment causes differences in learning performance or instead, inherent differences in learning ability predetermine rank remains to be tested.

3.2 Introduction

Characterising variation in cognitive performances is pertinent to our understanding of the evolution of cognition (Thornton et al., 2014; Thornton & Lukas, 2012). An individual's cognitive performance may correspond to their social rank. Social rank arises from interactions between dominant and subordinate individuals in groups (Drews, 1993), and can influence an individual's access to resources (Whitehead & Dufault, 1999), stress (Creel, 2001), and opportunities for learning (Bunnell, Kenshalo, Czerny, & Allen, 1979; Chalmeau & Gallo, 1993), all of which may influence an individual's performance on a cognitive task.

Dominant individuals perform more efficiently on operant learning (starlings, *Sturnus vulgaris,* Boogert, Reader, & Laland, 2006), spatial learning (mice, Barnard & Luo, 2002; Francia et al., 2006; meadow voles, *Microtus pennsylvanicus,* Spritzer, Meikle, & Solomon, 2004) and spatial memory tasks (mountain chickadees, *Poecile gambeli*, Pravosudov, Mendoza, & Clayton, 2003). However, such studies have relied on dyadic relationships between pairs of individuals, or concentrated on small groups, which may be simplistic and hence not reflect the network of relationships naturally observed in larger social groups (Chase, 1982). Therefore, we are lacking an understanding of how variation in cognitive performance may be manifested in relation to real-world social dynamics.

When learning performance has been considered in the context of a large group, results have been found that are contrary to the prediction that the more dominant individuals would be better learners. Subordinate individuals outperformed dominant individuals by making fewer errors on complex problem solving (long-tailed macaques, *Macaca fascicularis,* Bunnell & Perkins, 1980) and reversal learning tasks (Bunnell et al., 1980). It is possible that this switch in the direction of the relationship is due to the difference in tasks deployed. For example, reversal learning and inhibitory control tasks can be used to assay cognitive/behavioural flexibility (Bond et al., 2007; Tebbich, Sterelny, & Teschke, 2010). The ability to flexibly respond to changes when contingencies are altered is governed by separate neuronal pathways to acquisition learning (Ghahremani et al., 2010). Alternatively, the relationship between cognitive performance and social rank reported in the Bunnell et al.'s studies may have been complicated by the experimentally induced instabilities in social structure. Individuals were continually removed and re-introduced to the social group during the study period, therefore increasing social pressure for dominants who were attempting to maintain their rank (Bunnell et al. 1980), thus potentially confounding the relationship between social rank and cognitive performance.

Our understanding of the relationship between social rank and cognitive performance can also be confused by the use of inappropriate methods to construct hierarchies, particularly those that don't consider whole groups of individuals or which rely on the outcomes of small numbers of interactions. This may explain why a number of studies failed to find a relationship between social rank and learning performance (Bouchard, Goodyer, & Lefebvre, 2007; Christensen et al., 2012; Croney, Prince-Kelly, & Meller, 2007). Critically, there are few guidelines for assessing the reliability of an inferred dominance hierarchy (Sánchez-Tójar et al., 2017). In order to understand how an individual's social rank relates to their cognitive performance, it is necessary to remove these confounds of variable test design and consider social status in more naturalistic multi-individual groupings.

The pheasant, *Phasianus colchicus*, provides a suitable system to explore the relationship between group social rank and variation in learning performance. In the wild, pheasants exhibit non-resource defense polygyny in which males compete for territories to attract females. Competition for territories takes the form of agonistic interactions and territorial display (Mateos & Carranza, 1997; Ridley & Hill, 1987), and begins as early as December (Whiteside et al., 2018). Females preferentially choose dominant males (see Mateos, 1998 for review), and non-harem holding males sexually harass females and achieve copulations through force (Mateos & Carranza, 1995; Ridley & Hill, 1987). Breeding season begins in March. Pheasants exhibit variation in spatial memory (Whiteside, Sage, & Madden, 2016), although it is unclear whether this may be more important for territory holding males who know a specific area and its neighbouring areas in detail, or for satellite males who fail to command a territory and so utilize a much larger area more ephemerally. In captivity, males form stable dominance hierarchies for short periods (3 months) but which are somewhat flexible, especially at the start of the breeding season (Mateos & Carranza, 1999). Winners of dyadic interactions in the field match those in captivity, thus, male dominance in captivity reflects the situation in the wild (von Schantz et al., 1989).

We tested adult male pheasants on a spatial discrimination task while they were members of a captive, multi-individual social hierarchy during the breeding season. We expect that measures of social rank are more meaningful during the breeding season while competition for resources is intense, compared with the winter months in which males aggregate (Robertson, 1997) and measures of social rank may be more difficult to detect. We included the time it took individuals to begin the task as a measure of motivation to participate; a factor that may differ between individuals of different ranks. Males tend to occupy particular areas of the pen and so complete mixing does not always occur (personal observation - EJGL). This may result in sparse interaction data, a problem when inferring social hierarchies (Gammell et al., 2003; Neumann et al., 2011). To account for this we used a novel method of hierarchy inference which allowed us to determine the reliability of our inferred social hierarchy (Sánchez-Tójar et al., 2017). Previous studies compared the task performances of dyads (mice, Barnard & Luo, 2002; Francia et al., 2006; mountain chickadees, Pravosudov et al., 2003; meadow voles, Spritzer et al., 2004) and show that the dominant individuals outperform the subordinate individuals. If we extend these findings, then we expect that spatial learning performance will be positively related to social rank in a complex, established and more realistic social environment.

3.3 Methods

3.3.1 Subjects and housing

In March 2015 at North Wyke Rothamsted Research Farm, Devon (50^{0} 77’N, 3^{0} 9’W), we caught wild adult pheasants and housed 18 males and 16 females in a large pen (20m x 20m) to give a sex ratio approximately mimicking that observed in the wild (Grahn, Goransson, & von Schantz, 1993). This pen contained refuges, branch shelters, perches and multiple feeders and drinkers. Individuals were identifiable by numbered patagial wing tags.

3.3.2 Cognitive testing

From the 9th – 13th April 2015, 15 males completed the ‘left-right tunnel’ cognitive task; one male did not engage with the task and two males were deliberately not tested because we expected their participation in a different experiment to influence their performance on this task. The task assayed discrimination learning in which individuals learned to associate a location (left or right) with the reward of leaving the testing arena (4m x 4m, Figure 3.1). The testing arena was located within the housing pen but was in visual isolation from the regular housing. The testing arena comprised a main chamber which contained a pair of tunnels (arch shaped; H 20cm, W 28cm, L 60cm), one on the left and right sides, 3.4m apart, equidistant from a centre ‘starting point’. One tunnel was consistently blocked on the exit end (incorrect) while the other returned the individual to a holding area (correct), away from the experimenter and from which males could return to their regular housing at will. This chamber was novel to all individuals. During a trial, individual males were caught with a mesh net and placed on the starting point and oriented forwards. These procedures may have caused stress to the birds, however upon placement on the starting point individuals did not exhibit behavioural indicators of stress such as panting or flight behaviour (inclusive of running). We recorded time to leave the starting point (t1), but due to lost data, only consider t1 from the first six trials per individual as a measure of motivation to participate in the task. Males were unable to see the far end of either tunnel without lowering their head and individuals were considered to have made a choice when either: 1) they were within 1m of the tunnel and lowered their head; or 2) when a part of their body entered the tunnel. The correct tunnel (left or right) was designated randomly for each individual. When individuals entered inside the incorrect tunnel they could return to the main testing chamber by their own volition and a trial was finished when the male exited through the correct tunnel. Therefore, males experienced exiting through the correct tunnel on every trial. For analyses, we only considered an individual’s initial choice. Each individual received 14 trials in total. The first seven trials were conducted within one day; individuals were randomly selected for the first trial and then this order of testing was maintained for the remaining trials. The second seven trials were carried out four days later, following the same protocol as above. Therefore, inter-trial intervals were consistent between individuals.

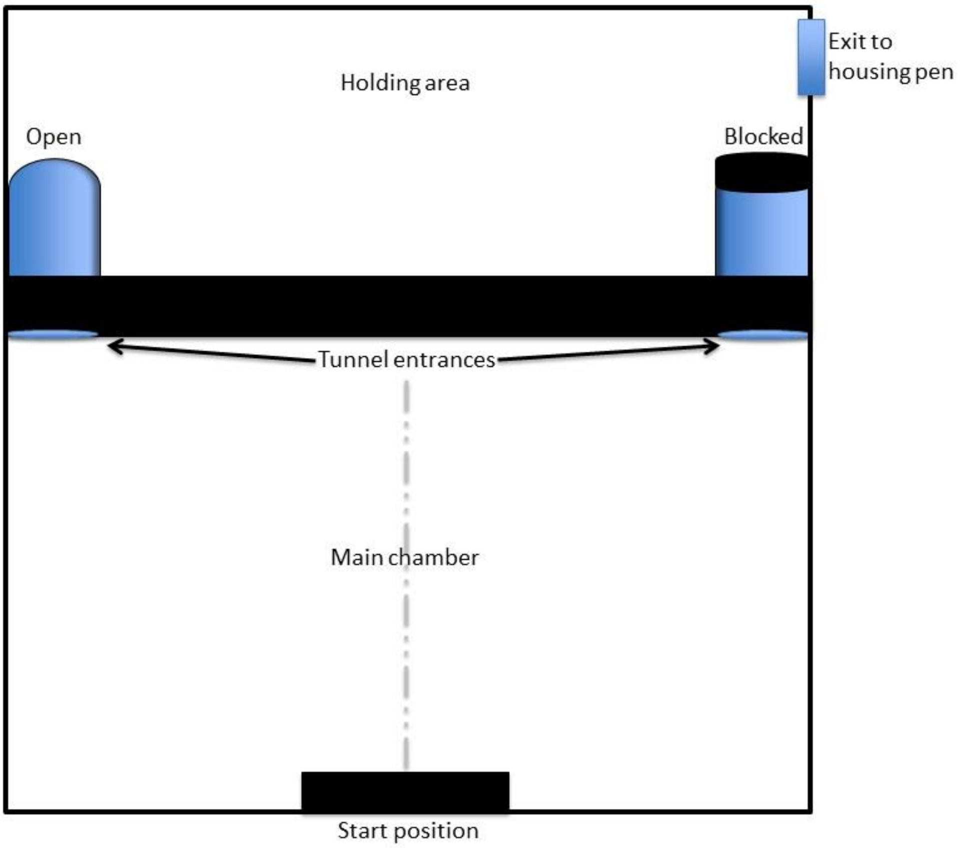

Figure 3.1: Aerial view of the left-right tunnel task testing arena (4m x 4m).

3.3.3 Dominance interactions

From the 20th – 28th May, we observed 367 agonistic interactions between males (Table 3.1) via *adlib* sampling conducted by four visually concealed observers. This method of sampling is suitable to capture event behaviours, such as aggressive interactions (Altmann, 1974). Interactions had a clear winner and loser. Each observer focused their efforts on one quarter of the pen and communicated via two-way radio when interactions occurred across these quarters to ensure observations were not duplicated. During the first day of observations we watched the birds for 2.5 hours and on the remaining seven days, we conducted two observation sessions of 30 minutes each (AM and PM). To generate the social ranks we used an extension of the Elo-rating method. In the original Elo-rating method, individuals begin with the same start rating and this is updated after each agonistic interaction (Albers & de Vries, 2001; Neumann et al., 2011). The value each rating is updated by is dependent on the outcome of the interaction (won or lost) and the probability of that outcome occurring, relevant to both individuals' current Elo-rating. From these ratings individuals are organised into a hierarchy, allowing one to conduct parametric statistics if necessary because individuals' social ranks are associated with a continuous variable. The extension of this method; the Randomized Elo-rating method (Sánchez-Tójar et al., 2017), then allows one to assess whether an adequate number of interactions were recorded to infer a social hierarchy and quantify uncertainty in the inferred hierarchy from the generation of randomized interaction data. Due to the subjects participating in other separate experiments, there was a gap of approximately 5 weeks between cognitive testing and recording of dominance observations, but based on previous work (Mateos & Carranza, 1999) we expect that the social hierarchy remained relatively stable within the breeding season. We believe that by conducting observations while the group size was constant (and birds were not removed for brief periods because of cognitive testing) and there was no interference from researchers, interactions would be more representative of natural dominance relationships.

Table 3.1: Ethogram of agonistic interactions between male pheasants

Agonistic	
Chase	aggressor (winner) runs towards opponent and opponent flees (loser)
Threat	aggressor (winner) steps forwards and makes a sharp movement towards opponent, opponent flees or avoids (loser). Similar to the start of a chase but aggressor does not continue to run
Contact	aggressor (winner) pecks opponent (loser) with the bill, usually directed at the head or neck, or aggressor (winner) jumps at opponent feet first to direct spurs at opponent (loser)
Submissive	
Avoid	individual (loser) rapidly changes trajectory while walking and is within 3m of another individual (winner) that is not showing any apparent signs of aggression

3.3.4 Statistical analysis

All analyses were conducted using R v.3.1.1 ("The R Foundation for Statistical Computing, Vienna, Austria," 2015). Using the *aniDom* package (Damien R. Farine & Sanchez-Tojar, 2017) we generated 'Randomized Elo-ratings' and assessed hierarchy uncertainty using the two methods described in Sanchez-Tojar et al. (2017): we firstly estimated repeatability of the individual Elo-ratings generated from replicated datasets (n = 1000) using the *rptR* package (Schielzeth, Stoffel, & Nakagawa, 2017), with high repeatability scores indicating a steep hierarchy (high probability that a dominant individual wins a contest); secondly, we split the interaction dataset into two halves, computed 1000 individual ranks for each half using the randomized Elo-rating method and calculated the Spearman's Rank Correlation r_S between the ratings generated by the two halves. We report the mean r_S and 95% confidence interval range of the correlation values. These results indicated low levels of uncertainty in the data, therefore we used the mean of the randomized Elo-ratings from the full dataset in subsequent analyses, hereby referred to as 'mean Elo-rating'. We used the *rptR* package (Schielzeth et al., 2017) to assess whether males were repeatable in the time they took to engage in the task (t1). If individuals are consistent in the time taken to begin the task over multiple presentations, we can conclude that this assay is a meaningful measure of their motivation. Individuals exhibited a significant level of repeatability (R = 0.231 ± 0.104, $p = 0.005$). Therefore mean t1, which was log-transformed to normalise the distribution, was used in subsequent analyses. The inclusion of mean t1 rather than t1 per trial also reduced the complexity of the subsequent model, which was necessary given the small sample size. We fitted a generalized linear mixed model (GLMM) with a binomial error structure and a logit link function using the *lme4* package (Douglas Bates, Maechler Martin, & Walker, 2016) to assess whether social rank could explain learning performance with 'Correct' (1 yes / 0 no) as the response variable, and trial, mean Elo-rating, first trial performance (correct: 1 yes / 0 no) and mean time taken to begin the task (log mean t1), as explanatory variables. This model was fitted on 13 trials, after performance on the first trial was removed from the Correct variable and included as a separate explanatory variable. An interaction term between mean Elo-rating and trial was included to assess whether individuals of different social rank differ in their rate of learning. We included the first trial performance as an explanatory variable because the outcome of this trial was prior to the opportunity for learning but may affect subsequent performance on the task. The inclusion of mean t1 (log) controlled for motivation to participate in the task. The model failed to converge, this was resolved by standardising mean Elo-rating and trial by converting them to *z* scores (Gelman & Hill, 2007). Trial was nested within individual as a random effect to control for repeated choices of individuals, and to allow the explanatory variables to vary randomly between individuals (random slopes model). The minimum adequate model was reached by comparing models based on log likelihood using backward stepwise deletion of non-significant variables. Results of the full model are provided here (http://doi.org/10.24378/exe.21). We calculated Odds Ratios (OR) from the exponential of b_1 and deduced Confidence Intervals (CIs) for variables in the minimum adequate model. To visualise results we plotted curves predicted from binary logistic regression models for each third of the hierarchy. We did not correct for side biases and three males chose correctly on their first trial and may have been 'unaware' of the incorrect tunnel, hence we also repeated the analyses excluding these individuals. To ensure that we were capturing variation in cognitive performance rather than other factors, we attempted to fit subsequent GLMMs on performances of all males using a binomial error structure and logit link function. Firstly, we fitted a model to check whether individuals of varying rank differed in their motivation to participate, with Correct (1 yes / 0 no) as the response variable and an interaction term between mean Elo-rating with time to begin the task (log mean t1) as explanatory variables. Second, we fitted a model to check there were no rank-related biases; individuals of higher rank may have been more likely than lower ranking individuals to choose correctly on the first trial, with Correct as the response variable and an interaction term between mean Elo-rating and first trial performance (correct: 1 yes / 0 no). The models however, failed to converge. Therefore, we conducted a Spearman's rank correlation between mean Elo-rating and mean t1 (log); and used binary logistic regression models, fitted with a binomial error structure and logit link function with Correct (1 yes / 0 no) as the response variable and trial as an explanatory variable to generate learning curve coefficients. The model outputs are provided *here (*http://doi.org/10.24378/exe.21*).* From the coefficients of each model we calculated the predicted probability that individuals would choose correctly on the first trial (X=1) using the following formula 1/(1+EXP(-(b_0+b_1))). We conducted a Spearman’s rank correlation between mean Elo-rating and X=1.

3.3.5 Ethical considerations

During capture, traps were checked at least three times a day. Birds were habituated to the cognitive testing procedures which involved capture, but this was done quickly to mitigate stress. All captive bird husbandry adhered to the DEFRA Code of Practice (DEFRA, 2009). Birds were held in captivity for three months, after which they were released back onto the site. All work was approved by the University of Exeter Psychology Ethics Committee and the work was conducted under Home Office licence number PPL 30/3204 to JRM.

3.4 Results

3.4.1 Social hierarchy

Our observations were sufficient to produce a steep, reliable hierarchy. The repeatability score of our Randomized Elo-ratings was 0.978 and the mean correlation coefficient obtained by splitting the interaction data was 0.751 (95% C.I; 0.554, 0.909).

3.4.2 Spatial learning performance

The percentage of correct choices per individual on the 13 trials ranged from 21-100% correct. The interaction between social rank and trial was not significant (Table 3.2, Figure 3.2), indicating that individuals of different social rank did not learn the spatial discrimination task at different rates. However, social rank and trial number were significant main effects in the model (Table 3.2, Figure 3.2). Specifically, higher ranking males were more likely to choose correctly and the probability of choosing correctly increased with trial number, indicative of learning. Performance on the first trial was a significant main effect in the model (GLMM: first trial, Wald $X^2 = 4.956$, $df = 1$, $p = 0.026$); males that chose correctly on their first trial were more likely to choose correctly on subsequent trials (Table 3.2). Motivation to engage in the task did not affect the probability that a male would choose correctly (GLMM: mean t1 (log), Wald $X^2 = 1.815$, $df = 1$, $p = 0.178$).

When omitting the three males that performed at 100% correct and repeating these analyses, trial (GLMM: trial, Wald $X^2 = 7.189$, $df = 1$, $p = 0.007$) and social rank (GLMM: Mean Elo-rating, Wald $X^2 = 7.176$, $df = 1$, $p = 0.007$) were significant main effects. The interaction between social rank and trial was not significant (GLMM: trial * Mean Elo-rating, Wald X^2 = 0.999, df = 1, p = 0.318). The choice made on the first trial (GLMM: first trial, Wald X^2 = 0.293, df = 1, p = 0.588) and motivation to engage in the task (GLMM: mean t1 (log), Wald X^2 = 1.999, df = 1, p = 0.157) were not significant in explaining task performances.

When considering performances from all males, the motivation to engage in the cognitive task, deduced from mean t1, was not significantly related to social rank (Spearman's Rank Correlation: mean Elo-rating with mean t1 (log), r_s = - 0.042, n = 15, p = 0.887). The predicted probability of an individual choosing correctly on the first trial was not related to social rank (Spearman's Rank Correlation: mean Elo-rating and X=1, r_s = 0.176, n = 15, p = 0.531).

Table 3.2: Minimum adequate model from generalized linear mixed model on the effects of performance on first trial (correct 1 yes / 0 no), social rank (mean Elo-rating z-score) and trial (z-score) on success on a spatial discrimination task by male pheasants tested individually but while housed in a social group, with odds ratios (OR), lower (Lo CI) and higher confidence intervals (Hi CI). Individual (variance= 1.353) and trial (variance= 0.128) were included as random effects to allow explanatory variables to vary randomly between individuals (random slopes model)

	Estimate	SE	Wald X^2	*p*	OR	Lo CI	Hi CI
Explanatory variable							
Intercept	0.939	0.364					
First trial	1.372	0.580	4.956	0.026	3.942	0.128	2.616
Trial	0.637	0.241	7.391	0.007	1.891	0.120	1.154
Mean Elo-rating	1.023	0.309	9.282	0.002	2.781	0.360	1.686

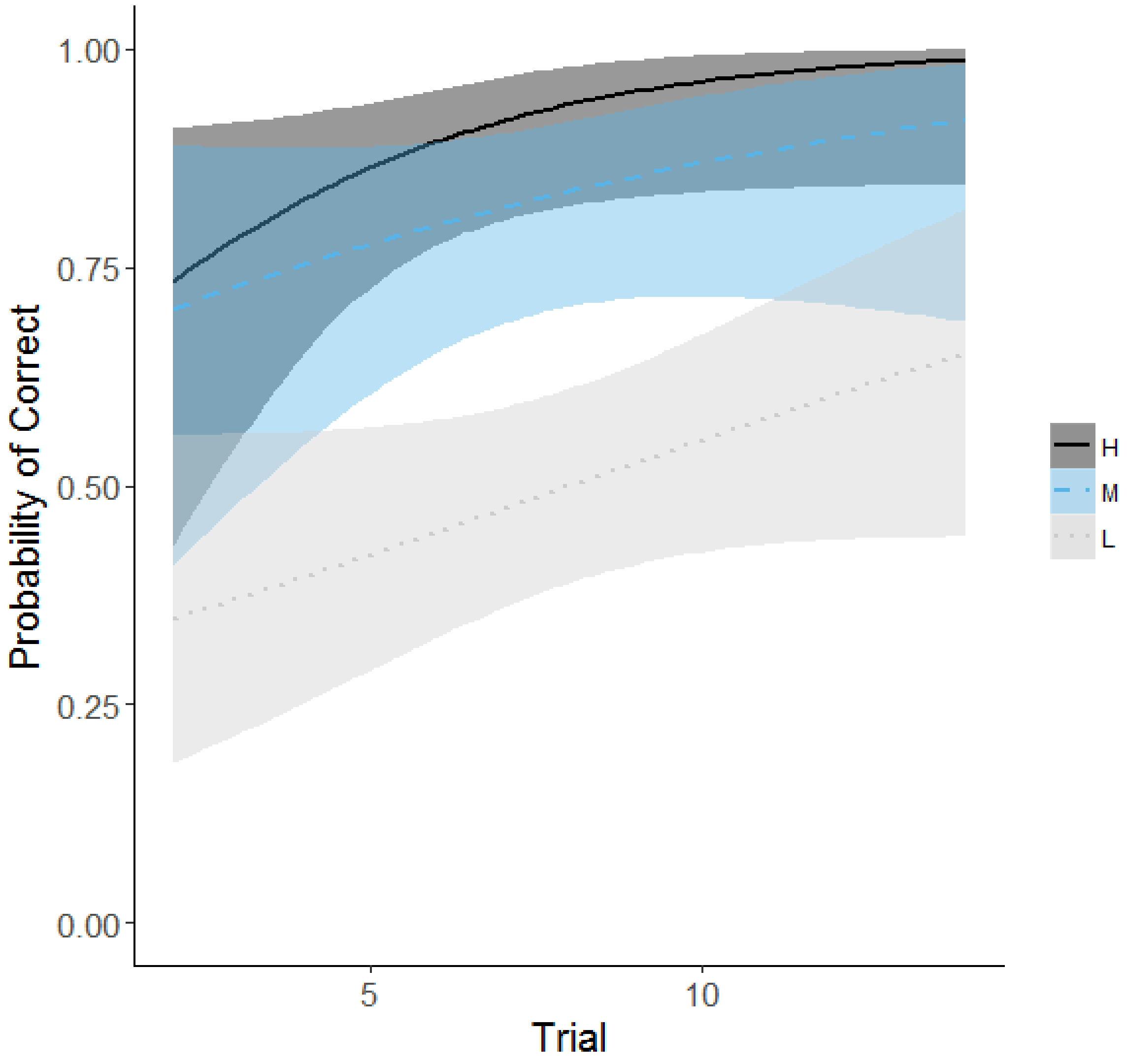

Figure 3.2: Predicted probability of choosing correctly on a spatial discrimination task with increasing trial number for male pheasants. Curves were drawn using a binary logistic regression model; for the three males that achieved a mean Elo-rating in the upper third (H); the five males that achieved a mean Elo-rating within the middle third (M); and the seven males that achieved a mean Elo-rating within the lower third (L), of the mean Elo-rating range. Mean Elo-ratings were deduced from 1000 Randomized Elo ratings. The shaded areas indicate 95% confidence intervals for each curve.

3.5 Discussion

The higher a male pheasant's social rank, the better their performance on a spatial discrimination task. Social rank was not related to the rate at which males chose correctly, but males' performances improved with experience, suggesting that the task captured capacities for spatial learning. Motivation to engage in the task was not related to social rank, nor did it relate to learning performance. There was no relationship between social rank and performance on the first trial, but individuals that chose correctly on their first trial had better performance overall. This suggests that in pheasants, the ability to learn to discriminate between spatial locations corresponds positively to an individual's social rank while in a group, rather than to differences in motivation or rank-related biases for a location. By considering the social hierarchy of a large group, these findings provide us with a broader view on how cognitive performances correspond to complex social systems, in which individuals have multiple relationships.

We did not correct for side biases during cognitive testing and although the rewarded tunnel side was determined randomly for each male, it is possible that a male may have had a pre-existing bias for the correct tunnel and their cognitive ability to *learn* the correct tunnel was not being assessed. When repeating the analyses including only males that experienced both the incorrect and correct tunnels, our findings were near identical to our results including all males, hence we are confident that the individuals that performed 'perfectly' do not affect our conclusions.

Our results complement findings from other species in which high levels of aggression and competitive ability exhibited by an individual have been positively linked to their learning and memory performance (Barnard & Luo, 2002; Boogert et al., 2006; Francia et al., 2006; Pravosudov et al., 2003). Contrary to these studies which concentrated on dyads (Barnard & Luo, 2002; Francia et al., 2006; Pravosudov et al., 2003) or small groups (Boogert et al., 2006), we considered a range of rank positions in a social hierarchy, providing more information. We may envisage that consistently winning or consistently losing contests effects cognitive performance positively and negatively, respectively. There is very little information however on how the intermediate ranks, which are those individuals that experience both winning and losing contests, may vary in their cognitive performance. Furthermore, studies of pairs or small groups neglect important social effects such as the role of bystanders on outcomes of social interactions (Chase, 1982). Therefore, these social ranks and their associated cognitive performances may not be fully representative of how this relationship manifests in natural situations. It is possible that the social hierarchy we inferred from the dominance observations had changed since the cognitive testing was conducted. However, previous work on pheasants shows that when group composition is held constant, hierarchies become well established (Mateos & Carranza, 1997b; Mateos, 2005), and although Mateos *et al*. do not comment explicitly on the duration of hierarchy stability, other galliformes demonstrate stable hierarchies when housed over similar periods to our study (up to 20 weeks in domestic chickens, *Gallus gallus domesticus,* Rushen, 1982; at least three weeks in jungle fowl, *Gallus gallus,* Chappell, Zuk, & Johnsen, 1999).

In contrast to our findings, Bunnell and authors report the opposite relationship between rank and cognitive performance, in which lower ranking macaques, *Macaca fascicularis*, were more proficient on reversal learning tasks (Bunnell et al., 1980; Bunnell & Perkins, 1980). This finding however, may be due to the unnatural and frequent changes made to the macaques' group composition. The unnatural changes in group composition may have had a more adverse effect on higher ranking individuals' cognitive performance than that of lower ranking individuals. Alternatively, the reversal test faced by the macaques may better indicate cognitive flexibility or inhibitory control; abilities important for lower ranking individuals as they regularly experience negative repercussions from those of higher rank (Strayer, 1976). It would be interesting to investigate if reversal learning is negatively related to social rank within our group system.

The positive relationship between performances on the cognitive task with social rank in our pheasants may be a consequence of our testing paradigm and not a result of differences between social ranks in cognitive ability. Motivation to engage in the task did not differ between males of different social rank, nor did this influence performance on the task. However, individuals may have differed in their motivation to leave the testing chamber (e.g. whether they have preferential access to females) and this is distinct from motivation to engage in the task. We assume that higher ranking males may have had less contested access to females in the communal pen, as females have been found to prefer dominant males (Mateos & Carranza, 1995). Although this is not something that we quantified, it is possible that higher ranking males habitually guarded females in the communal pen, causing them to be more motivated to choose the correct tunnel. Additionally, low ranking males may have been less motivated to return to the communal pen where they could be subject to aggression. However, the probability of choosing the correct tunnel generally increased with each trial for males of all social ranks so we suggest that males valued this reward equally.

Higher ranking individuals may have been more likely to choose correctly on their first trial, just by chance and thus had an advantage for the remainder of the task. However, the predicted probability of making a correct choice on the first trial was not related to social rank, suggesting that males of different rank were equally likely to choose correctly on the first trial. Furthermore, after choosing incorrectly on the first trial, individuals experienced the correct tunnel as they exited the main testing chamber. Therefore, we can rule out that individuals of higher rank had an advantage on this task.

Alternatively, low ranking males may have had poorer memory for the correct tunnel or were slower to learn its location because of the stress associated with living as a subordinate in a hierarchy (Blanchard et al., 1993; Creel, 2001) which impedes cognitive performances (de Kloet et al., 1999). It is likely that the lower ranking pheasants were in receipt of a higher level of aggression from conspecifics than higher ranking males (Mateos & Carranza, 1997a) and consequently, their performance on the task may be impaired. Future research could explore whether pheasants differ in stress levels according to their social rank and if this mechanism explains variation in learning performance. Tantamount to this, individuals may have also differed in their sensitivity to the testing procedures and the stress they experienced as a consequence. This variability in resistance to stress may have influenced cognitive performances and the later social rank that an individual occupied. We are not able to explore this possibility with our data as we did not record physiological measures of stress, nor did we observe any obvious behavioural indicators of stress. Whether differences in susceptibility to stress mediate the relationship between cognitive performance and social rank is an interesting idea for future work.

3.5.1 Conclusion

In an ecologically relevant, multi-individual mixed sex social environment, we found that, for male pheasants, variation in accuracy but not rate of individual learning performance on a spatial discrimination task was correlated positively with their social rank. Perhaps male pheasants that were inherently good at learning about space become dominant because they are better able to recall spatial features and so more efficiently establish and hold a territory. Alternatively, males may establish their dominance position independently of their performance in spatial memory tasks, but once they attain a dominant position, they may express better spatial learning because they have had more opportunity to learn spatial cues in a reliable and consistent territory (i.e. they are able to learn to learn). Whether social rank drives differences in cognitive performance or instead inherent differences in cognitive performance predetermine rank remains to be explored.

Chapter Four: The relationship between social rank and spatial learning*:* Cause or consequence?

4.1 Abstract

Individual differences in performances on cognitive tasks have been found to differ according to social rank across multiple species. However, it is not clear whether an individual's cognitive performance is flexible and the result of their current social rank, modulated by social interactions (social state dependent hypothesis), or that an individual's cognitive performance is determined prior to the formation of the social hierarchy and indeed contributes to determining an individual's rank (prior attributes hypothesis). We separated these two hypotheses by measuring learning performance of male pheasants, *Phasianus colchicus,* on a spatial discrimination task as chicks and again as adults. We inferred adult male social rank from observing agonistic interactions while housed in captive multi-male multi-female groups. Learning performance of adult males was assayed after social rank had been standardised; by housing males with only females. We predicted that if cognitive abilities determine social rank formation we would observe: consistency between chick and adult performances on the cognitive task; that chick performance would predict adult social rank; and variation in adult cognitive performances would correspond to group social rank even when males were alone and experienced no direct competition for rank. We found that learning performances were not consistent from chicks to adults, and chick learning performance was not related to adult social rank. Therefore, we could not support the prior attributes hypothesis of cognitive abilities aiding social rank formation. Instead, we found that individual differences in learning performances of adults were predicted by their most recent rank, measured in a social context, even though learning performance was assayed while males were in a standardized, non-competitive environment. This does not support the hypothesis that direct social pressures are causing the inter-individual variation in learning performances that we

observe. Instead, our results suggest that there may be carry-over effects of aggressive social interactions on learning performance. Our results also indicate that the number of females a male was housed with affected cognitive performances; males with four females had higher levels of learning performance than males housed with two females. Consequently, cognitive performances do not appear to influence social rank and cognitive performances are modulated by the current social environment, as well as by past social rank.

4.2 Introduction

To understand how cognitive abilities may have been shaped by natural selection, it is important to characterise the causes and consequences of individual differences in cognitive performances (Thornton et al., 2014; Thornton & Lukas, 2012). An individual's position in a social hierarchy is a critical determinant of an individual's fitness (Von Holst, Hutzelmeyer, Kaetzke, Khaschei, & Schönheiter, 1999) and is likely to be closely linked to their cognitive performance. Social rank greatly influences access to resources (Popp & DeVore, 1979; Wilson, 1975), stress (Abbott et al., 2003; Creel, 2001; Sapolsky, 2005) and opportunities for learning (Chalmeau & Gallo, 1993). However, it is not clear whether social rank and its associated fitness benefits are a cause of individual differences in cognitive abilities, or if social rank arises as a consequence of pre-existing individual differences in cognitive ability.

Social rank may be a consequence of cognitive ability with cognitively able individuals going on to achieve social success (Humphrey 1976; Bryne & Whiten 1988; Seyfarth & Cheney 2002). It has been suggested that an individual's social rank is predetermined by differences in their dominance ability, termed the "*Prior attributes hypothesis"* (Chase et al. 2002). Specific cognitive abilities may be important for the acquisition of dominance. Behavioural inhibition may enable individuals to respond appropriately to competitors and avoid unnecessary aggression (Strayer, 1976). Social learning can inform individuals about conspecifics motivations (Seyfarth & Cheney, 2002), as well as their fighting ability and consequently guide future social interactions (fighting fish, *Betta splendens,* Oliveira, McGregor, & Latruffe, 1998). Thus, individuals with more proficient social learning abilities have been found to be higher ranking (domestic chickens, *Gallus gallus,* Nicol & Pope, 1999). Similarly, we may expect that general learning ability is associated with social success (Humphrey, 1976). Learning allows individuals to adapt to changing (social) environments. Performances on operant foraging (starlings, *Sturnus vulgaris,* Boogert, Reader, & Laland, 2006) and spatial learning tasks are reported as superior in dominant individuals (pheasants, *Phasianus colchicus,* Langley et al. 2018, Chapter Three; mountain chickadees, *Poecile gambeli*, Pravosudov et al. 2003; mice, Fitchett et al. 2005; Francia et al. 2006). This may be because individuals that are inherently good at learning may be more efficient at beneficial behaviours such as foraging (bumblebees, *Bombus terrestris,* Raine & Chittka, 2008), mate choice (Dukas & Ratcliffe, 2009), and navigating the social environment which brings fitness benefits. However, evidence that these differences in performance existed prior to the establishment of dominance is lacking (Chichinadze, Chichinadze, Gachechiladze, Lazarashvili, & Nikolaishvili, 2014). There has not been an explicit test of whether individual differences in cognitive performance determine social rank. This is further complicated by the plasticity of cognitive performances. Adults generally outperform juveniles on cognitive tasks (meta-analysis, Thornton & Lukas, 2012), and this is likely because adults are more experienced and neural systems are more developed (Knudsen, 2004). Whether individual cognitive performances are consistent across life and if they are not, at which point cognitive performances are predictive of social rank, is unknown.

Alternatively, social rank may be a cause of variation in cognitive performances due to the associated demands of living in a social hierarchy; we term this the ‘*social-state dependent’* hypothesis. This may occur via stress (Abbott et al., 2003; Creel, 2001;

Sapolsky, 2005), that arises from the immediate social environment and is influential in shaping the expression of individuals' cognitive ability (De Kloet et al. 1999; Mendl 1999). First, stress may be caused by social pressures directly. In some cases, the dominant individuals may suffer from high stress and consequently exhibit poorer cognitive performances. When crab-eating macaques, *Macaca fascicularis,* were placed into different social groups, a natural decrease in rank was accompanied by a decrease in errors on object and colour discrimination and reversal tasks (Bunnell & Perkins 1980; Bunnell et al. 1980). The authors suggest that the differences in performance between high and low ranking macaques was due to the chronic social stresses experienced by dominant individuals when maintaining their social rank (Bunnell et al., 1980). Dominant crabs, *Chasmagnathus granulatus,* demonstrated shorter memory retention of a dangerous signal (context-signal-memory), but only after a dominance encounter, and not before (Kaczer et al., 2007), suggesting that the aggressive encounter was detrimental to the aggressor.

In some cases, the subordinate individuals may exhibit poorer cognitive performances due to aggression received. The acquisition of dominance status affected spatial learning ability in mice, *Mus musculus* (Barnard & Luo, 2002), with the individual of a dyad that became subordinate exhibiting impaired performance. The authors suggest this difference was mediated through aggression as there was a negative relationship between learning performance and the number of aggressive acts received after paired housing. Impairment in subordinate's spatial learning ability also persisted in mice, even after previously paired individuals were isolated and social pressures of rank had been removed (Fitchett et al. 2005).

A second source of stress, resulting from differences in social rank is that of nutritional stress caused by the unequal distribution of resources across a social hierarchy (Wilson 1975; Popp & DeVore 1979). Dominants are often larger than subordinates (red-deer, *Cervus elaphus*, Clutton-Brock, Guinness, & Albon, 1982; carrion crows, *Corvus corone corone*, Richner, 1989; red-winged blackbirds, *Agelaius phoenix*, Searcy, 1979) and in many cases more aggressive (Chase et al., 2002). Alternatively, in some species, social rank is maternally inherited and hence relatedness determines access to resources (Japanese macaques, *macaca fuscata,* Kawamura, 1958). Dominant individuals are reported to be in better body condition than subordinates (great tits, *Parus major,* Carrascal, Carlos Senar, Mozetich, Uribe, & Domenech, 1998; red-deer, Clutton-Brock, Albon, & Guinness, 1984). Improved nutrition may decrease stress overall and additionally dominant individuals may have more energy to invest in costly cognitive abilities (Aiello & Wheeler, 2009).

Social rank may influence opportunities for learning. Subordinate chimpanzees, *Pan paniscus,* were unlikely to interact with a cognitive task when the dominant individual was present (Chalmeau & Gallo, 1993). In addition to opportunity, social rank may affect the voluntary expression of cognitive ability. Subordinate rhesus macaques, *Macaca mulatta,* that had previously solved a food choice task, did not express these behaviours in the presence of dominant individuals (Drea & Wallen, 1999). These studies indicate how differences between the social ranks in stress (social and nutritional), opportunity and motivation can cause variation in cognitive performances.

The pheasant, *Phasianus colchicus*, offers a suitable system in which to explore causality in the relationship between cognitive performances and social rank. Pheasants are a precocial species and large numbers can be hatched on the same day and reared without parents. Pheasant chicks can be assayed for cognitive performance using batteries of psychometric tests under captive conditions (van Horik et al., 2016), prior to their release into the wild. Once in the wild, pheasants exhibit harem defense polygyny and males engage in agonistic interactions (Hill & Robertson 1988). Winners of these interactions are more likely to become dominant territory holders and attract females. Losers of these interactions become satellite males who do not hold fixed territories and are subordinate to territory holders and likely obtain low reproductive success. Territory acquisition begins as early as October (Ridley & Hill, 1987; Whiteside et al., n.d.) and territory holders have smaller, more concentrated home ranges than subordinate satellite males (Grahn et al., 1993). Male pheasants exhibit behavioural indicators of dominance, such as crowing (Ridley & Hill 1987; Heinz & Gysel, 1970) and lateral displays (Hill and Robertson 1988), and captive studies demonstrate that dominant males perform these dominance display behaviours at a significantly higher rate than subordinates (Mateos & Carranza, 1999). These displays are suggested to attract females (Mateos & Carranza 1999) and deter competitors (Hill & Robertson, 1988; Ridley & Hill, 1987). In captivity, when males are housed in groups they establish stable hierarchies over short periods at least (Mateos & Carranza, 1997a, 1997b), and the higher ranking males have preferential access to females and dominate particular areas of the housing aviary (personal observation – EJGL). We have previously shown that variation in performance on a spatial discrimination task is associated with social rank in adult male pheasants, which were tested while housed in a group with an established social hierarchy (Langley et al.

2018, Chapter Three). Perhaps, male pheasants that are inherently good at learning about space become dominant because they are better able to recall spatial features and so more efficiently establish and hold a territory. Alternatively, dominant males with smaller home ranges may express better spatial learning performances because they have had more opportunity to learn spatial cues in a reliable and consistent territory (i.e. they learn to learn).

We investigated whether learning performance on a spatial discrimination task suggests that this ability may determine a male pheasants' social rank, or whether it is more likely a consequence. We assayed the cognitive performance of pheasant chicks before we released them into the wild. Then, prior to the breeding season we captured adults from the wild. Individuals are captured at this time so that eggs can be collected for incubation, as part of a larger experiment. We expect that measures of male social rank are more meaningful during these months because this is when males are in intense competition for resources, i.e. access to females. We assessed adult males' group social rank while housed in a multi-male multi-female group aviary and also manipulated dominance rank by housing males singly, in a non-competitive, multi-female condition, which we term the 'perceived dominance' condition. Hence, in this condition, males were provided with an uncontested territory, a harem of females and no direct social pressure from other males. While males were in this perceived dominance condition and experiencing equivalent social ranks, we assayed their performance on the same spatial task that we had presented to the chicks. To test whether a male's cognitive performance may be the cause of, or a consequence of social rank, we asked three questions. First, is an individual's cognitive performance consistent from chick to adult? For a cognitive ability to be a prior determinant of social rank, we expected individual cognitive performances to be consistent from chick to adult, as this would indicate cognitive ability developed outside of and prior to dominance interactions. If cognitive performances are not consistent from chick to adult this suggests that they may be altered in response to an individual’s current social environment. Second, we asked whether chick cognitive performances predict their future social rank, suggesting that a prior ability in this domain may determine subsequent social rank. Positive results for questions 1 and 2 would provide support for the prior attributes hypothesis. Third, we tested adult males’ cognitive performances while they were housed in the perceived dominance condition and investigated whether this was related to their captive social rank. Critically, we assessed whether this perceived dominance condition was associated with increases in “*dominance-display*” behaviours; crowing and lateral struts, as an indication of the effectiveness of the rank manipulation. To test this statistically, we were looking for a non-significant result; if inter-individual variation in cognitive performance while experiencing this rank manipulation is not explained by an individuals’ most recent social rank, this provides support for the social state dependent hypothesis, because all males were experiencing the same social rank and therefore performance on the task is expected to be similar among males.

4.3 Methods

4.3.1 Study system, subjects & housing

This study was conducted from May 2015-June 2016 at North Wyke Rothamsted Research Farm, Devon (50^0 77’N, 3^0 9’W). We reared 194 pheasant chicks from hatching in one of four identical aviaries. These chicks were the offspring of adults we captured from the wild. Chicks were identifiable by numbered patagial wing tags (Roxan Ltd). For the first two weeks of life, chicks had access to an indoor 2m x 2m heated aviary. At three weeks they also had access to a covered but unheated 1m x 4m outdoor run and at four weeks they also had access to a 4m x 12m outdoor aviary. Throughout the aviaries, chicks had access to perches and food and water *ad libitum*. Within the indoor section of the aviary, chicks could enter a testing chamber through a sliding door and engage in cognitive testing and exit to the outdoor area via a lift-up door. One hundred and forty-nine chicks participated in the task described in this study. When the chicks were 10 weeks old, we released them on to the site that covers 250Ha of which there is lowland deciduous woodland, grassland, fen meadow and 40 artificial wheat feeders.

In March 2016 we caught adult pheasants (>10 months old) using baited funnel traps. The catching period lasted for three weeks and during this time traps were checked three times a day. By the end of the catching period we only sighted two males that we were unable to catch, suggesting that we had caught most of the pheasants on the site. We caught 22 males, 11 of which we had reared as chicks, hereby referred to as *known* males and the remaining 11 males were of unknown rearing history, hereby referred to as *unknown* males. Males that we reared as chicks and did not catch either died or dispersed off of the site. Mass and tarsus length measurements were collected from all individuals. Adult males were assigned to one of two different outdoor aviaries/social conditions, either; a large group aviary (19 m x 23 m), containing multiple females to give a male to female ratio of 60:40; or assigned to one of 10 smaller identical aviaries (4m x 8m), in which males were housed individually with either two or four females. The allocation of two or four females was determined at random and formed part of a separate experiment on female cognitive performance (Langley, van Horik, Whiteside, & Madden, 2018b, Chapter Two). Aviaries were in visual but not auditory isolation from each other. All aviaries contained elevated perches, refuge areas, and food and water *ad libitum.* A general overview of the method is shown in Figure 4.1.

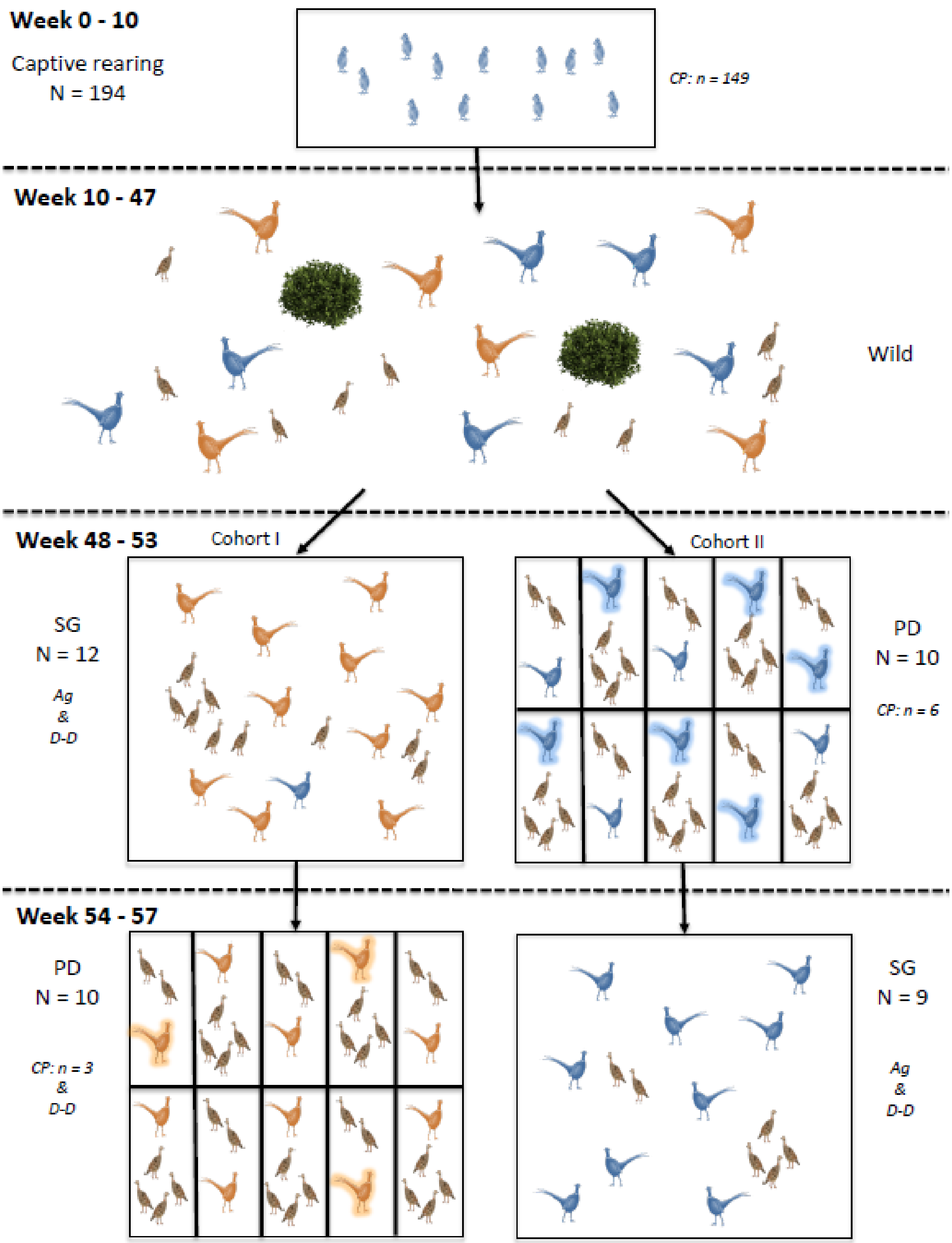

Figure 4.1: Timeline of experimental procedures. Blue birds = known; orange birds = unknown; SG = Social Group condition; PD = Perceived Dominance condition; N = Total sample size in each condition; CP = cognitive performance assayed; D-D = dominance-display behaviours observed; Ag = agonistic interactions between males observed; *n* = sample size of those tested on the spatial discrimination task (also shaded on the figure).

4.3.2 Cognitive test apparatus

Spatial learning and memory tasks on avian subjects typically investigate subjects' ability to reliably locate a food reward on a foraging apparatus containing wells (Western scrub jays, Aphelocoma californica, Pravosudov, Lavenex, & Omanska, 2005; zebra finch, *Taeniopygia guttata,* Sanford & Clayton, 2008; song sparrows, *Melospiza melodia,* Sewall, Soha, Peters, & Nowicki, 2013; New Zealand North Island robins, Petroica longpipes, Shaw, Boogert, Clayton, & Burns, 2015). Wells may be concealed by flaps (Sanford & Clayton 2008) or filled with sand (Pravosudov et al. 2005), requiring the subject to search and remember locations of food without them being visible. Our 'top-bottom' discrimination task required subjects to discriminate between two identical wells arranged vertically on a rectangular apparatus (38cm x 14cm x 4cm). The top well, furthest from the bird, contained a mealworm food reward. The bottom well, closest to the bird, was unrewarded and blocked by a bung. Both wells were covered with a layer of opaque crepe paper which chicks and adults were trained to peck through prior to testing. Both wells were unmarked and identical and were only distinguishable by their location on the task apparatus (top vs. bottom). During a trial we allowed individuals to make one choice per pair of wells. If individuals chose correctly, indicated by pecking at the crepe paper of the rewarded well, we allowed the individual to consume the food reward before the wells were removed. If individuals chose incorrectly, indicated by pecking at the crepe paper of the unrewarded well, the wells were promptly removed and a new pair of wells was presented.

4.3.3 Chick cognitive training and testing

From one day old, chicks were habituated to human experimenters. We trained chicks to enter a testing arena in groups and allowed them to become familiar with the testing apparatus by placing mealworms in open wells and on top of the apparatus so that they were visible to the chicks. In subsequent sessions we presented groups of chicks with mealworms only within the wells to encourage individuals to search for rewards within the wells. Following this, we added broken crepe paper onto the wells and over multiple sessions the wells became increasingly concealed until individuals spontaneously pecked through the crepe paper. At approximately three weeks old, chicks were trained to individually enter the testing chamber, located behind a sliding door, upon hearing an auditory command (whistling/humming from a human experimenter). Cognitive testing began when individuals could competently peck through the crepe paper to retrieve the mealworm reward. Each testing session consisted of 10 trials. Once the trials were completed, chicks were released through the exit door. During a testing session, chicks could voluntarily enter the testing chamber and the order in which they enter is consistent (van Horik et al., 2016). There were two morning sessions on consecutive days, beginning at 9am and lasting until approximately 11:30am once all chicks had been tested. Between these two sessions, chicks received one afternoon session beginning at 14:00pm and lasting until approximately 16:30pm. Food was removed from housing pens one hour prior to testing. The three testing sessions resulted in a maximum of 30 trials per individual. Seven of the 11 known males we caught as adults had completed 30 trials as a chick. Focusing on the first 20 trials (first morning and afternoon session) increased the sample size by one individual, therefore eight males that each performed 20 trials on this task were used in analyses.

4.3.4 Adult social conditions

Eleven unknown males and one known male (chosen at random) that we captured as adults were assigned to the ‘Social Group (SG)’ condition (the large group aviary). The remaining ten known males were assigned to the ‘Perceived Dominance (PD)’ condition (one of 10 individual aviaries; Figure 4.2). We housed known males in the same social condition so that we could compare their cognitive performances to their social rank, relative to the other males that they were reared with as a chick. Hence, we did not assign males to the conditions in a randomised way. Due to low participation on cognitive testing from known males while in the PD condition (see below), we also placed unknown males in to the PD condition to assay their learning performance in an attempt to increase our sample size. Hence, males experienced both conditions; those assigned to the SG condition first and then the PD condition are hereby referred to as ‘cohort I’, and those experiencing the conditions in reverse, are referred to as ‘cohort II’.

4.3.4.1 Social Group (SG) condition

We collected observations *ad libitum* on the outcomes of dyadic agonistic interactions between males for the inference of social rank (Table 4.1) and dominance-display behaviours as an indicator of perceived social rank (Table 4.2). There were two observers at a given time each monitoring different areas of the aviary to ensure all behaviours were recorded. Observers were visually concealed from the birds. For the recording of dyadic agonistic interactions, we assigned a winner and a loser. For the recording of dominance-display behaviours, we calculated rate (event/hour) of each behaviour performed by each male. We adjusted the rate of lateral displays directed towards females by controlling for female density by dividing the mean rate of displays performed by the number of females housed in the aviary. We only included lateral struts which were directed towards females so this was consistent between social conditions (females are present in both social conditions, whereas multiple males were only present in the SG condition and we did not want to introduce bias into our results); lateral displays that were clearly directed towards males or in cases where the receiver was ambiguous, were not included in analyses. For cohort I males, observations were collected from 21st March–6th May 2016, on 12 males, prior to cognitive testing in the PD condition. For cohort II males, observations were collected from 9th – 26th May 2016, on 9 males (one male died unexpectedly before being placed in the SG condition), after cognitive testing in the PD condition.

Table 4.1: Ethogram of agonistic interactions between male pheasants observed during the SG condition, for the inference of social rank

Agonistic	
Chase	aggressor (winner) runs towards opponent and opponent flees (loser)
Threat	aggressor (winner) steps forwards and makes a sharp lunge towards opponent, generally, opponent flees (loser). Similar to the start of a chase but aggressor does not continue to run
Contact	aggressor (winner) pecks opponent (loser) with the bill, usually directed at the head, or aggressor (winner) jumps at opponent feet first to direct spurs at opponent (loser)
Submissive	
Avoid	an individual (loser) rapidly changes trajectory while walking and is within 3m of another individual (winner) that is not showing any apparent signs of aggression

Table 4.2: Ethogram of dominance-display behaviours observed while pheasants were housed in both the SG and the PD conditions

Lateral strut	Male lowers head and flattens one wing toward receiver, sometimes primaries touch the ground while erecting ear tufts and inflating wattle. Tail is spread. Sometimes the display is accompanied with vibration of the tail to create audible sound.
Crow	Loud, sudden two-syllable call. Followed by a brief and loud wing flap (Heinz & Gysel 1970; Cramp & Simmons 1980)

4.3.4.2 Perceived Dominance (PD) condition

Housing in one of these 10 aviaries (Figure 4.2) provided the male with an exclusive territory, a harem and no direct social pressure from other males. Males were randomly allocated to a pen containing two or four females. This simulated the male holding a high social rank. Males had their cognitive performance assayed while in this condition. Outside of cognitive testing we also collected behavioural observations on dominance-display behaviours (Table 4.2) as an indication of a male’s perceived social rank, for cohort I males. Dominant males are found to perform these behaviours at a higher rate compared to subordinate males (Mateos & Carranza 1999). Five of the aviaries could be observed simultaneously and the dominance behaviours were conspicuous. Each day we determined randomly which five aviaries to observe for the first 30 minutes and then observed the remaining five aviaries for 30 minutes. Observations begun at variable times of the day in case there were differences between males in their activity levels. For each individual, we calculated rate per hour of each of the two dominance behaviours using the same methods as those used in the SG condition. We did not collect observations on dominance-display behaviours of cohort II males due to time constraints.

4.3.5 Adult cognitive training and testing

Performances on the spatial discrimination task were assayed while males were housed in the PD condition. We habituated all individuals to approach the test apparatus, located in the testing area of their aviary (Figure 4.2). The apparatus was located between two opaque screens so that it could only be approached and viewed by a bird ‘front-on’. These screens were necessary for the testing of adults because the females within the pen were also tested on this task, as part of a separate experiment (Langley et al., 2018b, Chapter Two); we wanted to prevent social learning of task affordances and these screens allowed only the bird being tested to view the apparatus. To signal to the males that the apparatus was available, a visual cue (black and white swirl pattern) was placed on the wall in the testing area, which was situated in the corner of the aviary. We used similar methods to the chick training regime by heavily baiting the box with mealworms so that they were visible to all birds within the aviary, with the gradual transition to only placing worms within the wells and the addition of crepe paper covering the wells. We attempted to train all 20 males while they were housed in the PD condition, but the males proved difficult to test and appeared distracted by females during the breeding season. We ceased in our attempts to train males that did not interact with the task apparatus on five consecutive training sessions. Three unknown males of cohort I and six known individuals of cohort II reliably participated in the task. During most test sessions, we were required to use a temporary mesh partition that stopped the females from approaching males while they were interacting with the test apparatus. The use of this mesh partition did not appear to be stressful as males readily engaged in cognitive testing shortly after the partition was implemented. Males were not caught or handled during testing. Each session consisted of 20 trials. Individuals received one session per day, for five days, resulting in 100 trials in total. We hoped that with the incorporation of a greater number of trials it would give us greater statistical power to detect differences in the rate of learning between males (interaction between trial and social rank). Cohort I and II were housed in the PD condition for 11 and 23 days, respectively, before cognitive testing begun. Adverse field conditions delayed cognitive testing for males of Cohort II (housed in the PD condition first) and we ran out of time to 'match' the duration that Cohort I were housed in the PD condition before beginning cognitive testing.

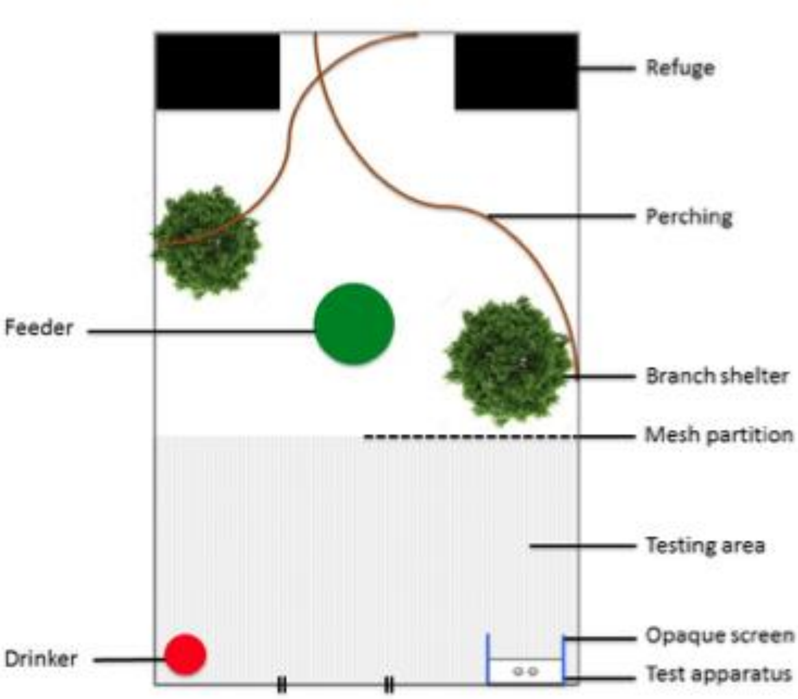

Figure 4.2: Aerial view of single housing pen (4m x 8m) for the Perceived Dominance (PD) condition with testing area and test apparatus.

4.3.6 Statistical analysis

All analyses were conducted using R v.3.2.1 (The R Foundation for Statistical Computing, Vienna, Austria, 2015).

4.3.6.1 Social rank

For each cohort we inferred the social hierarchy using the same methods as those in Langley et al. (2018a, Chapter Three) using the winner-loser data of agonistic and submissive interactions (Table 4.1). We generated ‘Randomized Elo-ratings’ using the *aniDom* package (Farine & Sanchez-Tojar, 2017) and assessed hierarchy uncertainty using the two methods described in Sanchez-Tojar et al. (2017). First, we estimated repeatability of the individual Elo-ratings generated from replicated datasets (n = 1000) using the *rptR* package (Schielzeth et al., 2017), with high repeatability scores indicating a steep hierarchy (high probability that a dominant individual wins a contest). Second, we split the interaction dataset into two halves, computed 1000 individual ranks for each half using the randomized Elo-rating method and calculated the Spearman’s Rank Correlation r_S between the ratings generated by the two halves. We report the mean r_S and 95% confidence interval range of the correlation values. These results indicated high levels of certainty in the data, therefore we used the mean of the randomized Elo-ratings from the full dataset in subsequent analyses, hereby referred to as ‘mean Elo-rating’.

4.3.6.2 Cognitive performance

We generated learning curves using a binary logistic regression model (GLM) for each individual that performed the top-bottom discrimination task as a chick (n=9) and as an adult (n=9) using the first 20 trials for both chicks and adults to ensure that learning curves are comparable. From these curves we calculated the probability that an individual would choose correctly on their final trial (X=Final), which is derived from solving the equation $Y = 1/(1+\exp[-(b_0+b_1X)])$, whereby b_0 depicts the intercept and b_1 depicts the slope estimate from the learning curve glm. We consider this measure indicative of how well an individual has learned the task by the end of the testing. We also calculated the predicted trial number when an individual reaches or will reach a learning criterion of 80% probability of choosing correctly (Y=80), this is derived by solving the equation $X = (-\ln 0.25 - b_0)/b_1$. We consider this indicative of how much experience an individual needs to adequately learn the affordances of the task. The X=Final and Y=80 measures were calculated for both chick and adult task performances. We asked three questions to distinguish between directionality in the relationship between cognitive performances and social rank. 1) We tested whether individual learning performances were consistent from chick to adult, using a Spearman's Rank Correlation between chick and adult X=Final; and chick and adult Y=80. This was conducted on six individuals that completed the task at both ages. 2) We tested whether chick learning performance predicted adult social rank using a Spearman's Rank Correlation between chick X=Final and their adult mean Elo-rating; and chick Y=80 and their adult mean Elo-rating. This was conducted on one individual of cohort I and seven individuals of cohort II, which completed the cognitive task as a chick (two additional individuals to those in question 1; that did not complete adult cognitive testing). 3) Finally, we fit a generalized linear mixed model (GLMM) with a binomial error structure and a logit link function to assess whether adult learning performance (correct: 1 yes / 0 no) was predicted by group social rank (mean Elo-ratings). We also included cohort, the number of females housed with while in the PD condition, choice on first trial (correct: 1 yes / 0 no), body condition and trial number (2-100) as explanatory variables. A two-way interaction between mean Elo-rating and trial number was included to examine whether individuals differ in their rate of learning in relation to their group social rank. We define rate of learning as the speed at which individuals switch from making a series of incorrect choices to a series of correct choices and is deduced from the steepness of the learning slope (trial* social rank; b_1). A main effect of trial indicates that there was an increase in the probability that males would choose correctly as trial number increased. A main effect of social rank on learning performance indicates that social ranks differ in their overall accuracy of task performance, inclusive of performance on all trials. We included cohort to account for the order in which males experienced the social conditions, as well as their rearing history (i.e. whether they had experience with this task as a chick). We included the number of females males were housed with during the PD condition because we have previously shown that group size affects female learning performance (Langley et al., 2018b, Chapter Two) . We included choice on first trial (correct: 1 yes / 0 no) to control for random choice on this first trial; as this trial was prior to the opportunity for learning but may affect subsequent performance on the task and this left the trial variable with trial number 2 – 100 (after trial 1 was removed). The residual values from a regression of tarsus and mass was included as a measure of body condition (Jakob, Marshall, Uetz, & Estimating, 1996). To facilitate convergence we converted all continuous variables to z-scores (Gelman and Hill 2007). Individual was included as a random term (random intercepts, fixed slopes model). We assessed the fit of this model by comparing it to an equivalent random intercepts and random slopes model and found that the random intercepts only model was adequate ($X^2 = 0.261$, $p = 0.878$) and therefore used this for subsequent analyses. We tested the significance of explanatory variables using likelihood ratio tests. This model was conducted on eight adult males that each completed 100 trials; 3 males of cohort I and five males of cohort II. We also tested whether body condition and social rank were related for these males using a Spearman's Rank Correlation.

4.3.6.3 Dominance display behaviours

We also investigated the effectiveness of our rank manipulation and compared rates of dominance-display behaviours of males when they were in the SG condition with the rates of dominance-display behaviour when they were housed in the PD condition, using a Wilcoxon signed-ranks test on all 10 individuals of cohort I.

4.3.7 Ethical considerations

Chicks and adults were habituated to human observation and were subject to minimal handling. All training procedures were adopted to mitigate stress during cognitive testing and birds could choose whether or not to participate in tasks. Birds were reared at a lower density than that recommended by DEFRA's code of practice (DEFRA, 2009), thus reducing stress. During capture of adults from the wild, traps were checked at least three times a day. Adult birds were held in captivity for three months, after which they were released at the capture site. All work was approved by the University of Exeter Psychology Ethics Committee and the work was conducted under Home Office licence number PPL 30/3204 to JRM.

4.4 Results

4.4.1 Is learning performance consistent from chick to adult?

There was a non-significant positive relationship between chicks' predicted performances at the end of 20 trials on the spatial discrimination task and their equivalent adult performances (Spearman's Rank Correlation: X=Final, $r_s = 0.696$, $n = 6$, $p = 0.125$, Figure 4.3). There was a non-significant positive relationship between the trial number in which chicks' were predicted to reach an 80% probability of choosing correctly, with the equivalent adult performances, on the spatial discrimination task (Spearman's Rank Correlation; Y=80, $r_s = 0.200$, $n = 6$, $p = 0.714$, Figure 4.4).

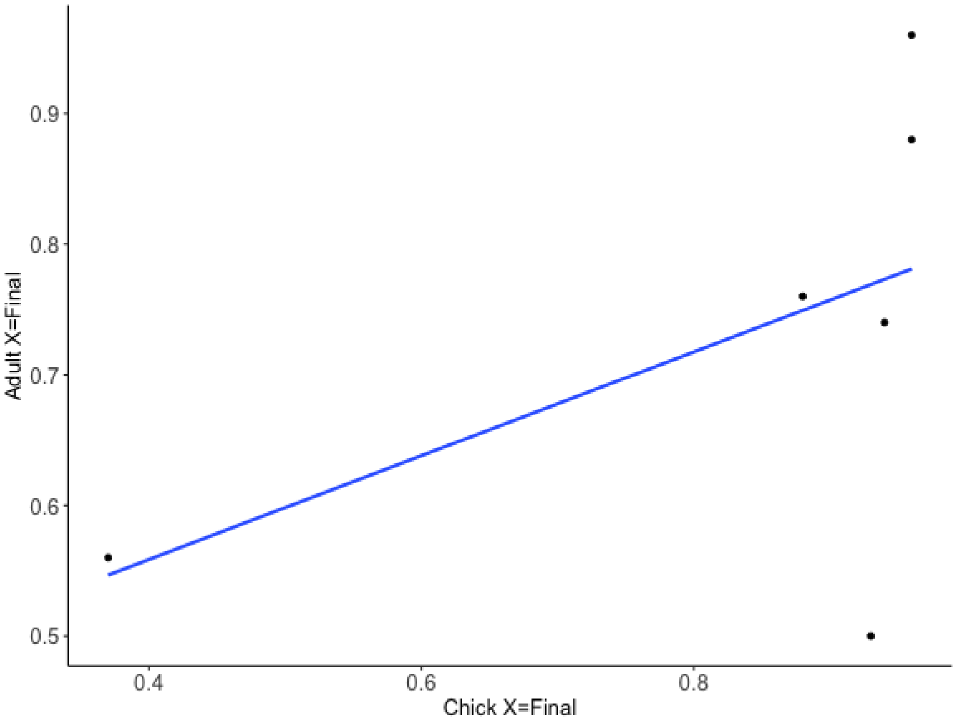

Figure 4.3: Relationship between the predicted probability of a correct choice on the final trial (X=Final) for chick and adult spatial discrimination performances (Cohort II, *n* = 6).

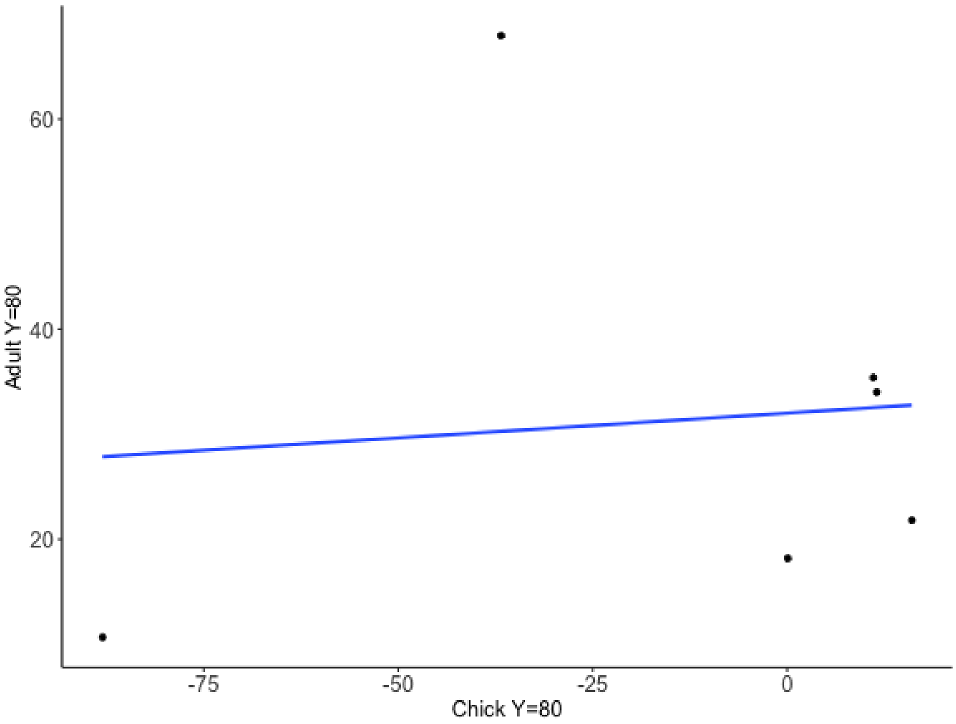

Figure 4.4: Relationship between predicted trial number when reached a learning criterion of 80% probability of a correct choice (Y=80) for chick and adult spatial discrimination performances (Cohort II, *n* = 6).

4.4.2 Does a chick's learning performance predict adult social rank?

The two uncertainty measures we obtained from using the Randomized Elo-rating method to generate hierarchies for both cohorts, indicate these inferred hierarchies were highly reliable indicators of social rank (Table 4.3). We found no relationship between mean Elo-rating and chicks' predicted performances at the end of the spatial discrimination task (Spearman's Rank Correlation: X=Final, $r_s = 0$, $n = 8$, $p = 0.99$). Similarly, there was no relationship between the trial number in which chicks were predicted to reach an 80% probability of choosing correctly and their adult social rank (Spearman's Rank Correlation: Y=80, $r_s = -0.524$, $n = 8$, $p = 0.197$).

Table 4.3: Hierarchy statistics for male pheasants of cohort I and II while housed in the social group condition (SG)

n	Cohort	No. interactions	Obs (days)	*r*	r^2		
					Mean	2.5%	97.5%
12	I	1044	47	0.984	0.948	0.881	0.993
9	II	701	14	0.996	0.976	0.917	1.000

r = repeatability estimate for individual Elo-ratings generated from replicated datasets; r^2 = correlation coefficient from Spearman's Rank Correlation between two halves of split dataset.

4.4.3 Does variation in cognitive performances relate to social rank once rank is standardised?

4.4.3.1 Evidence that the social rank manipulation was effective

Both indicators of dominance (crowing and lateral displays) were expressed at higher rates by males in single male groups than when housed in social groups. Of the ten males of cohort I, two males never crowed in either social condition and eight males increased their rate of crowing behaviour while housed in the rank manipulation (PD condition) compared with when they were housed in the social group (SG condition) (Wilcoxon Signed Ranks test: *n* = 10, *p* = 0.014, Table 4.4, Fig. 5).

Three of ten males performed fewer lateral struts while in the PD condition compared with when they were housed in the SG condition, whereas seven males performed struts at a higher rate while housed in the PD condition (Wilcoxon Signed Ranks test: *n* = 10, *p* = 0.002, Table 4.4, Figure 4.6).

Table 4.4: The rate per hour of dominance-display behaviour for male pheasants of cohort I while housed in each of the two social conditions, in relation to social rank while in the social group condition and the number of females housed with when in the perceived dominance condition.

	Mean		Lateral strut			Crow		
Male	**Elo-rating**	**Females**	**SG**	**PD**	**Increase**	**SG**	**PD**	**Increase**
1	773.8359	2	0.138	0.1	-0.038	6.655	11.333	4.679
2	403.1283	4	0.01	0.017	0.007	0.036	4.3	4.263
3	385.0008	4	0.096	0.167	0.071	0.145	0.333	0.188
4	207.2864	2	0.013	0.017	0.003	0	3.467	3.367
5	-16.0075	2	0.019	0.017	-0.002	0	5.4	5.4
6	-140.793	4	0.025	0.225	0.2	0	0	0
7	-302.046	2	0.006	0.133	0.128	0	10.767	10.767
8	-421.245	2	0.057	0.017	-0.041	0	0	0
9	-601.546	4	0.002	0.15	0.148	0	3.233	3.233
10	-891.792	4	0.01	0.05	0.04	0	0.067	0.067

SG = Social Group condition; PD = Perceived Dominance condition; Increase = (PD rate – SG rate); Lateral strut rate adjusted for female density = 19 females in the SG condition and 2 or 4 in the PD condition.

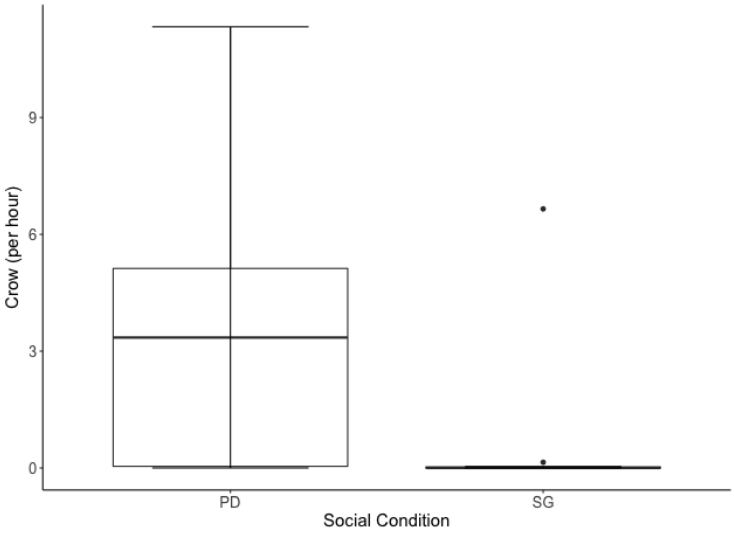

Figure 4.5: Median rate of crows per hour for 10 males of cohort I was higher when males were housed in the Perceived Dominance (PD) condition then when housed in the Social Group (SG) condition. The black horizontal line represents the median value. Whiskers represent the lower and upper quartiles (25% and 75%).

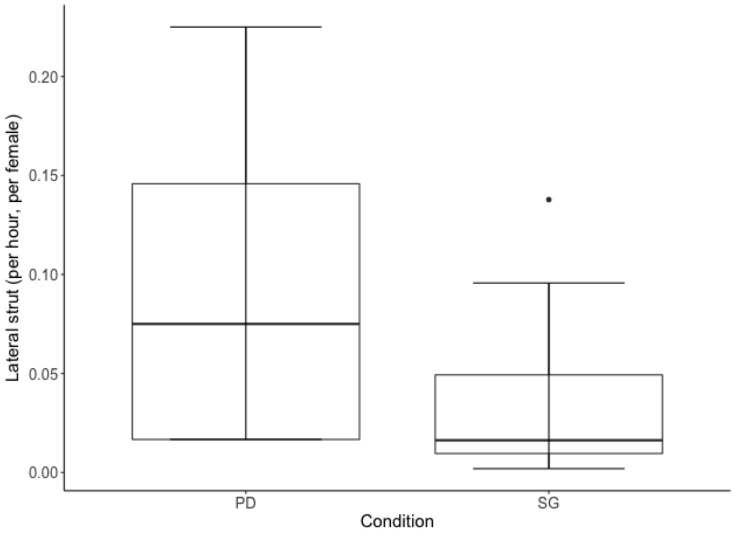

Figure 4.6: Median rate of lateral struts performed per hour (adjusted for female density) for 10 males of cohort I was higher in the Perceived Dominance (PD) condition compared to the Social Group (SG) condition. The black horizontal line represents the median value and whiskers represent the lower and upper quartiles (25% and 75%).

4.4.3.2 Cognitive performance during the rank manipulation

While adult males were housed in the perceived dominance condition (PD), individuals that had a high social rank when in the social group (SG) condition, learned the spatial discriminations at a faster rate than those of lower social rank (GLMM: Trial number*mean Elo-rating, $X^2 = 12.143$*, df = 1, p* < 0.001, Table 4.5, Figure 4.7). The number of females a male was housed with during the PD condition was a significant in predictor of spatial discrimination task performances (GLMM: number of females, $X^2 = 11.255$, *df* = 1, $p < 0.001$), with males housed with four females having a higher probability of choosing correctly (Table 4.5). High and low ranking males were equally as likely to be housed with four females (Table 4.6). Whether males were known or unknown did not relate to learning performances and this variable also controlled for the order in which the males experienced the two different social conditions (GLMM: cohort, $X^2 = 0.554$, *df* = 1, $p = 0.456$). Whether a male chose correctly on their first trial did not relate to performance on the remainder of the task (GLMM: first choice, $X^2 = 1.187$, *df* = 1, $p = 0.276$) and males across the hierarchy were equally as likely to choose correctly or incorrectly on their first choice (Table 4.6). Body condition was unrelated to social rank (Spearman's Rank Correlation, $r_s = 0.310$, $n = 8$, $p = 0.462$) and did not significantly relate to learning performance (GLMM: body condition, $X^2 = 2.794$, *df* = 1, $p = 0.095$; Table 4.5).

Table 4.5: Results from full and minimum adequate model of a generalized linear mixed model fitted on the effects of inferred social rank, cohort, body condition, the number of females housed with and trial number on binary spatial discrimination task performances for eight adult male pheasants tested while in the perceived dominance (PD) social condition (Cohort I: *n* = 3, Cohort II: *n* = 5). Random intercepts and fixed slopes model. Trial and mean Elo-rating were standardised (z-scores).

Predictor variable	Estimate	SE	OR	Lo CI	Hi CI
Full model					
Cohort	-0.349	0.306	0.705	-1.073	0.374
Body condition	-2.310	1.386	0.099	-5.587	0.967
Correct on first trial	0.203	0.187	1.231	-0.234	0.650
Minimum Adequate model					
Intercept	0.881	0.131			
Trial	0.844	0.101	2.326	0.605	1.083
Mean Elo-rating	-0.144	0.108	0.866	-0.399	0.111
Female (4 females)	1.002	0.216	2.723	0.491	1.513
Trial * R Elo-rating	0.318	0.094	1.374	0.096	0.540

Note. Estimate and standard (SE) for each variable with odds ratio (OR) with low (Lo CI) and high (Hi CI) confidence intervals.

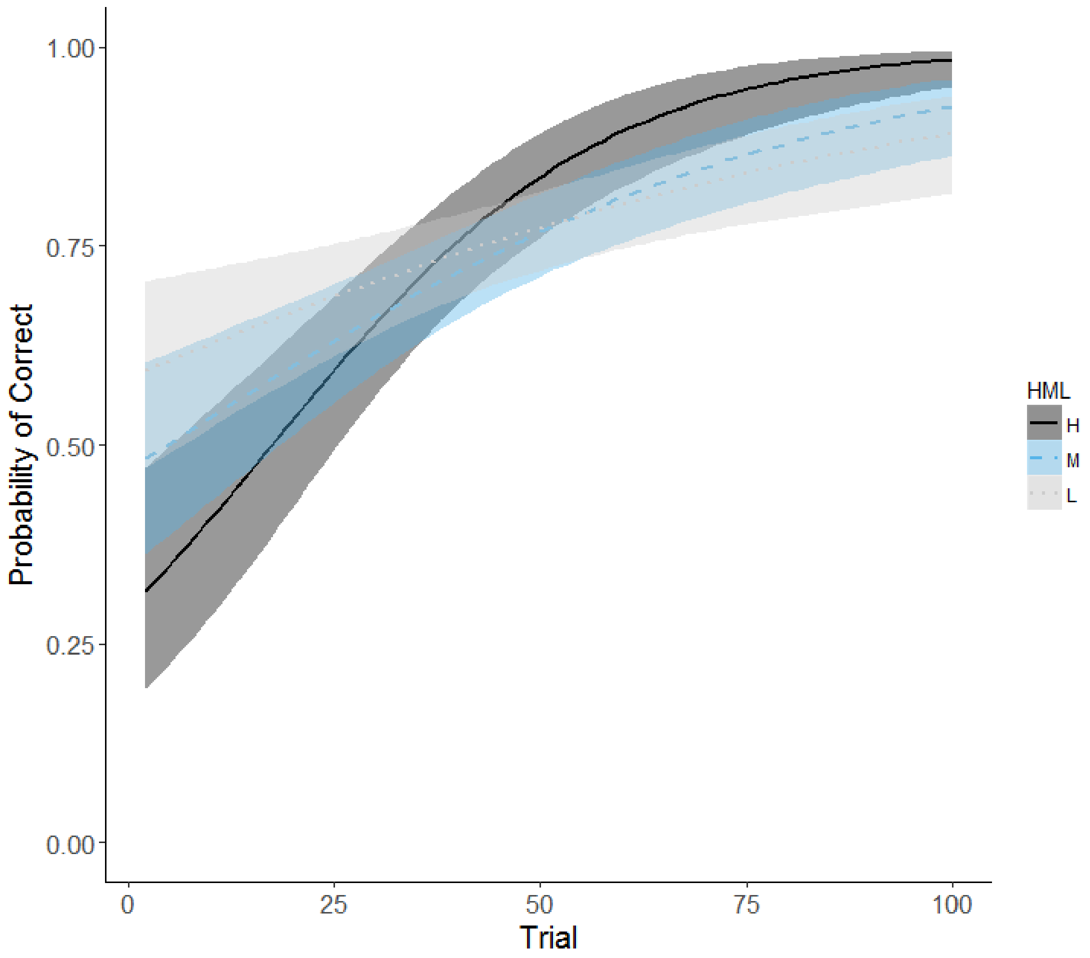

Figure 4.7: Predicted probability of choosing correctly on binary spatial discrimination task for adult males. Curves predicted from a generalised linear model with social rank included as a factor with three levels. Boundaries for high, middle or low rank determined by splitting full range of mean Elo-ratings in to thirds for each cohort. Solid, dashed and dotted lines represent high (Cohort II: *n* = 2), middle (Cohort I: *n* = 1; Cohort II: *n* = 2) and lowest (Cohort I: *n* = 2; Cohort II: *n* = 1) ranking males, respectively.

Table 4.6: Group social rank for adult male pheasants of both cohorts, the number of females they were randomly assigned (2 or 4) during the perceived dominance condition (PD) and first choice on a binary spatial discrimination task (prior to the opportunity for learning). Males of cohort I were unknown birds that experienced the social group condition (SG) before cognitive testing in the perceived dominance condition (PD). Males of cohort II are known males that experienced these conditions in reverse.

Cohort	Rank	Females	First choice
II	2	4	0
II	3	4	1
II	4	2	0
II	5	2	1
II	6	4	0
I	7	4	1
I	10	2	0
I	12	2	1

4.5 Discussion

The relationship between an individual's cognitive performance and their social rank is often reported but the issue of whether performance on a cognitive task is a cause or consequence of social rank, is seldom considered. We did not find evidence that cognitive performances on a spatial discrimination task were consistent across an individual's lifetime and chicks' performances failed to predict their adult social rank. Therefore, we cannot conclude that adult social rank is a consequence of a male's spatial learning performance. When we manipulated social rank so that all males experienced conditions synonymous with high dominance rank (uncontested territory and access to females), we found that a male's learning performance was predicted by the number of females they were housed with and their captive group social rank. This latter relationship was evident even when social rank was scored after cognitive testing. This suggests that spatial learning performances and social rank become associated over time and the relationship persists even when the direct social pressures associated with social rank have been removed. Our findings do not allow us to decipher cause and consequence of the relationship.

The variation in adult cognitive performances may not be representative of the whole population. Of the 104 males that we reared from hatching and released as juveniles, we caught 12 of these males as adults. This low return may be due to one of three factors. First, individuals may have died before the capture season. Pheasant survival to the first breeding season is low and approximately 42% of the ~50 million released in the UK each year die from predation or disease (see Madden et al., 2018 for review). Second, we may have failed to capture more of our released males because they dispersed off of the site, possibly in search of unoccupied territories. Third, males that remained on the site that we did not capture may have been neophobic to the artificial traps. Irrespective of the reasons for non-capture, the captured males are therefore from a biased sample of males that are able to survive to the first breeding season, unlikely to disperse off of the site and are not neophobic to the traps. Furthermore, participation in cognitive testing from the captured males was low; a common problem in cognitive testing experiments (<50% see van Horik et al., 2016). However, because variation in cognitive performances was explained by social rank, which is a relative measure, we argue that this is an informative measure within our study sample.

The prior attributes hypothesis describes that a high correlation coefficient between an attribute and social rank, is indicative of that attribute having assisted in rank formation (Chase, 1974). This hypothesis originally focused on morphological attributes that were developed prior to the formation of the hierarchy but were measured while the dominance hierarchy is established and active, with the inference that these traits assisted in the establishment of the dominance hierarchy. Cognitive performances have been suggested to determine social success (Byrne & Whiten, 1988; Call, 2001; Cheney et al., 1986; Dunbar, 1998a; Humphrey, 1976; Seyfarth & Cheney, 2002; Taborsky & Oliveira, 2012). However, testing whether cognitive performances predict social rank at the individual level is difficult, and to date, this has not been shown through experimental manipulation (Chinchinadze et al. 2014). For cognitive or behavioural attributes, which are highly plastic, measures must be collected prior to the formation of the hierarchy to avoid the confounding possibility that the expression of the attribute is simply a result of social rank. If the ability to discriminate between spatial cues is beneficial to determining social rank in pheasants, then we expected that cognitive performance of chicks early in life, would predict their future social rank. Generally, our findings do not support this because we did not detect individual consistency in cognitive performances and furthermore, chick performances did not predict adult social rank. The lack of significance may be related to the small sample size, further testing with a greater sample size and increased statistical power is required to make more robust conclusions.

If our findings represent general patterns, we offer two explanations for the lack of a relationship between early life spatial learning performances and adult social rank. First, spatial learning ability may be subject to cognitive development (Knudsden 2004), and influenced by experience (Rowe & Healy, 2014) in the wild. Thus, learning performances assayed during early life while individuals were housed in controlled and identical conditions may not be representative of learning performances that influence a male's ability to attain/maintain a particular social rank as an adult, i.e. spatial learning performances may predict social rank but is not necessarily consistent across an individual's life. Further testing of spatial learning abilities at various life stages and at which point it predicts social rank, is required to better understand consistency (if any) in cognitive performance and the potential influence on social rank.

Second, this may suggest that spatial learning ability, specifically the ability to discriminate between two locations in a food-motivated task is a skill that is not critical or even influential in attaining a high social rank. Although high levels of aggression are associated with superior spatial learning performances in adult animals (pheasants, Langley et al. 2018a, Chapter Three; mice, Francia et al., 2006; meadow voles, Spritzer, Meikle, & Solomon, 2004; mountain chickadees, Pravosudov et al., 2003), spatial learning performances early in life may not correspond to later social interactions involved in hierarchy formation. If learning performances in the spatial domain are unrelated to learning performances in other domains, then performances in other cognition tasks may better predict an individual's future social rank. For example, social learning abilities may better inform individuals' partner choices and the outcome of social interactions (fighting fish, Oliveira et al., 1998). The lack of a relationship between early life spatial learning performances and adult social rank suggest that the relationship between these factors that we observe in the adults may be driven by the influence of aggression on spatial learning performances, rather than the reverse.

In previous studies supporting the social-state dependent hypothesis (Bunnell et al. 1980 and Bunnell & Perkins 1980; Barnard and Luo 2002 and Kaczer et al. 2007), performance on a cognitive task was observed after natural rank changes occurred and social rank was not manipulated. Our finding that variation in performance on a learning task corresponds to rank even following a rank manipulation, indicates that the relationship between social rank and cognitive performance is not necessarily driven by current social pressures. We suggest three explanations for these findings.

First, the effects of social rank on cognitive performances may persist even when the immediate social setting has changed. The effects of social defeat/success on performance on a spatial learning task in mice were found to persist, up to 13 weeks after social pressures had been removed and mice were housed individually (Fitchett et al. 2005). Pheasants' agonistic and submissive interactions in the wild may have contributed to variation in cognitive performances. If carry-over effects of past social interactions are driving inter-individual differences in learning, the time it takes for these differences in learning performance to diminish may also give an indication of how long the effects of social defeat, or success, persist (Laskowski et al. 2016; Hsu, Earley, & Wolf, 2006). Further, the relationship between cognitive performances and social rank was observed regardless of whether social ranking was scored before cognitive testing (cohort I) or afterwards (cohort II). This suggests that individuals may be consistent in their social rank experienced in the wild and in captivity. It is also important to note that the two cohorts experienced the adult social conditions for variable amounts of time due to adverse field conditions which delayed cognitive testing for males of cohort II. Consequently, cohort II males experienced the artificial dominance condition first and for 12 days longer before cognitive testing began than males of cohort I. This may have led to a difference between the cohorts in the predictive power of their inferred social rank on cognitive performances, i.e. living in the artificial dominance condition, away from the direct social pressures of competitors, may have reduced the explanatory power of social rank on cognitive performances, compared with individuals that lived in the group condition for longer. The inclusion of cohort in the model controls for this difference between the groups and this was not significant. For future work, it would be interesting to house individuals in the artificial dominance condition for different durations and assess the increases or decreases in the predictive power of social rank on cognitive performances.

Second, the relationship between social rank and spatial learning may be mediated by a third variable that we did not measure or modify. Body condition was unrelated to social rank and did not predict learning performance. However, this measure was calculated upon the birds' capture and may not be representative of their body condition during cognitive testing. Future studies may benefit from including physiological measures taken at the time of observations to examine whether these are contributing factors of performances on cognitive tasks and the outcomes of social interactions.

Third, social-rank-related variation in spatial learning performances may have been evident even while individuals were isolated from other males because the manipulation of social rank was not as successful as we believed. Although we observed increases in dominance behaviours (crowing and lateral struts) from singly housed males, the males were still in auditory communication with neighbouring males. Crowing is a behaviour performed by dominant males and may act to indicate territory ownership to conspecifics (Heinz & Gysel 1970; Ridley 1987). It is possible that male crows communicate dominance status to conspecifics and males were able to assess their relative rank through neighbouring males' crows and so maintain some form of perceived hierarchy even when housed away from direct social contact. To our knowledge, the specific information that pheasant crows communicate has not been formally tested.

Our findings offer some support that the current social environment causes individual variation in cognitive performances. Inter-individual variation in learning performance was affected by the number of females a male was housed with during cognitive testing. Males housed with four females had a higher probability of choosing correctly than males housed with only two females. The mechanisms behind this effect are unknown (see Langley et al., 2018b, Chapter Two), but this suggests that the current social environment, specifically access to more females, has direct influences on individual variation in cognitive performances.

Further indication that the social environment influences variation in cognitive performances, comes from the comparison between this study and Langley et al. (2018a, Chapter Three). Langley et al. (2018a, Chapter Three) found that higher ranking males demonstrated greater learning accuracy but did not learn at a faster rate than lower ranking males. In the current study, more dominant males learned spatial discriminations at a faster rate than lower ranking males; shown by the significant interaction between trial and social rank. The subtle differences between the two studies may be due to the differences in the social conditions experienced while cognitive performance was assayed. Langley et al. (2018a, Chapter Three) assayed cognitive performance while males were living in a social hierarchy and under direct pressures of maintaining and acquiring resources. In this study, cognitive performance was assayed while males were not experiencing direct social pressure from other males. This suggests that the rate of learning differs between males of different social rank only when males are tested away from the direct pressures of the social hierarchy. Alternatively, such differences may be due to the different tasks used. Langley et al. (2018a, Chapter Three) investigated learning performance in an escape-type task, as opposed to the food motivated learning task used in this study. Finally, differences between the two studies may have arisen because of a difference in the number of trials that were conducted; here we conducted 100 trials which gives us much stronger statistical power when determining rate of learning. To further understand the effects of social rank on spatial learning performances, repeatedly testing individuals while experiencing different social environments (social hierarchy and manipulated social rank), on cognitive tasks targeting the same cognitive domain with the same task affordances and the same number of trials, may be a fruitful approach.

4.5.1 Conclusion

Performance on a spatial discrimination task during early life does not convincingly predict performance on the same task in adulthood, nor does it predict adult social rank in male pheasants. Therefore, it is possible that the ability to discriminate between locations may be flexible across an individual's life and does not necessarily provide an advantage in acquiring a high social rank. When adult, an individual's spatial learning performance relates to their position in a social hierarchy, and this variation exists even when direct contests with other males are prevented. We also demonstrate that the number of females accompanying a male, affects the spatial learning performance of males. These two results indicate that the social environment, past and current, explains variation in spatial performances. An individual's cognitive performance is unlikely to be fixed from early life, but rather may develop over their lifespan, possibly mediated by their social interactions, and even in mature adults retain some level of plasticity depending on their immediate social conditions. It remains unclear to what extent spatial learning performance and social rank are causally linked.

Chapter Five: Individual differences in learning performances during early life on spatial and non-spatial tasks are unrelated to aggression, sex or body condition

5.1 Abstract

The relationship between behavioural attributes and individual cognitive performances can elucidate how variation in cognition may have arisen. Positive relationships between aggression and spatial learning and memory performances are reported in adult male animals. To further understand this relationship, investigation during early life (necessary to better understand causality), in females (necessary to understand behavioural and hormonal mechanisms) and further, on cognitive tasks involving non-spatial cues (necessary to understand neural or psychological mechanisms of the relationship) are required. We investigated aggression and learning performances on spatial (four-arm maze) and non-spatial (colour discrimination) learning tasks in male and female captive pheasant, *Phasianus colchicus,* chicks, during their first few weeks of life. We considered sex differences in aggression and task performances, as well as body condition. We found that the most aggressive individuals were male, but body condition was not related to aggression. Performance on both tasks improved at the population level as trials progressed, indicative of learning. However, inter-individual variation in the accuracy and rate of learning on both the spatial and non-spatial task were not related to aggression given or received, sex or body condition. In contrast to adult pheasants, in which there is a positive relationship between dominance and spatial learning performances, aggression and learning performances were not related in early life in chicks. This suggests that the relationship between aggression and cognitive performance that we observe in adult males develops later in life and may arise from experiences and individual developmental trajectories. This study highlights the importance of investigating the relationship between cognitive performances and behavioural attributes at various life stages and on different tasks if we are to

understand the causality of such relationships and factors influencing the expression of cognitive abilities.

5.2 Introduction

An understanding of how cognitive ability co-varies with behavioural attributes may indicate how individual differences in cognitive abilities may have arisen and be maintained. Aggression is a ubiquitous behavioural attribute that is associated with an individual's hormonal profile (Wingfield, Ball, Dufty, Hegner, & Ramenofsky, 1987), their access to resources (Popp & DeVore, 1979) and ultimately, their fitness (field cricket, *Gryllus assimilis*, Loranger and Bertram 2016; rhesus macaques, *Macaca mulatta,* Brent et al. 2013). Aggression may also be linked to cognitive performance. High levels of aggression (mice, radial arm maze task, Barnard and Luo 2002; Morris water maze, Francia et al. 2006; T-maze, Fitchett et al. 2005; meadow voles, *Microtus pennsylvanicus,* water maze tasks, Spritzer et al. 2004) and dominance inferred from aggressive and submissive interactions (pheasants, *Phasianus colchicus,* Langley et al. 2018a, Chapter Three Langley et al. in review, Chapter Four), have been positively related to inter-individual variation in spatial learning performances. However, these studies have focused on adult males and their learning and memory of spatial cues. This restriction of test subjects and tasks means that we cannot understand the mechanisms and causal relationships that link aggression with cognition.

The relationship between aggression and spatial learning performances may arise because early life experiences of aggression alter neural development. During early life, neural structures are highly plastic (Knudsen, 2004) and chronic stress caused by the receipt of aggression during development governs adult cognitive performances (mice, *Mus musculus,* Sterlemann et al. 2010). Aggressive interactions during early life also determine adult aggression (Laskowski, Wolf, & Bierbach, 2016). Therefore, the relationship between spatial learning performance and aggression we see in adults may be a consequence of experiences that alter a factor common to both and over time cognitive and behavioural attributes become associated. Hormone profiles may provide a second linking factor. High levels of aggression (Rosvall et al. 2012) and superior spatial learning performances (rats, *Rattus norvegicus* Spritzer et al. 2011) are both associated with elevated testosterone. However, it is not clear whether hormonal profiles change over time in conjunction with changes in aggression and cognitive abilities, or if the hormonal changes prompted by aggressive interactions cause corresponding cognitive changes. By understanding if the patterns of aggressive interactions during early life are related to cognitive performances we can reveal how the relationship between aggression and cognition develops.

Investigation into adult cognitive performances and aggression focuses on male subjects. Sexes usually vary in levels of aggression with males typically exhibiting higher levels of aggression (Bales and Carter 2003) and it is unclear if this same pattern between aggression and cognitive performances is applicable to females. If the sexes diverge in their cognitive-behavioural relationships, such that aggression and cognitive ability are not linked in females, we might assume that the linkage of aggression and cognition has arisen as a product of different sexual selection pressures. Generally, males are reported as having better spatial learning performances than females (guppy, *Poecilia reticulata*, Lucon-Xiccato 2017; Gaulin and Fitzgerald 1986; review, Jones et al. 2003), with the exception of species in which female cognition is specialized for specific ecological problems (tungara frog, *Physalaemus spp.*, Liu and Burmeister 2017; cowbirds, *Molothrus ater*, Guigueno et al. 2014). By contrast females are reported to outperform males on observational learning tasks (great tits, *Parus major,* Brodin and Urhan 2015), and reversal learning tasks (guppies, *Poecilia reticulata*, Lucon-Xiccato and Bisazza 2014, Petrazzini et al. 2017), although similar performances by males and females were found on non-spatial discrimination tasks (guppy, *Poecilia reticulata*, Lucon-Xiccato et al. 2016; mosquitofish, *Gambusia affinis,* Etheredge et al. 2017). Although the link between spatial ability and aggression is well documented in males, with more aggressive individuals also having better spatial learning ability (mice, radial arm maze task, Barnard and Luo 2002; Morris water maze, Francia et al. 2006; T-maze, Fitchett et al. 2005; pheasants, *Phasianus colchicus,* Langley et al. 2018a, Chapter Three, Langley et al. in review, Chapter Four; meadow voles, *Microtus pennsylvanicus,* water maze tasks, Spritzer et al. 2004), much less is known about these relationships in females. Further, whether sex differences in cognitive-behavioural relationships exist during development, prior to sexual maturity, is also unknown. Cognitive developmental trajectories are also related to sex, but the differences seen in adults are not mirrored in juveniles (see Thornton and Lukas 2012). A meta-analysis across species on individual differences demonstrated that in juveniles, female performances on physical cognition tasks exceeded that of males, yet in adults this pattern is reversed (Thornton and Lukas 2012). We currently know very little about how differences between the sexes in cognitive performances manifest during early life.

Investigating the relationships between aggression and cognitive performances in different test paradigms beyond the commonly studied spatial tasks, will elucidate whether the relationship between aggression and cognition is specific to spatial domains or a more general one, suggesting that learning performances in different domains are governed by general processes (Burkart et al. 2016). Few studies have considered the relationship between aggression and non-spatial cognitive domains. Less aggressive crabs, *Chasmagnathus granulatus*, retained the memory for a dangerous signal longer than more aggressive crabs (Kaczer et al., 2007). Less aggressive kittiwakes outperformed more aggressive conspecifics on a visual associative learning task (Kitaysky et al. 2003). If this negative relationship between aggression and non-spatial cognitive performance is a general pattern, then it contrasts markedly with the positive relationships seen between aggression and spatial performances. This suggests that cognitive-behavioural relationships are domain-dependent, indicating distinct relationships for some types of cognition and not others.

Relationships between aggression and cognitive performances may be moderated by body condition. Cognitive processes are energetically demanding (Ames, 2000; Reuven Dukas, 1999) and aggression may benefit individuals in contests and the acquisition of resources needed to meet these energetic requirements. In some species the receipt of aggression is more energetically costly than giving it (cichlid fish, *Tilapia zillii*, Neat et al. 1998; copperheads, *Agkistrodon contortrix*, Schuett and Grober 2000). Therefore, more aggressive individuals may have greater energy reserves obtained from increased access to resources, and individuals that receive aggression pay higher energetic costs. Consequently, more aggressive individuals may have more energy to invest in learning processes. Aggression given has been positively linked to body size (rainbowfish, *Melanotaenia duboulayi*, Colléter and Brown 2011; common waxbill, *Estrilda astrild*, Funghi et al. 2014) and body condition (Icelandic horses, *Equus caballus,* Vervaecke et al. 2007). Body condition was negatively associated with cognitive performance, indicated by the number of trials to reach criterion on a detour reach task, in the New Zealand robin, *Petroica longipes* (Shaw 2017). Conversely, body condition was not linked to colour discrimination learning performances in Zenaida doves, *Zenaida aurita* (Boogert et al. 2010). The associations between aggression, body condition and cognitive performances appear species and task dependent. Hence, investigations into these features within a single species are required.

We investigated whether cognitive performances on two learning tasks; a non-spatial learning task (colour discrimination) and a spatial learning task (four-arm maze), were related to aggression in captive reared pheasants early in life. Pheasants are precocial, can be reared in large numbers without parents and can be tested individually on psychometric tasks (Meier et al., 2017; van Horik et al., 2018, 2016). Thus, the pheasant system allows us to investigate cognitive-behavioural relationships during early life and with a large sample size. We first explored the non-cognitive features that are characteristic of individuals displaying high levels of aggression and those that receive more aggression; specifically, their sex and body condition. Male pheasant chicks are more aggressive than females (Whiteside et al. 2017). We expected that aggression given would be positively related to the body condition of the aggressor, and although there were many food sources within the pens, aggressive pheasants would have greater levels of uncontested access to food resources and consequently be in better body condition. We then investigated whether aggression given and received, sex and body condition were related to learning performances on the non-spatial and spatial cognitive tasks. We expected that if the adult relationship between aggression and spatial learning performances (Langley et al. 2018a, Chapter Three; Langley et al. in review, Chapter Four) is the consequence of experiencing or administering aggression, affecting development, then this relationship would not manifest during early life. If aggression is related to task performances during early life, this may suggest that cognitive abilities are associated with behavioural attributes via a shared mechanism (perhaps genetic or hormonal), unrelated to an individual's experience and development. If aggression is related to performances on the spatial learning task and not on the non-spatial learning task, this could suggest that the cognitive processes that underlie learning of different cue types (spatial and non-spatial), are associated with aggression via separate mechanisms. We expected that if sex differences in learning performances are subject to learning experiences and/or sexual maturation, then there would be no differences between males and females on either task because their performances were assayed before sexual maturity. We also expected that if there is a relationship between performance on either task and aggression, this may be mediated by a difference in body condition, with individuals in good body condition outperforming those in poor body condition.

5.3 Methods

5.3.1 Subjects and housing

This study was conducted from May – July 2017 at North Wyke Rothamsted Research farm (Devon, 50^{0} 77’N, 3^{0} 9’W). Two hundred and twenty-eight pheasant chicks were hatched and placed in one of four identical aviaries (57 individuals per aviary). Each aviary consisted of an indoor holding area that was heated (2m x 2m) and contained perches and saw-dust bedding. This area was separated from an unheated but sheltered outdoor run area (1m x 4m) by a guillotine partition. Adjacent to the holding area was a visually isolated testing arena (0.75m x 0.75m), divided from the holding area by a sliding entrance door and connected to the outdoor area by a lift-up exit door (Figure 5.1). At three weeks old, chicks also had access to an outdoor enclosure (4m x 12m) connected to the sheltered run, containing perches and branch shelters. Chicks were provided with age-specific chick crumb (Sportsman game feed) and water *ad libitum* throughout all areas of the aviary, except the testing arena. Chicks were marked by individually numbered patagial wing tags (Roxan Ltd, Selkirk, U.K).

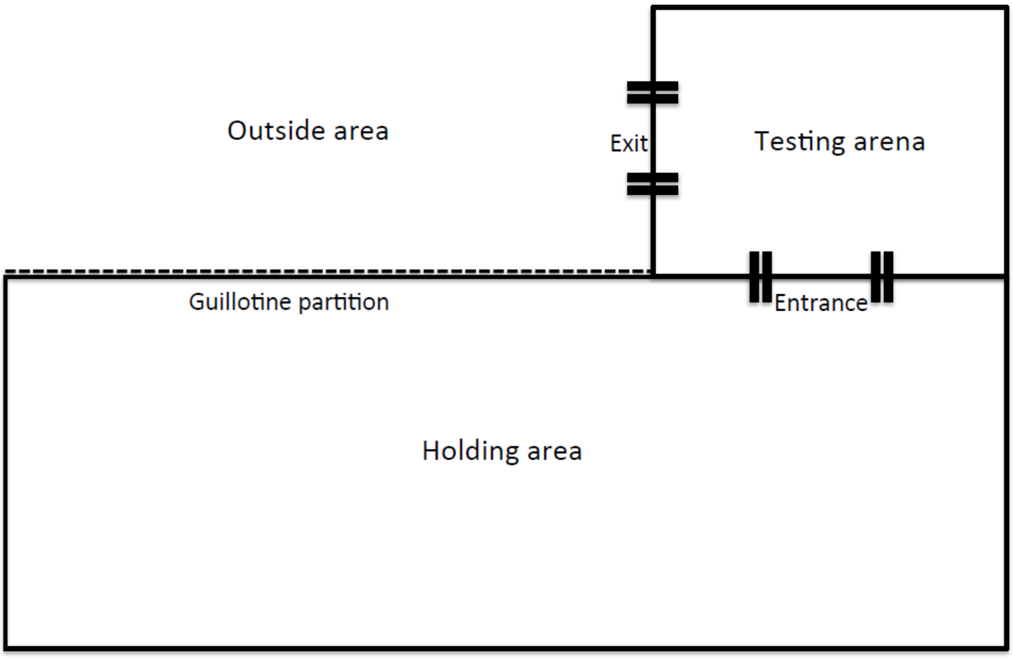

Figure 5.1: Pheasant chicks' indoor holding area (2m x 2m) and testing arena (0.75m x 0.75m).

When chicks were three weeks old, nine birds were removed from each aviary and placed into a separate 'overspill' aviary. This reduced the density of individuals within the aviaries in order to avoid high levels of aggression that may be detrimental to the welfare of the birds. The birds that we selected to be removed from the four main aviaries were those that exhibited signs of stress during cognitive training and / or did not interact with task apparatus. We aimed to assay the cognitive performances of 192 individuals (48 individuals per pen) and the two tasks described in this study had varying levels of participation.

5.3.2 Cognitive training and testing procedures

From one week old, chicks were trained to enter the testing arena upon the opening of the sliding door and hearing an auditory cue (observer humming). All chicks received equal opportunities to enter the testing arena and did so for every training and testing session. After entering the testing arena, the sliding door was closed and a chick was tested individually while an observer recorded their interactions with the task. Upon completion of the training or testing, or if individuals did not participate within 2min, or exhibited signs of stress (lost-calling, pacing, flapping), they were released into the outside area of the aviary. The chicks were tested on six different cognitive tasks: social learning, spatial memory, colour discrimination, eight arm maze, four-arm maze and an inhibitory control task, of which the colour discrimination task (non-spatial task) and four-arm maze task (spatial task) are described here. The other tasks were not considered in this study because our question focused on *individual learning* ability, rather than social learning, memory or executive function.

5.3.2.1 Non-spatial task; colour discrimination task

This task was designed to test visual discrimination abilities (non-spatial learning performances) and we deployed a task similar to those used for other avian subjects (Boogert et al., 2011; Shaw et al., 2015). The test apparatus was a rectangular box (38cm x 14cm x 4cm) that contained were two circular wells (diameter 2.8cm), 1.2cm apart, both concealed by a layer of opaque crepe paper. When nearly three weeks old, the chicks were trained to peck through the crepe paper that covered wells on the testing apparatus. Initially, we presented chicks with wells covered with broken crepe paper and over subsequent presentations, the size of the breaks in the paper were decreased until birds opened completely ‘closed’ wells spontaneously. For training and testing a mealworm food reward was presented in a central position on the apparatus, in front of the wells and this centralised chicks to the apparatus before they engaged with the task. For testing, each well was encircled by either a blue or green colour cue. Wells surrounded with blue were rewarded and contained a live mealworm (correct, S+). Wells surrounded with green were unrewarded and blocked with card that could not be pecked through (incorrect, S-). The rewarded colour was not counterbalanced across aviaries. The location of the rewarded colour was counterbalanced across trials so that it was not presented in the same position for more than three consecutive trials. During a trial, if individuals pecked at the correctly coloured well, they were allowed to consume to food reward before a new binary choice was revealed (the next trial began). If an individual pecked at the incorrect well, we removed the binary choice and revealed a new binary choice. Hence, individuals were scored as ‘correct’ (1 yes / 0 no) for each trial. Individuals were four weeks old when presented with this task. Individuals received two ten-trial sessions per day, morning and afternoon over four consecutive days, totalling 80 trials.

5.3.2.2 Spatial task; four-arm maze

The maze consisted of four arms extending from the centre of the testing chamber and at the end of each arm was a partition, behind which a food reward could be concealed (Figure 5.2). The food reward was located behind the second arm of the maze (for individuals of two aviaries the reward was located on the left and for two aviaries this was located on the right, hence reward location was counter-balanced across individuals). Four-arm maze tasks are used to assess spatial learning abilities (goats, Hosoi et al. 1995; fiftneen spined sticklebacks, *Spinachia spnachia,* Hughes and Blight 2000; mice, *Mus musculus,* Locurto et al. 2003, Galsworthy et al. 2005).

When six weeks old, the chicks were habituated to the new structure in which the testing arena contained freely available mealworms along the arms and behind the arm-partitions, this encouraged chicks to search all arms. During a testing trial, the starting platform, central to the arms of the maze held a white dish which contained a mealworm food reward. This standardised the chicks approach to the arms of the maze before beginning the task. During a testing trial, individuals were observed while exploring the arms. A chick was scored as making an error when they walked to the end of an unrewarded arm and placed their head behind the partition or moved into a position to look behind the partition. When a chick located the food reward, they were allowed to consume the food before the exit door was opened. Hence, individuals were scored as the number of errors (unrewarded arms searched) during each trial. Individuals were seven weeks old when presented with this task. Individuals received two or three single-trial sessions per day, over five days, totalling 12 trials; on the first, second and fifth day of testing, individuals received two trials per day, and on days three and four, individuals received three single-trial sessions per day. Due to unforeseen circumstances, chicks were not tested on the binary spatial discrimination task used in previous chapters.

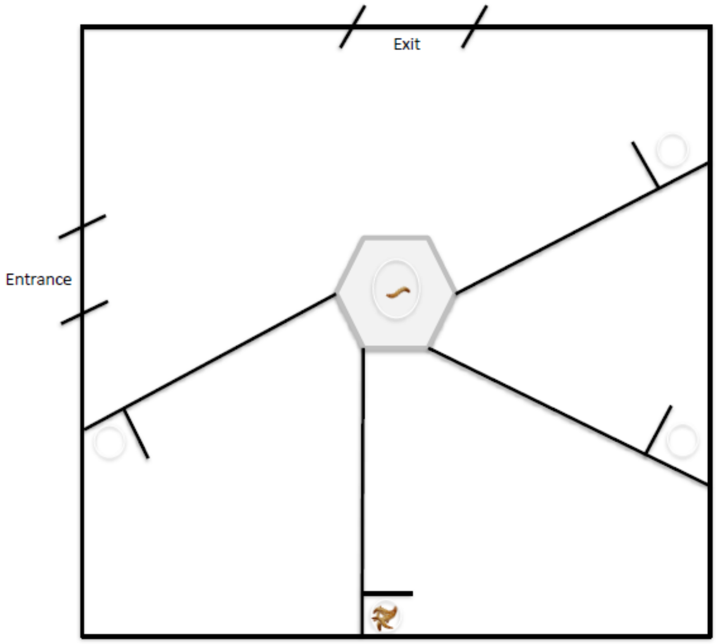

Figure 5.2: Four-arm maze task presented to pheasant chicks at seven weeks old. Grey shaded hexagon depicts starting platform (9 cm W) containing a food reward. Black lines depict walls (32 cm L, 40cm H). A single arm contained a food reward concealed behind a partition. Two aviaries received the layout depicted here, the other two aviaries received a mirror image of this layout.

5.3.3 Aggression

Aggressive interactions comprised: *aggressive pecking,* in which an initiator uses the beak to peck and pinch a feather or the skin of recipient, usually accompanied by a sharp movement toward recipient and recipient flees; *threat/lunge;* initiator adopts tall posture and lunges towards the recipient, but it does not develop into a chase, recipient avoids the initiator; or a *chase;* initiator runs towards recipient for more than 1 metre and recipient flees. When the birds were aged between four to six weeks old, we recorded aggressive interactions *ad libitum* during 30-minute observation sessions; recording the initiator, receiver and interaction type. There were 19 observation sessions of each aviary, conducted over 16 days, each lasting for 30 minutes, totalling 9.5 hours. On the first three days of observations, there were two sessions per day and on the remaining 16 days, there was a single session per day. During observations birds were restricted to a single section of the aviary so that all individuals could be viewed simultaneously; the first six sessions were conducted while birds were allowed access to the indoor aviary only and subsequently, observations were carried out while all birds within a single aviary were allowed only in the outdoor aviary. For all observation sessions, a single observer was situated in a position in which they could see the whole aviary section simultaneously. Observers were not concealed as birds were habituated to our presence for cognitive testing and concealment would have restricted the observer's view of the whole section of the aviary. For each observation session we counted the number of aggressive acts initiated and received by each individual. If an individual was not observed being aggressive or receiving aggression during an observation session, they received a score of 0. Due to the high number of 0's in the data, we summed aggression given and received per week and calculated the mean across all weeks of both given and received by dividing the total count of aggression acts given, by four (the number of weeks that the birds were observed). Therefore, each individual was assigned 'aggression given (mean per week)' and 'aggression received (mean per week)' and this was used in subsequent analyses. Due to the high number of individuals, we did not calculate social rank based on aggressive interactions as in Langley et al. (2018a, Chapter 3) and Langley et al. (in review, Chapter Four) because this would require a huge amount of data; the recommended ratio of interactions per number of individuals for a reliable estimate of social rank is 10:1 (Sánchez-Tójar et al., 2017).

5.3.4 Sex and body condition

We recorded mass (Slater Super Samson spring balance—precision 5 g) and tarsus length using callipers (precision ± 0.1mm) at 10 weeks old. Our previous study showed that mass recorded when the birds were two, four and ten weeks old were all highly correlated (van Horik et al. 2017), and therefore, we only collected mass when the birds were 10 weeks old. We calculated body condition for each individual as its residual of body mass against the cube of tarsus length (Jakob et al., 1996). Pheasants can be sexed visually from one day old (Woehler and Gates, 1970). Two individuals that were tested on the colour discrimination task died from natural causes before testing on the maze task and the final measuring day; hence they were excluded from subsequent analyses.

5.3.5 Statistical analysis

All analyses were conducted in R v3.4.3 (R Core Team, 2017).

5.3.5.1 Characteristics of aggression; physical and behavioural

We used Generalised Linear Mixed Models (GLMMs) fit with a poisson error structure and log link function to assess the characteristics of aggressive behaviour (Table 5.1). We modelled aggression given (mean per week) as a function of the aggression received (mean per week), sex and body condition (residual of body mass (g) against cube of tarsus length (cm)). We also modelled aggression received (mean per week) as a function of aggression given (mean per week), sex and body condition. Housing aviary was included as a random factor for both models. We report Wald statistics and p values from backward stepwise deletion of non-significant variables to deduce the minimum adequate model. Models were checked for normality of residuals and that homoscedasticity was not violated.

5.3.5.2 Learning performances and aggression

We conducted a Spearman's Rank Correlation between the total number of trials correct on the non-spatial task and the total number of errors made on the spatial task for all individuals. We investigated whether aggression given and received, sex and body condition explained individual performances on a colour discrimination task (non-spatial) and a four-arm maze task (spatial task) using 12 GLMMs; six models per task (Table 5.1). Performances on the non-spatial task (correct: 1 yes / 0 no) were modelled using a binomial error structure and logit link function. Performances on the spatial task (number of errors) were modelled using a poisson error structure and log link function. All GLMMs included aggression given (mean per week), aggression received (mean per week), sex and body condition (residual of body mass (g) against tarsus length (cm) ^3). All continuous variables were scaled to facilitate convergence (z-score) (Gelman & Hill, 2007) and to give model estimates of the average learning performance. The initial models for each cognitive task (non-spatial task; model 1.1 and spatial task; model 2.1), are hereby referred to as 'accuracy-models' and were used to investigate *accuracy* of task performances. We defined accuracy as how well an individual had learned the task by the end of testing; taking into account their performance on all trials (coefficient b_1). For the non-spatial task model (model 1.1), this is the average predicted probability that an individual would choose correctly, whereas for the spatial task model (model 2.1), this is the average predicted number of errors made. The accuracy-models did not contain interactions between variables. We compared random intercepts and fixed slopes model to the equivalent random intercepts and random slopes models using the *lmerTest* package (Kuznetsova et al. 2017). For the non-spatial accuracy-model (model 1.1), the random slopes and random intercepts model (trial nested within individual) showed a significantly better fit than the equivalent random intercepts and fixed slopes model ($X^2 = 32.089$, $df = 1$, $p < 0.001$). Hence, we used a random intercepts and random slopes model for non-spatial task models to maintain consistency within the GLMMs for the same task. The random intercepts and random slopes accuracy model for the spatial task (model 2.1) was not a better fit ($X^2 = 5.711$, $df = 1$, $p = 0.058$). Hence, we used random intercepts and fixed slopes models for all spatial task models to maintain consistency within tasks. All models also contained housing pen as a random intercept. To investigate whether individuals of certain characteristics (aggression given and received, sex and body condition), differed in their 'rate' of learning, defined as the speed at which individuals switch from making a series of incorrect choices to a series of correct choices (steepness of the learning slope), we fitted four subsequent models for each task, identical to accuracy-model of the same task but which differed in a single two-way interaction between trial and one of the four other variables (aggression given, aggression received, sex and body condition). These models are referred to as the 'rate-models'. We did not include all two-way interactions between each variable with trial in the same model because the model was too complex and failed to converge. The final model per task, included a three-way interaction between trial, aggression given and sex to investigate whether there was a sex-specific relationship between aggression and rate of learning. For all models we determined which variables were significantly related to task performance by using backward stepwise deletion of non-significant terms; deduced using the drop1 function in the R base package. For accuracy-models we also report the full model summaries. For rate-models we only report the test statistics for the removal of the interaction term because subsequent removal of the remaining variables will be identical to that of accuracy models. We checked that there were no patterns in the data by plotting the residuals against each variable. We checked for collinearity between continuous explanatory variables using the *usdm* package (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) to calculate Variance Inflation Factors (VIFs). VIFs >3 are a cause for concern as they increase type II errors, however VIFs were ~1 for each variable. Using the *MUMIn* package (Barton 2018), we calculated the conditional r-squared (R^2c); the proportion of variance in the response variable that is explained by the explanatory and random variables (Nakagawa and Schielzeth 2012), for all models. The non-spatial task models (binomial models) were fitted using performances from 189 individuals; 184 individuals completed all 80 colour discrimination trials but three of these individuals had a missing value for a single trial due to human error; one individual completed 75 trials, one individual completed 74 trials, one individual completed 70 trials, one individual completed 69 trials, and three individuals completed <14 trials. The spatial task models (poisson models) were fitted on performances from 190 individuals; 174 individuals completed all 12 trials, nine individuals completed 11 trials, 3 individuals completed 10 trials, two individuals completed nine trials, one individual completed eight trials and one individual completed seven trials. One individual refused to enter the testing chamber and did not complete any trials and two of the deceased individuals (mentioned above) died before the maze task was conducted.

Table 5.1: Model information for GLMMs investigating behavioural and physical attributes in relation to aggression and cognitive performances of pheasant chicks

Model	Question	Response	Explanatory variables	Random	Error
Characteristics of aggression					
0.1	What behavioural or physical attributes relate to aggression given?	Aggression given (mean per week)	Aggression received + Sex + Body condition	1|Aviary	Poisson
0.2	What behavioural or physical attributes relate to aggression received?	Aggression received (mean per week)	Aggression given + Sex + Body condition	1|Aviary	Poisson
Non-spatial task					
1.1 (Accuracy)	Does aggression, sex or body condition relate to accuracy of learning?	Correct (1 yes / 0 no)	Trial + Aggression given + Aggression received + Sex + Body condition	Trial|individual 1|Aviary	Binomial
1.2 (Rate)	Does aggression given relate to learning rate?	Correct (1 yes / 0 no)	Trial * Aggression given + Aggression received + Sex + Body condition	Trial|individual 1|Aviary	Binomial
1.3 (Rate)	Does aggression received relate to learning rate?	Correct (1 yes / 0 no)	Trial * Aggression received + Aggression given + Sex + Body condition	Trial|individual 1|Aviary	Binomial
1.4 (Rate)	Do the sexes differ in their learning rate?	Correct (1 yes / 0 no)	Trial * Sex + Aggression given + Aggression received + Body condition	Trial|individual 1|Aviary	Binomial
1.5 (Rate)	Does body condition relate to learning rate?	Correct (1 yes / 0 no)	Trial * Body condition + Aggression given + Aggression Received + Sex	Trial|individual 1|Aviary	Binomial
1.6 (Rate)	Is the relationship between aggression and learning sex-specific?	Correct (1 yes / 0 no)	Trial*Aggression given * Sex + Aggression Received + Body condition	Trial|individual 1|Aviary	Binomial
Spatial task					
2.1 (Accuracy)	Does aggression, sex or body condition relate to accuracy of learning?	Number of errors	Trial + Aggression given + Aggression received + Sex + Body condition	1|Individual 1|Aviary	Poisson
2.2 (Rate)	Does aggression given relate to learning rate?	Number of errors	Trial * Aggression given + Aggression received + Sex + Body condition	1|Individual 1|Aviary	Poisson
2.3 (Rate)	Does aggression received relate to learning rate?	Number of errors	Trial * Aggression received + Aggression given + Sex + Body condition	1|Individual 1|Aviary	Poisson
2.4 (Rate)	Do the sexes differ in their learning rate?	Number of errors	Trial * Sex + Aggression given + Aggression received + Body condition	1|Individual 1|Aviary	Poisson
2.5 (Rate)	Does body condition relate to learning rate?	Number of errors	Trial * Body condition + Aggression given + Aggression Received + Sex	1|Individual 1|Aviary	Poisson
2.6 (Rate)	Is the relationship between aggression and learning sex-specific?	Number of errors	Trial * Aggression given * Sex + Aggression Received + Body condition	1|Individual 1|Aviary	Poisson

5.3.6 Ethical considerations

Chicks were habituated to human observation and were checked for any signs of stress or discomfort during and outside of cognitive testing. If chicks appeared stressed or in discomfort, we moved them to a smaller holding aviary with a lower density of birds to be closely monitored. Chicks were not subject to handling, unless absolutely necessary and on the final measuring day. Any handling was done quickly and efficiently to mitigate stress. All training procedures were adopted to mitigate stress during cognitive testing and birds could choose whether or not to participate in tasks. The birds were reared at a lower density than that recommended by DEFRA's code of practice (DEFRA, 2009), thus reducing stress. All work was approved by the University of Exeter Psychology Ethics Committee and the work was conducted under Home Office licence number PPL 30/3204 to JRM.

5.4 Results

5.4.1 Aggression and physical and behavioural attributes

The mean number of observed aggressive acts given ranged from 0 – 5 acts per week. One hundred and eight individuals were recorded as being aggressive at least once, compared to 84 individuals that were never observed being aggressive. Sex significantly predicted the amount of aggression given (GLMM, model 0.1, Sex: $X^2 = 13.089$, $df = 1$, $p < 0.001$, Table 5.2), with males being 80% more aggressive than females (Figure 5.3). Neither levels of aggression received (GLMM, model 0.1, aggression received: $X^2 = 2.273$, $df = 1$, $p = 0.132$, Table 5.2), nor body condition (GLMM, model 0.1, body condition: $X^2 = 0.595$, $df = 1$, $p = 0.440$, Table 5.2) were significantly related to aggression given.

One hundred and forty-one individuals received aggression at least once. Sex (GLMM, model 0.2, sex: $X^2 = 0.006$, $df = 1$, $p = 0.939$, Table 5.3), body condition (GLMM, model 0.2, body condition: $X^2 = 1.100$, $df = 1$, $p = 0.294$, Table 5.3), and aggression given were not related to aggression received (GLMM, model 0.2, aggression given: $X^2 = 1.306$, $df = 1$, $p = 0.253$, Table 5.3).

Table 5.2: Full model summary of model 0.1; what behavioural or physical attributes relate to aggression given in pheasant chicks? Aggression given (mean per week) is modelled as a function of the amount of aggression received (mean per week), sex and body condition. Random intercepts model fit with a poisson error structure and log link function. We report the estimate (b_1) and standard error for each variable with the exponential of the estimate ($Exp(b_1)$), which indicates how much aggression given changes in response to each explanatory variable, with low (lo CI) and high (Hi CI) 95% confidence intervals.

	Estimate	**SE**	**Exp(b1)**	**Lo CI**	**Hi CI**
Explanatory variable					
Intercept	-1.295	0.208			
Aggression received (mean per week)	0.150	0.105	1.162	-0.057	0.357
Sex (male)	0.800	0.240	2.226	0.327	1.270
Body condition	0.080	0.103	1.083	-0.123	0.283

R^2_c = 0.107

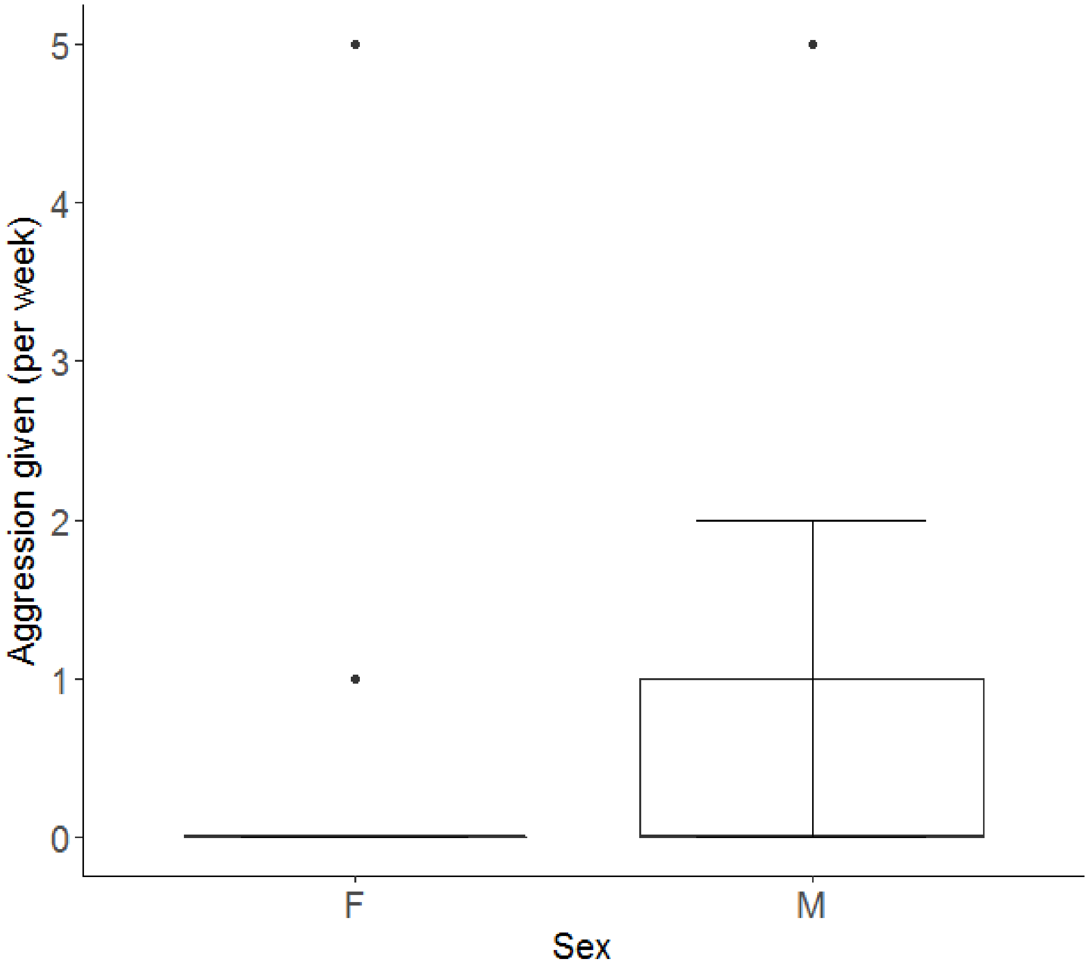

Figure 5.3: Sex differences in the amount of aggression given (mean per week) for male and female pheasant chicks. The black horizontal line represents the median value. Whiskers represent the lower and upper quartiles (25% and 75%).

Table 5.3: Full model summary of model 0.1; what behavioural or physical attributes relate to aggression received in pheasant chicks? Aggression received (mean per week) is modelled as a function of aggression given (mean per week), sex and body condition. Random intercepts model fit with a poisson error structure and log link function. We report the estimate (b_1) and standard error, with the exponential of the estimate ($Exp(b_1)$), which indicates how much aggression received changes in response to each explanatory variable, with low (lo CI) and high (Hi CI) 95% confidence intervals.

	Estimate	**SE**	**Exp(b1)**	**Lo CI**	**Hi CI**
Explanatory variable					
Intercept	-0.027	0.111			
Aggression given (mean per week)	0.075	0.069	1.078	-0.061	0.211
Sex (male)	-0.012	0.153	0.988	-0.314	0.288
Body condition	0.078	0.074	1.081	-0.068	0.224

$R^2_c = 0.017$

5.4.2 Cognitive performances

There was a weak negative relationship between performances on the non-spatial and spatial learning tasks, indicating that there was a trend for individuals that made more correct choices on the colour discrimination task to make fewer errors on the maze task, but this was not significant (Spearman's Rank Correlation, *r* = - 0.111, *n* = 189, *p* = 0.128; Figure 5.4).

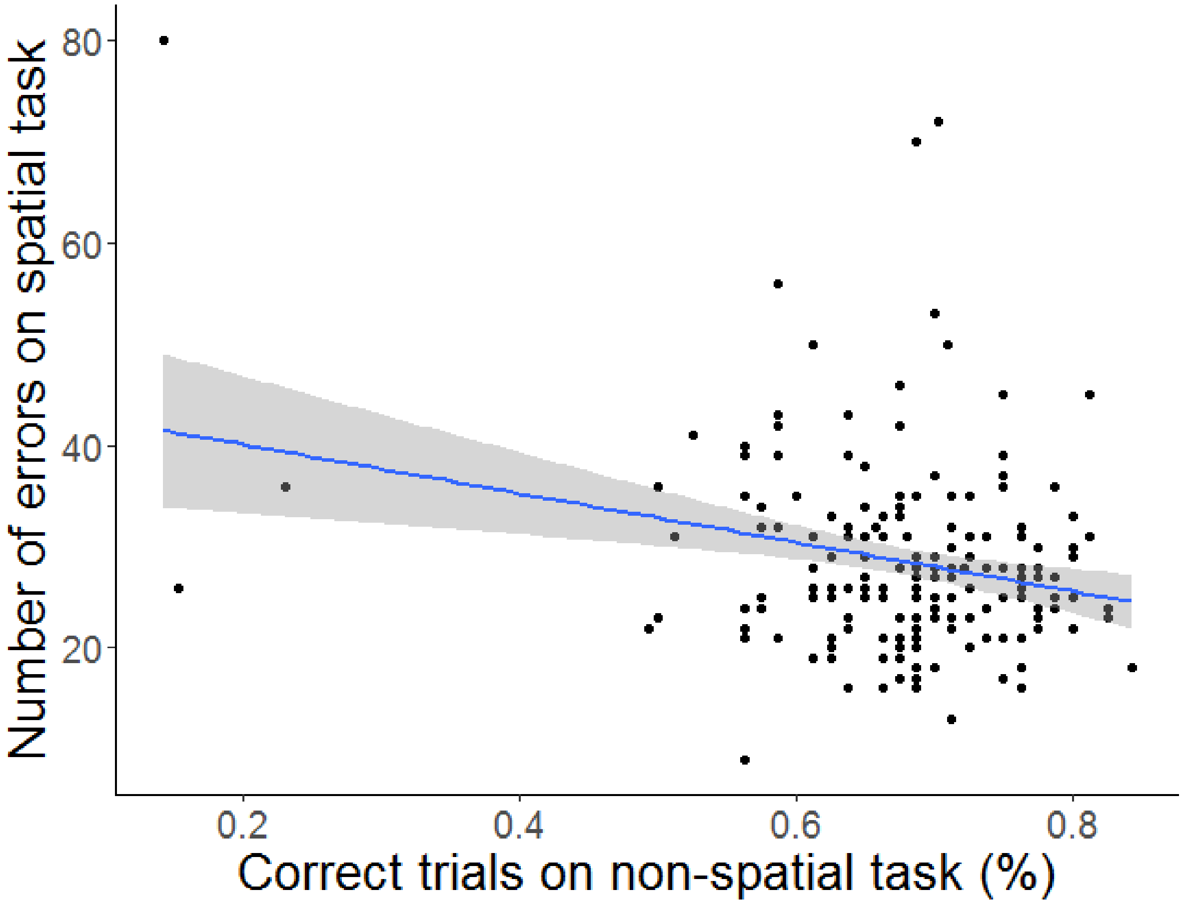

Figure 5.4: Relationship between performances on the non-spatial learning task (proportion of total trials correct on the colour discrimination task) and the spatial learning task (total number of errors on the four-arm maze task). Line of best fit drawn from GLM on learning performances of 189 chicks. Grey shading represents 95% Confidence Interval.

5.4.2.1 Non-spatial task performances

During the first 10 trials of the colour discrimination task the mean percentage of correct choices made was 46 ± 0.012 (mean ± se). This increased to 80 ± 0.010 mean percentage of correct choices for the final 10 trials. Hence, trial was a significant main effect in the accuracy model, indicative of learning (GLMM, model 1.1, trial: X^2 = 265.880, *df* = 1, p < 0.001, Table 5.4, Figure 5.5). Aggression given was negatively related to accuracy of learning performance, suggesting that more aggressive individuals were less likely to choose correctly, however this relationship was not significant (GLMM, model 1.1, aggression given (mean per week): X^2 = 1.386, *df* = 1, *p* = 0.239, Table 5.4, Figure 5.6) and neither was the relationship between aggression given and learning rate (GLMM, model 1.2, trial * mean aggression per week: X^2 = 0.481 *df* = 1, *p* = 0.488). Aggression received was positively related to accuracy of learning performance, indicating that individuals that received more aggression were more likely to choose correctly, however this was not significant (GLMM, model 1.1, aggression received (mean per week): X^2 = 1.380, *df* = 1, *p* = 0.240, Table 5.4, Figure 5.7) and neither was the relationship between aggression received and learning rate (GLMM, model 1.3, aggression received (mean per week): X^2 = 1.061, *df* = 1, *p* = 0.303). The sexes did not differ in their learning accuracy (GLMM, model 1.1, Sex: X^2 = 0.165, *df* = 1, *p* = 0.685, Table 5.4), nor did they differ in their learning rate (GLMM, model 1.4, Trial * Sex: X^2 = 0.411, *df* = 1, *p* = 0.521). Body condition was not related to learning accuracy (GLMM, model 1, Body condition: X^2 = 0.0.42, *df* = 1, p = 0.838, Table 5.4), or learning rate (GLMM, model 1.5, Trial * Body condition: X^2 = 1.283, *df* = 1, *p* = 0.257).

Table 5.4: Full model summary of model 1.1; does aggression, sex or body condition relate to accuracy of learning on a colour discrimination task by pheasant chicks? Learning performance (Correct: 1 yes / 0 no) was modelled as a function of trial number, aggression given (mean per week), aggression received (mean per week), sex and body condition as explanatory variables. Random intercepts and random slopes model. Model was fit with a binomial error structure and logit link function. We report the model estimate (b_1) and standard error, with the odds ratio (OR) indicating how much the odds of a correct choice increase with each explanatory variable and low (lo CI) and high (Hi CI) 95% confidence intervals.

	Estimate	**SE**	**OR**	**Lo CI**	**Hi CI**
Explanatory variable					
Intercept	0.828	0.052			
Trial	0.586	0.025	1.797	0.537	0.635
Aggression given (per week)	-0.033	0.026	0.967	-0.084	0.011
Aggression received (per week)	0.033	0.026	1.034	-0.018	0.084
Sex (male)	0.021	0.053	1.021	-0.084	0.126
Body condition	0.005	0.026	1.005	-0.046	0.056

R^2c = 0.122

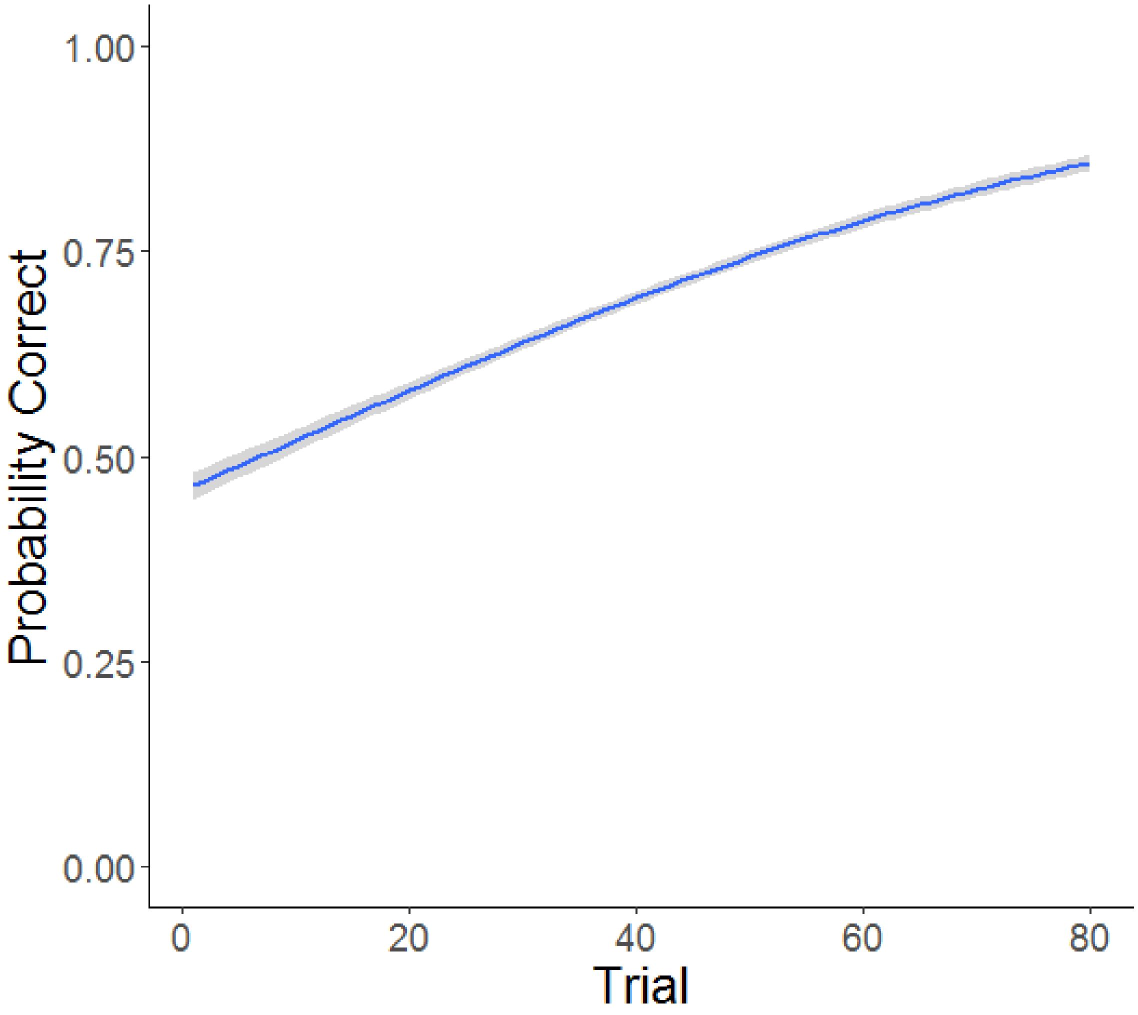

Figure 5.5: The increasing probability of choosing correctly on a colour discrimination task of pheasant chicks as trial number increases. Curve drawn from binomial GLM on learning performances of 189 chicks. Grey shading represents 95% Confidence Interval.

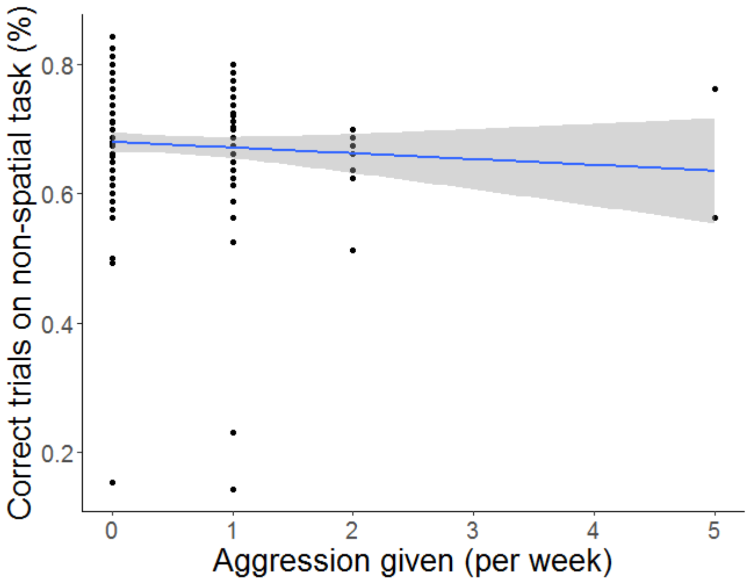

Figure 5.6: The relationship between the proportion of correct trials on the non-spatial task (colour discrimination) and aggression given per week by 189 pheasant chicks. Grey shading represents 95% confidence interval.

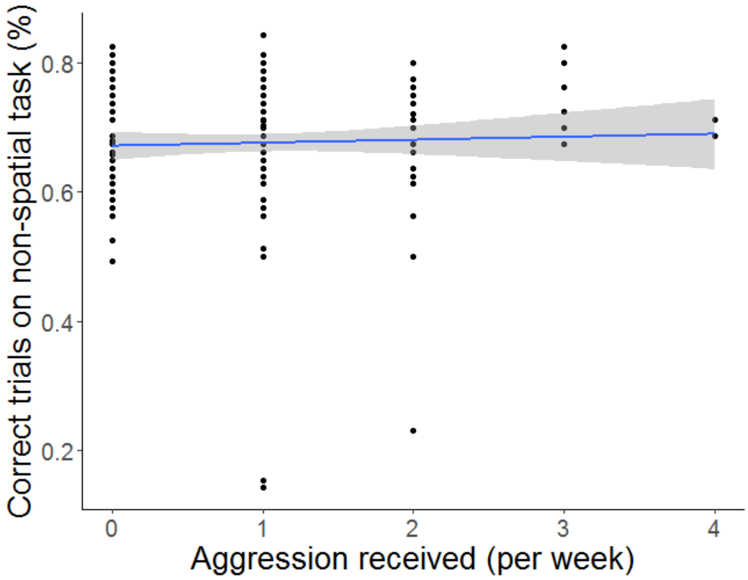

Figure 5.7: The relationship between the proportion of correct trials on the non-spatial task (colour discrimination) and aggression received per week by 189 pheasant chicks. Grey shading represents 95% confidence interval.

5.4.2.2 Spatial task performances

On the first trial, the mean number of errors made on the four-arm maze task was 3.176 ± 0.192 (mean ± se). This decreased to 1.829 ± 0.069 (mean ± se) mean number of errors for the final trial. Trial was a significant main effect in the accuracy model (GLMM, model 2.1, trial: $X^2 = 157.560$, $df = 1$, $p < 0.001$, Table 5.5; Figure 5.8), indicative of learning. Aggression given was positively related to accuracy of learning performance, suggesting that more aggressive individuals made more errors, however this was not significant (GLMM, model 2.1, aggression given (mean per week): $X^2 = 0.042$, $df = 1$, $p = 0.838$, Table 5.5, Figure 5.9) and neither was the relationship between aggression given and learning rate (GLMM, model 2.2, trial * aggression given (mean per week): $X^2 = 0.166$ $df = 1$, $p = 0.684$). Aggression received was negatively related to accuracy of learning performance, suggesting that individuals that received more aggression also made fewer errors, however, this was not significant (GLMM, model 2.1, aggression received (mean per week): $X^2 = 0.135$, $df = 1$, $p = 0.714$, Table 5.5, Figure 5.10) and neither was the relationship between aggression received and learning rate (GLMM, model 2.3, trial * aggression received (mean per week): $X^2 = 1.162$ $df = 1$, $p = 0.281$). The sexes did not differ in their learning accuracy (GLMM, model 2.1, Sex: $X^2 = 0.281$, $df = 1$, $p = 0.596$, Table 5.5), nor did they differ in their learning rate (GLMM, model 2.4, trial * sex: $X^2 = 1.018$, df = 1, p = 0.313). Body condition was not related to learning accuracy (GLMM, model 2.1, body condition: $X^2 = 0.011$, df = 1, p = 0.916, Table 5.5), or learning rate (GLMM, model 2.5, trial * body condition: $X^2 = 0.984$, $df = 1$, $p = 0.321$).

Table 5.5: Full model summary of model 2.1; does aggression, sex or body condition or relate to accuracy of learning on a four-arm maze task by pheasant chicks? The number of errors made during a trial were modelled as a function of trial number, aggression given (mean per week), aggression received (mean per week), sex, body condition and (mean test order). Individual and housing aviary were fit as random intercepts. The model was fit with a poisson error structure and log link function. We report the model estimate (b_1) and standard error, with the exponential of the estimate (Exp(b_1)) which indicates how much the count of errors change in response to each explanatory variable, with low (lo CI) and high (Hi CI) 95% confidence intervals.

	Estimate	**SE**	**Exp(b1)**	**Lo CI**	**Hi CI**
Explanatory variable					
Intercept	0.824	0.084			
Trial	-0.172	0.014	0.842	-0.200	-0.144
Aggression given (per week)	0.003	0.016	1.003	-0.029	0.035
Aggression received (per week)	-0.006	0.016	0.994	-0.038	0.026
Sex (male)	0.015	0.032	1.015	-0.048	1.081
Body condition	-0.002	0.016	0.998	-0.034	0.029

R^2c = 0.139

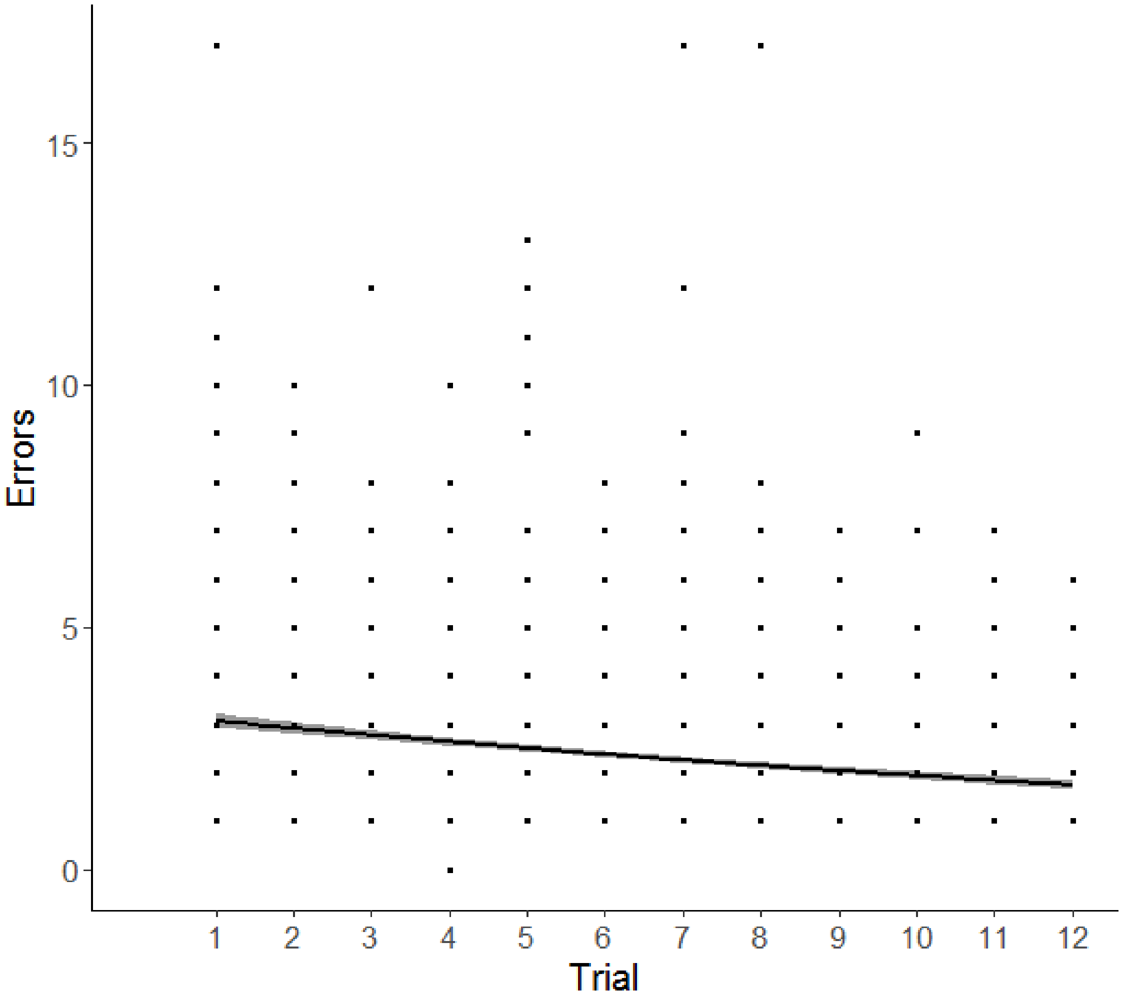

Figure 5.8: The decreasing number of errors made on a four-arm maze task by 190 pheasant chicks as trial number increased. Curve drawn from a generalised linear model fit with a poisson error distribution. Grey shaded area represents 95% Confidence interval.

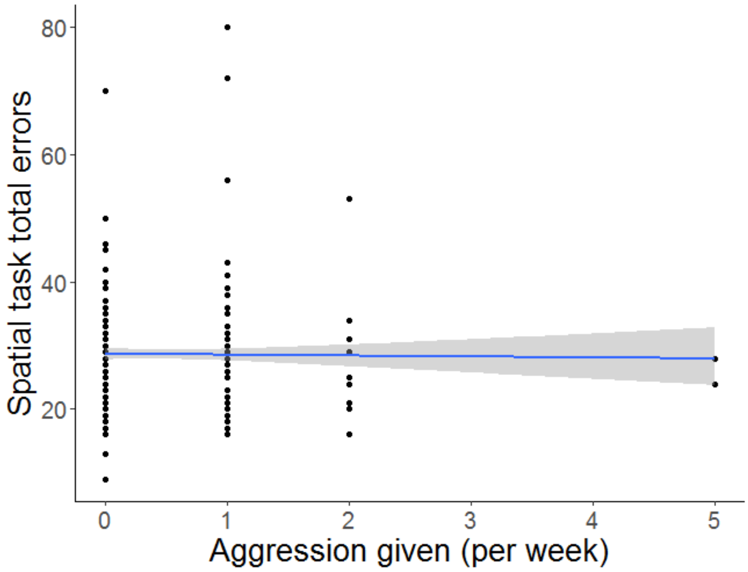

Figure 5.9: The relationship between the total number of errors made on the spatial task (four-arm maze) and aggression given per week by 189 pheasant chicks. Grey shading represents 95% confidence interval.

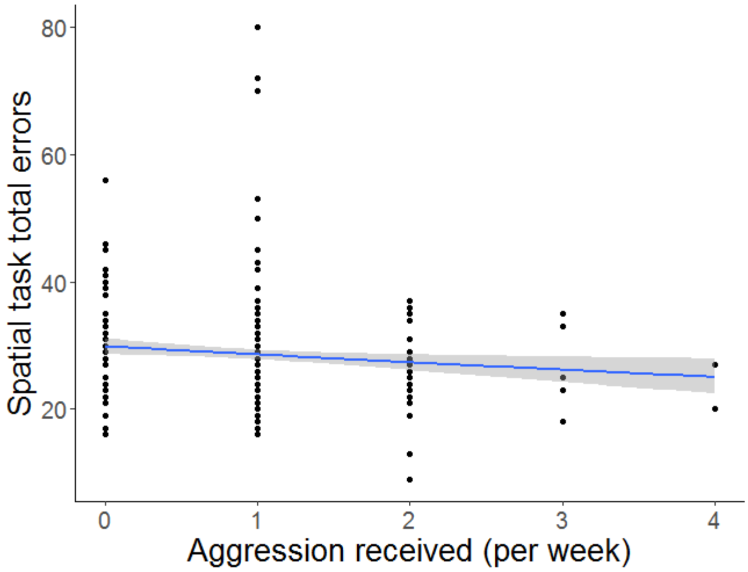

Figure 5.10: The relationship between the total number of errors made on the spatial task (four-arm maze) and aggression received per week by 189 pheasant chicks. Grey shading represents 95% confidence interval.

5.5 Discussion

Pheasant chick performances on both spatial and non-spatial learning tasks improved with trial number, indicative of learning at the population level. These learning performances were weakly but not significantly related, suggesting that individuals that performed well on the non-spatial learning task were not more likely to perform well on the spatial learning task. Male pheasant chicks were more aggressive but neither sex nor aggression given were related to performances on either the spatial or the non-spatial task. Males and females of different body condition were equally likely to receive aggression and aggression received was not related to performances on either task. Finally, body condition was not related to aggression given or received and did not relate to performances on either task. These findings highlight that the positive associations between spatial learning performances and aggression in males, and task-dependent sex differences in cognitive performances that we observe in adult pheasants and widely across species, may not be present in early life and thus are the consequence of cognitive development prompted by other experiences or conditions later in life.

Although the relationships between aggression given and learning performances of the pheasant chicks were not significant, the directions of these relationships are of interest. Aggressive individuals performed more poorly on both the spatial tasks and non-spatial tasks. Similarly, in kittiwake chicks, aggressive individuals were less successful on a visual discrimination task (Kitaysky et al., 2003). Pheasants that received the most aggression were slightly more successful on both the spatial and non-spatial task, although this relationship was not significant. These patterns contrast with relationships we observe in adult males of pheasant and other species. Aggression given is positively related to spatial learning performances (mice, Barnard and Luo 2002; Francia et al. 2006; T-maze, Fitchett et al. 2005; meadow voles, *Microtus pennsylvanicus,* Spritzer et al. 2004). In pheasants, more dominant individuals have superior learning performances compared to more subordinate individuals (Langley et al. 2018a, Chapter Three; Langley et al. in review, Chapter Four) and more dominant individuals are also more aggressive (unpublished data). This suggests that the relationship between being aggressive and superior learning performance develops over an individual's life, perhaps subject to spatial learning experiences in the wild and, or further aggressive interactions.

The differences between young and adult pheasants in their cognitive-behavioural relationships, may be due to the difference in the definitions of aggression that were used relevant to each age group. In the adults, the relationship between dominance and learning performance was investigated. Adult dominance was inferred from aggressive and submissive interactions. Here, submissive interactions are ambiguous with the density of chicks, hence we investigated aggressive behaviour only in relation to learning performances. Being aggressive and receiving submissive behaviour is highly correlated in adult pheasants (unpublished data), therefore we are confident that aggression during early life is comparable to dominance in adulthood.

The differences between young and adult pheasants in their cognitive-behavioural relationships could also be due to the differences in spatial tasks that were deployed. Adult pheasants were presented with an escape type task (Langley et al. 2018a, Chapter Three) and a foraging grid (Langley et al. in review, Chapter Four), in which both tasks required individuals to discriminate between two locations. Whereas here, the chicks were presented with a four-arm maze task that required them to navigate and find a reward in one of four arms. Although, all tasks presented to adults and chicks aimed to assess the ability to learn spatial locations, and performances on similar tasks to the two that we describe have been associated with activity in the avian hippocampus (foraging grid, Pravosudov et al. 2005; maze, Colombo et al. 1997), it is possible that the difference in the number of cues (2 versus 4) may be related to aggression differently. For instance, spatial learning and memory performances do not always correspond. More aggressive male meadow voles have better spatial learning ability but there were no differences between males in their spatial memory performances (Spritzer et al., 2004). Hence, if the four-arm maze task requires a greater working memory capacity than the binary grid task, this may cause a decoupling between the cognitive-behavioural relationship due to a third cognitive mechanism.

Males were more aggressive than females during early life, however, neither sex, nor aggression given was related to variation in learning performances on either task. The directions of the relationships suggest that males were slightly better on both the spatial and non-spatial task but these differences were not significant. This pattern contrasts with what we see in juvenile animals of other species, with females outperforming males on physical cognition tasks (reviewed in Thornton and Lukas 2012). In adults, males of polygynous species are commonly reported as outperforming females on spatial learning tasks (Gaulin & Fitzgerald, 1986; Jones et al., 2003; Tyrone Lucon-Xiccato & Bisazza, 2017), but not on non-spatial performances (Brodin & Utku Urhan, 2014; Etheredge et al., 2017; Lucon-Xiccato & Bisazza, 2014; Tyrone Lucon-Xiccato, Dadda, & Bisazza, 2016; Miletto Petrazzini, Bisazza, Agrillo, & Lucon-Xiccato, 2017). If there are sex differences in cognitive performances of adult pheasants then it would suggest that sex-specific cognitive performances emerge as individuals' age/develop. However, this remains to be tested.

We predicted that the more aggressive individuals would be in better body condition as they monopolised food resources more efficiently via aggressive interactions and this improved body condition would facilitate learning due to sufficient energy reserves (Ames, 2000; Reuven Dukas, 1999). Although the relationship was positive it was non-significant. Body condition was not related to aggression given or received and body condition was not related to variation in learning performances. Although our measure of body condition is commonly used in birds (Jakob et al., 1996), it may not successfully capture variation in nutrient reserves that are allocated to neural processes involved in cognitive functions. Alternatively, it may take time for differences in the acquisition of resources to influence cognition.

5.5.1 Conclusion

In summary, male pheasant chicks were more aggressive than females, but the young of both sexes did not differ in their learning performance on a spatial and non-spatial cognitive task. Therefore, the relationships between spatial learning performance and aggression that we have observed in pheasants and are reported more generally, as well as the sex differences in adult cognitive performances reported across species, are likely the consequence of experience and the developmental trajectory that an individual undergoes.

Chapter Six: Disassortative mixing by cognitive performances in wild pheasants

6.1 Abstract

The fine-scale social structure of a population has potential implications for evolutionary processes. Social structure is commonly associated with variation in cognitive abilities across species and both individual social relationships and social structure have fitness implications for individuals. Whether individual variation in cognitive abilities influences social structure is unknown. We assayed the general cognitive abilities of 155 pheasant, *Phasianus colchicus,* chicks on an inhibitory control and a visual discrimination learning task. We released these individuals into the wild and observed their associations at feeding stations, constructing monthly mixed-sex networks and single-sex networks, over five months. For each network we calculated weighted assortativity coefficients for each cognitive performance measure to determine whether individuals assort or disassort by cognitive ability. We also examined network centrality in relation to each cognitive performance measure. We found that performances on the inhibitory control and visual discrimination task were unrelated and females outperformed males on the inhibitory control task. We observed disassortative mixing by inhibitory control performances, suggesting that individuals with poor performance on the task had stronger associations with individuals that were more successful on the task and this was evident in mixed-sex and female-only networks. Disassortative mixing by visual discrimination performance was evident in all networks (mixed-sex, female and male networks). Superior inhibitory control performances predicted high network centrality in mixed-sex and female-only networks, whereas, individuals with greater success on the visual discrimination task were less central in mixed-sex and female-only networks. Hence, social structure was influenced by individual variation in cognitive abilities. We propose that this structure may reflect differences between individuals in their foraging strategy based on

cognitive abilities and such social structure may have implications for the outcome of selection on traits governing cognitive abilities.

6.2 Introduction

Social structure is defined as the content, type and quality of relationships between dyads within a population (Hinde 1976). Social structure influences an individual's access to information (great tits, *Parus major,* Aplin, Farine, Morand-Ferron, & Sheldon, 2012; black-capped chickadees, *Poecile atricapillus*, Jones, Aplin, Devost, & Morand-Ferron, 2017), novel problem solving abilities (great tits, Aplin et al., 2014; ravens, *Corus corax*, Kulahci et al., 2016), likelihood of contracting disease (Tasmanian devils, *Sarcophilus harrisi*, Hamede, Bashford, McCallum, & Jones, 2009) and ultimately may have consequences for the evolution of behavioural traits (Croft, Krause, & Darden, 2009a). Hence, factors that influence social structure are of key importance to an individual's fitness.

Social structures are influenced by individual variation in physical, behavioural and relational attributes (Newman, 2003), with individuals preferring to associate with or avoid others based on such attributes. This results in non-random assortative mixing based on kinship (meerkat, *Suricata suricatta,* Madden, Nielsen, & Clutton-Brock, 2012), age (baboon, *Papio ursinus*, Carter et al. 2015), sex (Tasmanian devil, *Sarcophilus harrisii*, Hamede et al. 2009; pheasants, *Phasianus colchicus,* Whiteside et al. 2018), body size (chub, Krause 1994; golden shiner *Notemigonus crysoleucas*, and banded killifish *Fundulus diaphanous*, Krause et al. 1996; Hoare et al. 2000) and consistent behavioural traits (female Trinidadian guppies, *Peocilia reticulate*, Croft et al. 2009; male great tits, *Parus major,* Aplin et al. 2013; baboons, Carter et al. 2015; chimpanzees, *Pan paniscus,* Massen and Koski 2014). Assortment may occur through active or passive processes. For instance, individuals that are behaviourally similar may passively interact or associate more often than by chance due to preferences for the same habitat (pumpkinseed sunfish, *Lepomis gibbosus*, Wilson et al. 1993). Conversely, individuals may assort through active processes and seek out individuals of similar phenotypes. For example, females may preferentially associate with the same sex and, or, actively avoid the opposite sex to avoid costs of male aggression (Japanese quail, *Coturnix japonica*, Ophir and Galef 2003). Assorting by age may promote useful behaviour, such as play in young or juvenile animals (Bekoff & Byers, 2011). These predictable assortative social structures have positive fitness implications (Cameron, Setsaas, & Linklater, 2009; Croft, Krause, & Darden, 2009b; Frère et al., 2010; Fu, Nowak, Christakis, & Fowler, 2012). For example, associating with individuals of similar size reduces predation risk (Krause, 1994), and increases foraging efficiency (Krause 1994; Utne-Palm and Hart 2000). Associating with individuals of similar behavioural type facilitates cooperation (guppies, Croft et al. 2006) and behavioural synchronisation (zebra finches, *Taeniopygia guttata*, Schuett et al. 2011). Associating with individuals of different behavioural type can also be beneficial. For example, in populations of foraging individuals, those with a tendency to scrounge resources, only benefit if they preferentially associate with producers (Barnard & Sibly, 1981; Caraco & Giraldea, 1991; Vickery et al., 1991), and stable and consistent frequencies of producers and scroungers were seen in a wild population of great tits, *parus major* (Aplin & Morand-Ferron, 2017). Little work has considered how individuals may disassort by cognitive abilities (but see studies of human mate choice based on general intelligence e.g. Phillips et al. 1988; Rushton & Nicholson 1988), and thus how cognitive abilities may structure social networks.

Cognitive abilities describe the mechanisms by which animals perceive, process, store and respond to sensory information in the environment (Shettleworth, 2010) and cognitive abilities and the social environment are inextricably linked (Byrne & Whiten, 1988; Dunbar, 2003; Humphrey, 1976; Seyfarth & Cheney, 2002). Cognitive abilities cannot be measured directly but manifest in behaviour. We consider two broad and common cognitive domains that may influence social relationships and the resulting social structure. First, we consider inhibitory control: the ability to inhibit prepotent responses in favour of more beneficial behaviour. This ability is deemed critical in changing social environments (Amici et al., 2008) whereby one cost of group living is increased competition for resources (Krause & Ruxton, 2002). Individuals able to inhibit aggression and, or food theft, may be more attractive social partners. In pigtail macaques, individuals that performed well on a reversal learning task, suggesting that they had good inhibitory control, were low ranking, less aggressive individuals (Strayer 1976). However, it is not clear that low levels of aggression lead to more social connections. In carrion crows, *Corvus corone,* individuals that displayed good inhibitory control were actually more aggressive, but had a higher rate of affiliative and agonistic interactions (Wascher, 2015). Hence, superior inhibitory control abilities are related to a greater number of connections, but it is unclear how this may influence overall social network structure.

Second, we consider variation in individual learning ability. Individual's with superior learning abilities may be better at learning and remembering favourable or unfavourable social partners (spotted hyena, *Crocuta crocuta*, Drea & Carter, 2009), profitable food patches (bumble-bees, *Bombus terrestris*, Raine & Chittka, 2008), and locations with high predation threat (snail, *Physa acuta*, Turner, Turner, & Lappi, 2006;

rainbow fish, *Melanotaenia spp*., Brown 2003). This ability to learn may make individuals preferred social partners and so affect their position within the social network. Individual lemurs, *lemur catta,* that were observed acquiring food in a draw-pulling task, became more central in the social network as a consequence (Kulahci et al., 2018b). The authors suggest that individual differences in learning and the use of novel information may influence who bonds with whom. Although the authors show a causal link, the lemurs were housed in this social group prior to the experiment and individuals to solve the task were self-selecting. Hence, social factors may have already shaped individuals' tendency to become solvers or not. Alternatively, learning performances may determine an individual's behavioural strategy and this indirectly influences network position. For example, learning performances have been associated with an individual's foraging strategy. In wild populations of great tits, *Parus major,* individuals slow to learn a foraging task adopted the scrounging foraging role (Aplin & Morand-Ferron, 2017). Consequently, these individuals also had a greater number of social connections, presumably to exploit more producers. However, these cognitive performances and foraging strategy data were collected simultaneously on a socially learnt foraging task, therefore social connections may have caused individuals to behave as scroungers and exhibit poor learning performances. One study suggests that learning ability may precede foraging strategy or that these two factors are associated early in life, prior to the social context in question; house sparrows, *Passer domesticus,* displaying better performances on a colour discrimination task early in life were more likely to forage as a producer while in a group after fledging (Katsnelson et al., 2011). In order to better understand whether cognitive abilities may determine social structures, we require a system in which cognitive abilities can be assayed independently of the social structure in question.

Pheasants, *Phasianus colchicus*, offer a suitable system to explore the influence of cognitive abilities on social structure. They readily learn and their individual performances can be assayed on psychometric tasks early in life from a few weeks old (Meier et al., 2017; van Horik et al., 2018; van Horik, Langley, Whiteside, & Madden, 2016; Whiteside, Sage, & Madden, 2016). They are omnivorous generalists feeding on grass, galls, seeds and insects and there is some reliance on supplementary cereals provided at artificial feeders (Whiteside, Sage, & Madden, 2015). Such diverse foraging involves learning about a range of potential food items to be preferred and avoided. Foraging may involve recalling feeder locations. Pheasants are gregarious and assort by sex during the winter months (Hill & Robertson, 1988; Ridley & Hill, 1987) and demonstrate these non-random associations by sex at artificial feeders (Whiteside et al., 2018). Social associations may be important in order to facilitate collective vigilance in groups (Whiteside, Langley, & Madden, 2016), or when groups of females collectively visit males to assess them and form harems (Hill & Robertson, 1988). It is also likely that there is much individual variation in pheasant social associations. It is not clear how cognitive performance relates to foraging behaviour in pheasants or other species, nor whether cognitive performances may predict social associations.

We investigated whether pheasants' social associations at feeding stations in the wild are structured according to cognitive abilities (inhibitory control and general associative learning ability) assayed during early life. Following cognitive testing, individuals were released into the wild, where their associations at feeding stations were monitored from October-February, before the breeding season began. Associations at feeding stations are commonly used to infer the social structure of wild bird populations (Farine, Garroway, & Sheldon, 2012). Due to the sexual assortment in this population (Whiteside et al. in review), we generated mixed-sex networks as well as single sex networks, to investigate the effects of cognitive abilities on network structure for the sexes independently. We calculated assortment coefficients for each network, which provides an index that indicates whether associations involve similar or dissimilar individuals (Newman 2003; Farine 2014). We also explored whether individual variation in cognitive performance predicts network centrality. To our knowledge, no previous studies have investigated whether individual variation in cognitive abilities prior to the formation of the social structure in question, influences social structure. Therefore, we could not predict whether populations would show assortative or disassortative mixing for cognitive performances. Previous findings indicate that carrion crows with good inhibitory control performances received more social interactions (Wascher 2015), therefore we predicted that individuals with superior inhibitory control would be more centrally located in the association network. Similarly, ring-tailed lemurs that exhibited good problem-solving ability were more central in the social network (Kulachi et al. 2018), therefore we predicted that individuals with proficient early life learning performances would also be more central in their association networks. By studying these patterns in various systems and improving our understanding of social phenotypes, cognitive phenotypes and the relationship between the two, we can endeavour to appreciate how these relationships arise and are maintained.

6.3 Methods

6.3.1 Subjects and housing

This study was conducted from May 2014 – February 2015 at North Wyke Rothamsted Research Farm, Devon (50°77'N, 3°9'W). Two hundred pheasant chicks were purchased from a commercial game dealer and placed into one of four identical pens (50 individuals per pen). Each pen consisted of an indoor holding area that was heated (2m x 2m) and contained perches and saw-dust bedding. This area was separated from an unheated but sheltered outdoor run area (1m x 4m) by a guillotine partition door. Adjacent to the holding area was a visually isolated testing arena (0.75 m x 0.75 m), divided from the holding area by a sliding entrance door and connected to the outdoor area by a lift-up exit door (Figure 1). At three weeks old, chicks also had access to an outdoor enclosure (4m x 12m) connected to the sheltered run, containing perches and branch shelters. Chicks were provided with age-specific chick crumb (Sportsman game feed) and water *ad libitum* throughout all areas of the pen, except the testing arena. Chicks were identifiable by numbered patagial wing tags (Roxan Ltd, Selkirk, U.K). Chicks were reared in these conditions for 10 weeks while we assayed their cognitive performances.

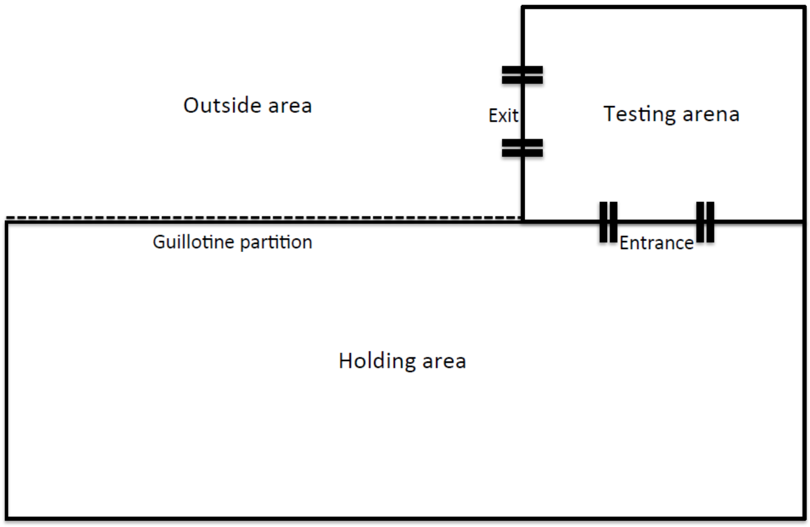

Figure 6.1: Pheasant chicks' indoor housing pen (2m x 2m) and testing arena (0.75m x 0.75m) with sliding entrance and lift-up exit doors.

6.3.2 Cognitive testing procedures

During a testing period, all chicks were ushered into the holding area of the pen and the guillotine door was closed. Chicks were trained to enter the testing arena individually upon hearing an auditory cue (observer humming/whistling) and the opening of the sliding door. All chicks received equal opportunities to enter the testing arena and did so for every testing period. After entering the testing arena, the sliding door was closed and individuals could retrieve a freely available mealworm located central to the task apparatus, thus standardising their approach to the task. An observer then recorded the chick's interactions with the task. Upon completion of the task, or if individuals did not participate within 2min, or exhibited signs of stress (lost-calling, pacing, flapping), they were released into the outside area of the pen via the lift-up exit door. Hence, each chick entered the testing arena once during a testing period. There were two testing periods each day; one morning and one afternoon, Monday to Friday. Chicks were tested on six different cognitive tasks, of which, the first two tasks are described here.

6.3.2.1 Inhibitory control task

The detour reach task assesses an individual's inhibitory control (Diamond 1990; Vlamings et al. 2010). It requires an individual to reach around a transparent barrier to obtain a reward, while inhibiting the response of reaching directly for the reward, which would result in hitting the barrier. The task apparatus was a cylindrical tube (9 cm L), open at both ends (6 cm diameter) and fixed to a white Perspex base. Contained within the cylinder were mealworm food rewards. The openings of the cylinder were oriented toward the exit door and opposite end of the testing area so that on entry to the chamber, the subject could see the reward through the transparent wall of the tube but was required to detour around the wall of the cylinder and reach within the tube to obtain the rewards. Individuals first received two training sessions on an opaque version of the task in which the tube was covered in black tape, previous to testing. This standard training procedure on an opaque version of the task facilitates habituation to a novel object and allows individuals to learn the motor action of reaching into a tube from one end (Boogert et al., 2011; Diamond, 1990; Vlamings et al., 2010). Individuals successfully removed the food reward from within the cylinder at least once before testing. During a test session, individuals were presented with the transparent version of the task whereby they could see the reward and needed to retrieve it without pecking at the outside wall of the cylinder. Individuals received two test sessions, one morning and afternoon session on the same day. Between every test session the apparatus was cleaned to remove dust that may have reduced its transparency. Individuals had not experienced any transparent materials prior to testing; a factor known to affect performances on inhibitory control tasks (van Horik et al., 2018). We took the mean number of pecks (sum of pecks on both tests / 2) before obtaining the reward as our measure of inhibitory control, with individuals that make few pecks to the cylinder considered to possess high levels of inhibitory control and individuals that make many pecks to the cylinder considered to possess low levels of inhibitory control. This task was conducted when the birds were four weeks old.

6.3.2.2 Visual discrimination task

To measure general associative learning ability, we assessed visual discrimination performances. A commonly used paradigm to assess visual discrimination performances of avian subjects, are foraging grids containing wells surrounded with different colour cues (Boogert et al., 2011; Shaw et al., 2015). Individual pheasants were presented with a square apparatus (20 cm L x 20 cm W x 5cm D), containing 20 circular wells. A layer of opaque crepe paper covered each well. Chicks were trained to peck through the crepe paper that covered wells on the testing apparatus; initially, we presented chicks with wells covered with broken crepe paper and over subsequent presentations, the size of the breaks in the paper were decreased until birds' opened completely 'closed' wells spontaneously. During testing, half the wells were encircled with a red '#' shape and contained mealworm food rewards, the other half of the wells were encircled with a black hexagon and were blocked by a bung, so that the paper could not be pecked through. The locations of rewarded and unrewarded wells were random and differed between sessions. Observers recorded the number of correct choices made in 10 choices, in each session. A choice was denoted as when a bird pecked at the crepe paper of a well. When 10 choices had been made, the exit door was opened and the test apparatus was removed. Chicks received a morning session and an afternoon session for five days, resulting in 10 sessions per individual. Our learning performance score was the percentage of correct choices made during the final three sessions (30 choices); this represents how well individuals had learned which stimuli was rewarded by the end of testing. We used a composite measure of learning (percentage correct) which contrasts with previous chapters in which statistical models were fit to the raw data because here, the choices were not binary and the probability of an individual choosing correctly changes after every choice on the 10-well apparatus. Thus, binary logistic regression models using data on all choices are not appropriate in this study. This task was conducted when the chicks were five weeks old.

6.3.3 Release and social associations

In July, when the pheasants were approximately 10 weeks old, they were released on to the site. The site covers 250Ha containing lowland deciduous woodland, grassland, fen meadow and 40 artificial wheat feeders. The minimum and maximum distance between feeders was approximately 0.01km and 1.9km, respectively. Feeders that were closest together were separated by dense woodland. The site is not subject to game shooting or predator control. Initially, the birds were placed in an open-topped release-pen ~2500m^2 situated near to the centre of the farm. The release-pen was surrounded by an electric fence, which excluded terrestrial predators but was exposed to aerial predation. Pheasants could disperse from the pen at will but in the two months following release, the pen was checked at dawn, mid-day and dusk; our presence deterred predators and encouraged birds to return to the safety of the pen. From October onwards, these regular checks ceased.

We continuously monitored feeder use by birds from October 2014 until February 2015 with Bushnell Trophy motion-activated cameras. All images were viewed manually and the time that a bird was at the feeder was recorded. Individual pheasants could be identified from their wing tag numbers. Untagged birds or those whose wing tags could not be seen were excluded from further analysis. It was hard to determine the number of untagged birds that were recorded because individuals could not be reliably identified. Due to the large distance between feeders and, or woodland between closely situated feeders, pheasants could not see conspecifics at neighbouring feeders easily. We used social associations at feeders observed from October to February because prior to this (August and September), associations were almost exclusively in the release pen where birds were living at unnaturally high densities. While some birds remained in the release pen, most birds had dispersed from the pen by October and we consider these associations more natural. During March we began trapping adults and housing them in captivity as part of a separate experiment so we ceased collecting association data.

6.3.4 Statistical analysis

We investigated whether there were sex differences in task performances and used Mann Whitney U tests due to unequal variances in task performances between females and males. To investigate whether task performances were related to each other we used Spearman’s Correlation for females and males combined and within each sex independently. These were conducted on 46 females and 82 males that completed both tasks.

Weighted association networks, based on co-occurrence at feeder sites, were constructed for five calendar months (October 2014 to February 2015) using the *asnipe* package (Farine, 2017). We chose to generate networks per month as we had no prior assumptions of how social connections may change over time. We used a fixed 600s time window such that birds appearing at a feeder within 10 minutes of one another were considered to be in association. Observations of social associations away from feeders confirm the validity of this time window (Madden et al. unpublished data). A gambit of the group approach was used to calculate group by individual matrices (Whitehead & Dufault, 1999), and the strength of association between two individuals was calculated based on simple ratio indices (Cairns & Schwager, 1987). We constructed the networks for female and male associations combined and we also did this for same-sex only networks due to sexual segregation exhibited by pheasants during these months (Whiteside et al. in review). This resulted in 15 weighted networks. For each network, we calculated assortativity coefficients and their standard errors (Newman, 2003), using the *assortnet* package (Farine, 2016). ‘Weighted assortativity’ (*r*) is a coefficient that depicts the proportion of associations that are between similar phenotypes and is deemed to be more robust against influential and rare events on perceived social structure, than assortativity coefficients derived from binary networks (Farine 2016). The coefficient ranges from 1 (perfectly assorted, i.e. all edges connect two nodes of the same phenotype) to −1 (perfectly disassortative, i.e. all edges connect two nodes of different phenotype), whereby values of 0 are neutrally assorted (Newman, 2003). Currently, there is no statistical test to examine the effects of multiple phenotypic measures on a weighted network’s assortativity, hence we assessed cognitive performance scores separately for each task in relation to each network. From each monthly association network, we also calculated individual centrality based on two network metrics: ‘degree’, which is the number of associations an individual has, as well as the ‘strength’ which is the sum of association weights. We used General Linear Models (LM) to investigate whether each network metric was predicted by either cognitive performance measure, separately.

Social network data represents relational data that is non-independent, thus violating assumptions of many statistical approaches. To generate appropriate null models and determine statistical significance of network assortativity coefficients and social centrality measures in relation to each cognitive performance measure, we compared the observed coefficients of each network, to a distribution of expected coefficients, generated from 10,000 data stream permutations. Data stream permutations involve repeatedly swapping the observations of individuals between groups but maintains group sizes and individual gregariousness (Croft, Madden, Franks, & James, 2011). We conducted 10 ‘swaps’ per permutation. Mixed-sex random networks were generated while restricting the permutations within day, sex and feeder location. We restricted within day to control for death or dispersal of individuals. We restricted within sex because pheasants assort according to sex during these months (Whiteside et al. in review). We restricted within location to control for intrinsic preferences from individuals for specific locations, independent of preferences for foraging partners. For the same-sex networks we generated random networks while restricting permutations within day and feeder location.

6.3.5 Ethical considerations

Pheasant chicks were imprinted on experimenters so as to mitigate stress during cognitive testing and birds could choose whether or not to participate in tasks. Chicks were reared at a lower density than that recommended by DEFRA’s code of practice (DEFRA, 2009). Released birds were provided with supplementary wheat from feeders for the duration of the study. All work was approved by the University of Exeter Psychology Ethics Committee and the work was conducted under Home Office licence number PPL 30/3204 to JRM.

6.4 Results

6.4.1 Cognitive testing

Pheasant chicks' participation in cognitive testing varied with task and participation declined as testing progressed. Hence, the inhibitory control task, which was the first task that individuals were tested on, had 169 individuals participate and the visual discrimination task had 125 individuals participate.

The median number of errors made on the inhibitory control task was 6 (IQR: 1 to 11) and there was a significant difference between the sexes in the number of errors made (Mann Whitney U test: $W = 2491$, $n = 172$, $p < 0.001$; Figure 6.2), with females making fewer errors (median, IQR: 4, 0 - 8) than males (median, IQR: 8, 4 - 13).

From the first to the final session on the visual discrimination task, there was a mean ± se of 24% ± 0.01% improvement in correct choices. Final performance scores (percentage correct on final three sessions) on the visual discrimination task varied (median, IQR: 0.657, 0.579 to 0.781), but there was no significant difference between female and male performances (Mann Whitney U test: $W = 2523$, $n = 125$, $p = 0.100$).

Overall, there was no relationship between inhibitory control task performances and visual discrimination task performances (Spearman's Correlation: $r_s = 0.155$, $n = 126$, $p = 0.081$). When investigating this within each sex, there was no relationship between inhibitory control task performances and visual discrimination task performances in females (Spearman's Correlation: r_s = 0.056, n = 46, p = 0.713), or in males (Spearman's Correlation: r_s = 0.145, n = 82, p = 0.193).

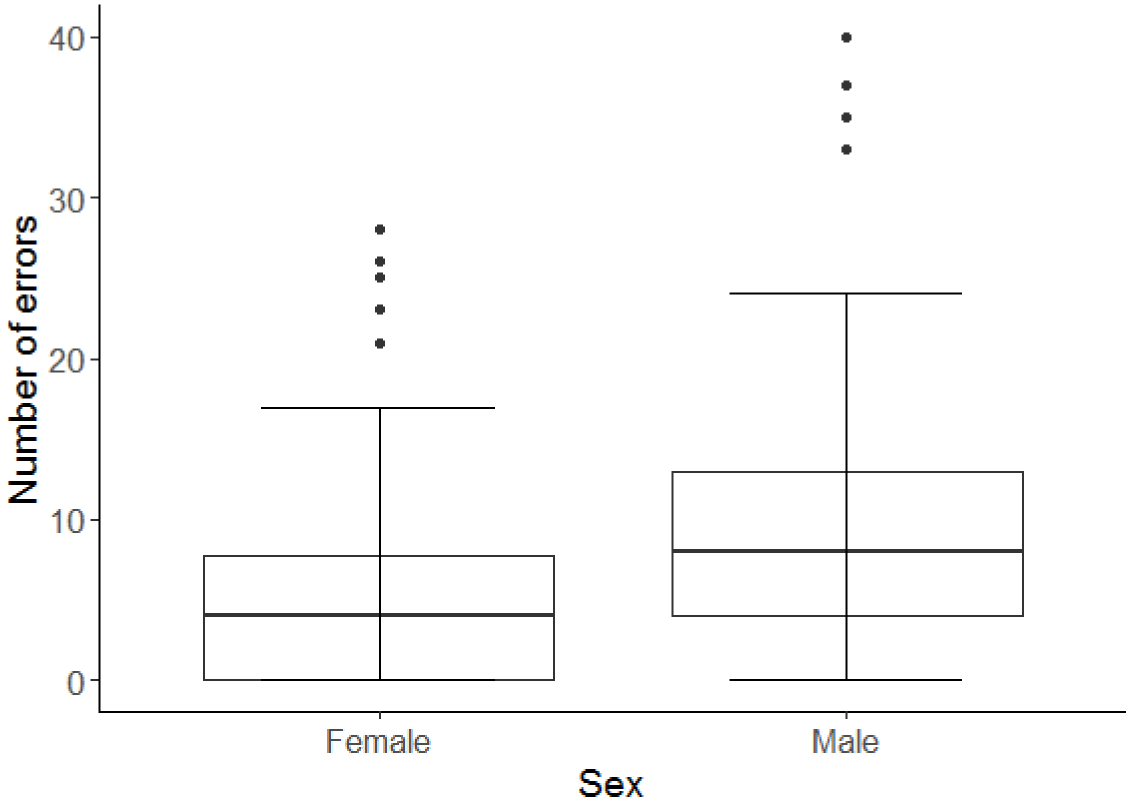

Figure 6.2: The number of errors made by female and male pheasant chicks on the inhibitory control task (mean of two sessions) at four-weeks-old. The boxes represent the lower and upper quartiles (25% and 75%). Black lines represent the median number of errors for each sex and whiskers represent the 10th and 90th percentiles.

6.4.2 Association network structure

We recorded 30,931 visits across 40 feeding stations, occurring between October 2014 and February 2015 (Table 6.1). One hundred and four birds that we reared as chicks were recorded as visiting a feeder or the close surrounding area of a feeder (within view of the cameras), during these months. Each of these individuals were observed a mean ± se of 240.767 ± 15.576 times. We assume that the remaining reared birds died or dispersed off of the site. The number of individuals observed at feeding stations and that participated in either of the cognitive tasks reduced as the months progressed (Table 6.1) and this was similar for both females (Table 6.2) and males (Table 6.3).

Table 6.1: Descriptive statistics for mixed-sex networks generated from associations at feeding stations by female and male pheasants each month. Total number of individuals per network, the number of groups (gambit-of-the-group approach) and number of individuals within each network to complete the inhibitory control and visual discrimination tasks.

Network	Individuals *n*	Groups *n*	Inhibitory *n*	Visual *n*
October	101	3500	84	67
November	76	3295	59	42
December	72	3936	55	39
January	67	3622	51	37
February	63	2694	48	35

Table 6.2: Descriptive statistics for female-only networks generated from associations at feeding stations each month. Total number of individuals per network, the number of groups (gambit-of-the-group approach) and number of individuals within each network to complete the inhibitory control and visual discrimination tasks.

Network	**Individuals** ***n***	**Groups** ***n***	**Inhibitory** ***n***	**Visual** ***n***
October	53	1262	41	29
November	38	1791	28	18
December	37	1667	27	18
January	35	1580	27	17
February	32	1319	23	16

Table 6.3: Descriptive statistics for male-only networks generated from associations at feeding stations each month. Total number of individuals per network, the number of groups (gambit-of-the-group approach) and number of individuals within each network to complete the inhibitory control and visual discrimination tasks.

Network	**Individuals** ***n***	**Groups** ***n***	**Inhibitory** ***n***	**Visual** ***n***
October	54	2838	48	42
November	38	1941	31	25
December	35	2268	28	22
January	32	2041	26	21
February	25	1374	25	20

6.4.3 Association network structure and inhibitory control performances

There was disassortative mixing by performance on the inhibitory control task in mixed-sex networks, with pheasants that made few errors being more likely to associate with pheasants that made many errors on the task (Table 6.4, Figure 6.3). The assortment coefficients were negative in all months, and the standard errors did not overlap 0 for October, November and December networks. Furthermore, the observed coefficients for October to January networks were significant, determined from data stream permutation tests. The same pattern was observed in female-only networks for four of the monthly networks (Table 6.4). This disassortment was stronger than that in the mixed-sex networks. The standard error did not overlap 0 for any of the networks and assortment coefficients for October, November, December and February networks were significant. In male-only networks, there was significant disassortative mixing by inhibitory control performances during October (Table 6.4). This changed to random mixing in November, to significant assortative mixing in December, to random mixing in January and significant assortative mixing in February. However, assortativity coefficients and the standard errors were close to 0 for all networks, hence, biological relevance of the data stream randomizations should be interpreted with caution (Farine, 2014). This suggests that the disassortative mixing observed in mixed-sex networks is at least partially driven by inter-sexual associations because females had significantly better task performances than males. However, these sex differences in performances do not explain the stronger disassortment seen within female networks, in which the sex differences in mean performances could not manifest.

Table 6.4: Weighted assortment (*r*) by inhibitory control abilities within each monthly social network calculated from associations at feeding stations in the wild by released female and male pheasants in mixed-sex and single-sex networks. Values in bold represent significant *p-values* (*p* < 0.05) deduced from comparison of observed coefficient to a distribution of expected coefficients (generated from 10,000 data stream permutations)

Month/s	Mixed-sex	Female-only	Male-only
Oct r	-0.111 ± 0.043	-0.308 ± 0.064	-0.057 ± 0.056
p	**0.003**	**0.003**	**0.036**
Nov r	-0.130 ± 0.047	-0.294 ± 0.080	0.059 ± 0.098
p	**0.001**	**0.009**	0.110
Dec r	-0.122 ± 0.058	-0.208 ± 0.086	0.026 ± 0.104
p	**0.035**	**0.050**	**0.017**
Jan r	-0.060 ± 0.076	-0.138 ± 0.097	0.064 ± 0.114
p	**0.034**	0.262	0.285
Feb r	-0.050 ± 0.093	-0.197 ± 0.096	0.173 ± 0.231
p	0.290	**0.033**	**0.011**

6.4.4 Association network structure and visual discrimination performances

There was disassortative mixing by visual discrimination performances in the mixed-sex networks, with pheasants that learned the discrimination more accurately being more likely to associate with pheasants that were less accurate by the end of the task. This disassortment was observed in October, November and December networks, determined by data stream permutation tests (Table 6.5; Figure 6.4). In female-only networks, all assortment coefficients were negative and the standard error only overlapped 0 for the December network. There was significant disassortative mixing by visual discrimination task performances for October and November networks, determined by data stream permutations (Table 6.5). In male-only networks, the assortment coefficients for visual discrimination task performances were negative for October, November, December and January networks (Table 6.5). The standard error crossed 0 only in the January network, but only the November network was significant, determined by data stream permutation tests. There were no sex differences in task performances, hence the disassortative mixing observed in the mixed-sex network is driven by both females and inter-sexual associations.

Table 6.5: Weighted assortment (*r*) by visual discrimination abilities within each monthly social network calculated from associations at feeding stations in the wild by released female and male pheasants in mixed-sex networks and single-sex networks. Values in bold represent significant *p-values* (p < 0.05) deduced from comparison of observed coefficient to expected coefficients (generated from 10,000 data stream permutations)

Month/s	Mixed-sex	Female-only	Male-only
Oct r	-0.256 ± 0.118	-0.412 ± 0.250	-0.129 ± 0.070
p	**0.001**	**0.001**	0.080
Nov r	-0.322 ± 0.093	-0.390 ± 0.128	**-0.449 0.244**
p	**0.001**	**0.041**	**0.001**
Dec r	-0.119 ± 0.160	-0.204 ± 0.221	-0.394 ± 0.335
p	**0.042**	0.155	0.352
Jan r	-0.353 ± 0.126	-0.422 ± 0.145	-0.258 ± 0.289
p	0.251	0.100	0.137
Feb r	-0.306 ± 0.130	-0.347 ± 0.144	0.009 ± 0.326
p	0.346	0.274	0.122

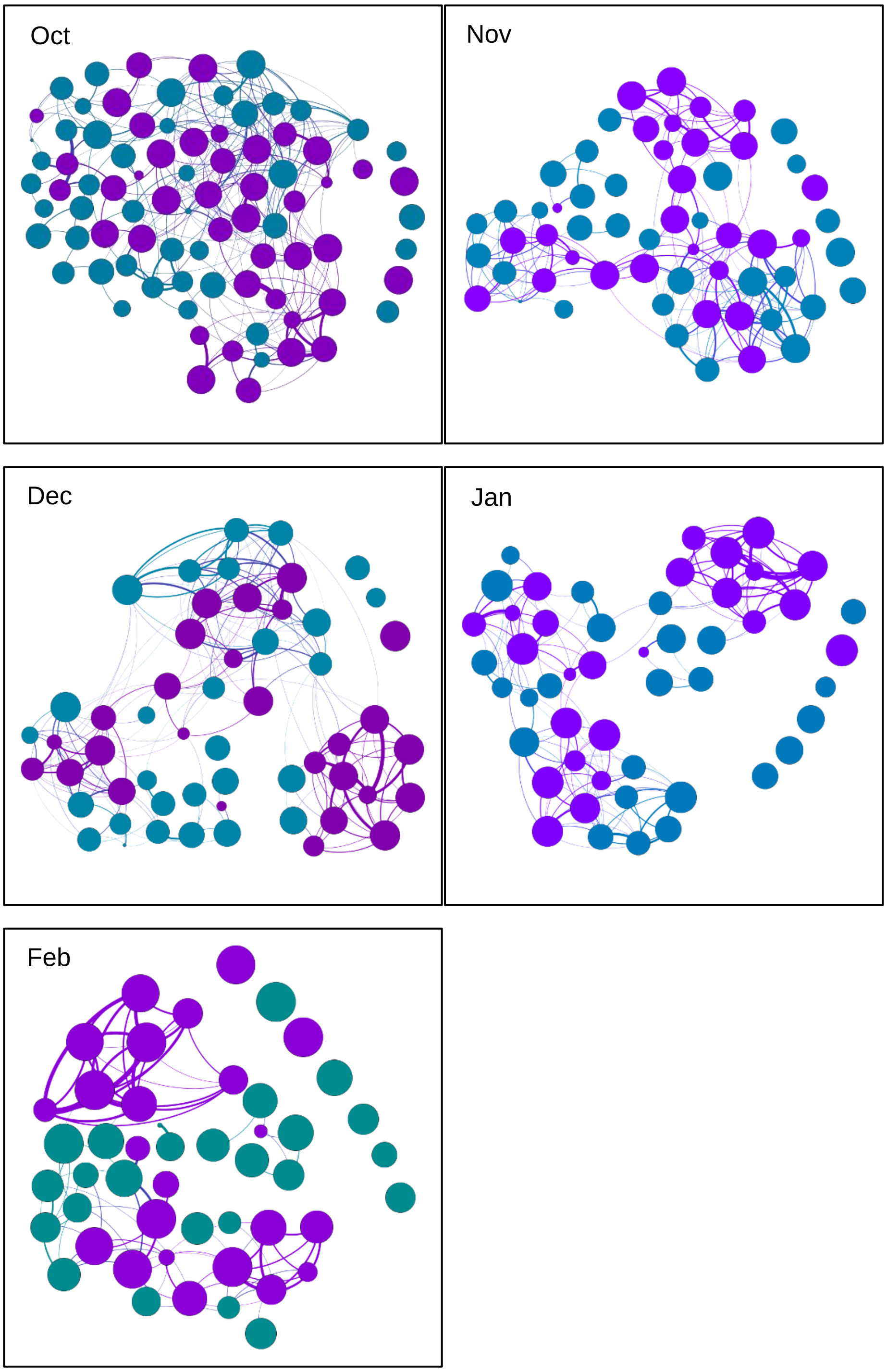

Figure 6.3: Social associations between female (purple nodes) and male (green nodes) pheasants at feeding stations in the wild for each month, showing disassortative mixing based on early life performances on an inhibitory control task. Size of nodes is inversely related to the mean number of errors made, i.e. large nodes represent fewer errors and small nodes represent many errors. Thickness of lines corresponds to strength of the relationship between two nodes.

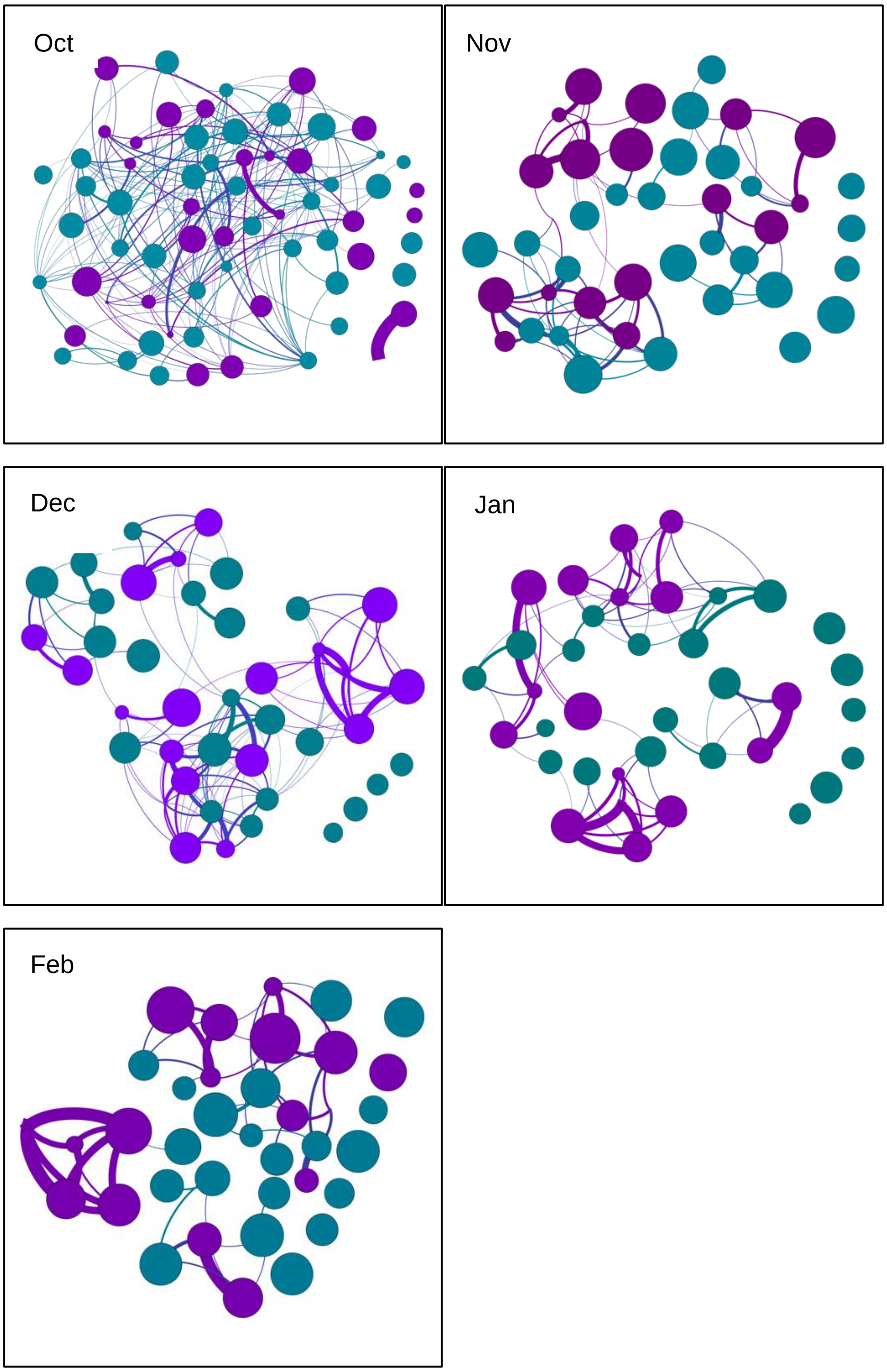

Figure 6.4: Social associations between female (purple nodes) and male (green nodes) pheasants at feeding stations in the wild for each month, showing disassortative mixing based on their early life performances on a visual discrimination task. Size of nodes corresponds to the % of correct choices on the final three sessions i.e. large nodes represent higher % correct and small nodes represent lower % correct. Thickness of lines corresponds to strength of the relationship between two nodes.

6.4.5 Cognitive abilities and network centrality

Pheasants that made few errors in the inhibitory control task were generally more central in the social network, having a higher number of associates and stronger links to their associations than pheasants that made more errors (Table 6.6, Figure 6.3). This was seen most strongly in mixed-sex networks and female networks (Table 6.6). In male networks, inhibitory control performances were unrelated to either the number or strength of connections, suggesting that inhibitory control abilities do not influence male network centrality.

Pheasants that learned the visual discrimination more accurately by the end of testing were generally less central in the networks, with fewer associates than pheasants which had learned the discrimination less well (Table 6.7, Figure 6.4). These relationships were stronger in mixed-sex and female only networks (Table 6.7). In male-only networks, good visual discrimination performances were negatively related to the number of associations for the November network only. This suggests that among males, network centrality is less affected by visual discrimination performances.

Table 6.6: Regression coefficients for the relationship between cognitive performances on an inhibitory control task and two measures of social centrality (degree: the number of associates and the strength of these associations) for pheasants in mixed-sex and single-sex networks. Negative relationships indicate that individuals that made few errors in the test have more or stronger links. Values in bold represent significant p-values (*p* < 0.05) deduced from comparison of observed coefficient to expected coefficients (generated from 10,000 data stream permutations)

Network	**Mixed-sex**		**Female only**		**Male only**	
	Degree	**Strength**	**Degree**	**Strength**	**Degree**	**Strength**
Oct r	-0.093	-0.006	-0.056	-0.004	0.036	-0.001
p	0.112	0.462	**0.002**	0.210	0.475	0.257
Nov r	-0.045	-0.004	-0.073	-0.001	0.001	-0.003
p	**0.006**	0.279	0.342	**0.026**	0.493	0.271
Dec r	-0.174	-0.013	-0.083	-0.005	-0.080	-0.004
p	0.397	0.288	0.111	**0.001**	0.096	0.305
Jan r	-0.146	-0.009	-0.062	-0.002	-0.050	-0.001
p	**0.019**	**0.023**	0.172	**0.048**	0.480	0.302
Feb r	0.096	-0.011	-0.090	-0.011	-0.029	0.002
p	0.219	**0.001**	**0.035**	**0.005**	0.241	0.463

Table 6.7: Regression coefficients for the relationship between cognitive performances on a visual discrimination task and two measures of social centrality (degree: the number of associates and the strength of these associations) for pheasants in mixed-sex and single-sex networks. Negative relationships indicate that individuals that were less accurate by the end of testing have more or stronger links. Values in bold represent significant p-values (*p* < 0.05) deduced from comparison of observed coefficient to expected coefficients (generated from 10,000 data stream permutations)

Network	**Mixed-sex**		**Female only**		**Male only**	
	Degree	**Strength**	**Degree**	**Strength**	**Degree**	**Strength**
Oct r	-5.161	-0.637	-3.345	-0.637	-2.506	0.108
p	**0.004**	0.271	**0.023**	0.234	0.231	0.068
Nov r	-8.843	-0.579	-7.006	-0.606	-0.550	-0.006
p	0.147	0.031	0.456	**0.003**	**0.001**	0.194
Dec r	-6.201	-1.038	-4.088	-1.322	-1.761	-0.072
p	**0.001**	0.001	0.078	**0.007**	0.324	**0.017**
Jan r	-8.748	-1.065	-4.342	-1.176	-9.034	-0.030
p	**0.011**	0.237	**0.015**	0.340	0.289	0.145
Feb r	-2.118	-0.686	-0.421	-0.619	-0.831	0.147
p	**0.047**	0.008	**0.001**	**0.005**	0.221	0.278

6.5 Discussion

An individual pheasant's cognitive performance early in life predicts their patterns of associations as an adult. Individuals that had poor inhibitory control ability had a greater proportion of associations with those with good inhibitory control ability in mixed-sex networks. Females had significantly better task performances than males and in female-only networks, there was also significant disassortative mixing by inhibitory control performances. In mixed-sex and female-only networks, individuals with good inhibitory control ability were more central in the network. In male-only networks, the patterns were not as congruent; males' assortment based on their early life inhibitory control performances fluctuated across months and inhibitory control abilities had no influence on centrality in male-only networks. Individuals that performed more accurately on a visual discrimination task associated more with those that were less accurate on the task. There was no sex difference in visual discrimination abilities and both the mixed-sex and single sex networks showed disassortative mixing by task performances, albeit more consistently in female-only than for male-only networks. In mixed-sex and female-only networks, individuals that had most accurately learned the visual discrimination task were least central in the network. This same pattern was seen in one of the monthly male networks.

This disassortative mixing by cognitive performances contrasts markedly with the general phenomena of assortative mixing by various non-cognitive attributes seen across taxa (kinship: meerkats, Madden et al. 2012; age: baboons, Carter et al. 2015; sex: Tasmanian devil, Hamede et al. 2009; pheasants, Whiteside et al. 2018; size: chub, Krause 1994; golden shiner and banded killifish, Krause et al. 1996; Hoare et al. 2000; consistent behavioural traits: female Trinidadian guppies, Croft et al. 2009; male great tits, Aplin et al. 2013; baboons, Carter et al. 2015; chimpanzees, Massen and Koski 2014). However, our results match the disassortative mixing for behavioural type that has been demonstrated in aggregations of foraging geese (Kurvers et al., 2010). Kurvers et al. (2010) explain that this type of mixing was the consequence of producer scrounger games (Barnard & Sibly, 1981; Caraco & Giraldea, 1991; Vickery et al., 1991), in which individuals of different behavioural type diverged in their tendency to independently locate food patches and their time spent foraging and as a consequence, producer scrounger dynamics emerged. We did not directly examine pheasant foraging strategies, but it is possible that cognitive abilities assayed during early life may be representative of an individual's foraging strategy in the wild. In captive house sparrows, individuals with more successful colour discrimination performances during early life behaved as 'producers' when foraging as adults (Katsnelson et al. 2011). If these same mechanisms are present in pheasants, then proficient learners may be behaving as producers, predominantly locating feeding stations, whereas poor learners 'follow' the producers to feeding stations and thus behave as scroungers. In social networks of wild great tits, individuals that adopt the scrounger role had poorer social learning performances and had a greater number and greater strength of social connections (Aplin & Morand-Ferron 2017). Individuals that are more centrally located in networks, receive the most information (Aplin et al., 2012), hence, individuals that are not good at learning (social or asocial), may benefit from being 'well-placed' in their social network to maximise scrounging opportunities (Aplin & Morand-Ferron 2017). In support of this but in contrast to our prediction, pheasants that had the lowest levels of success by the end of the visual discrimination task also had a greater number and strength of connections in the wild. Pheasants poor at learning are potentially adopting the scrounger role and thus had more and stronger social connections.

It is unclear why individuals disassort by inhibitory control performances. We suggest two potential explanations. First, individual variation in inhibitory control abilities may also be related to a divergence in foraging strategy (similarly to learning performance). For instance, individuals with poor inhibitory control performances may be more exploratory and so be more likely to locate novel food patches. Therefore, they may behave as producers in the network, in the same way that good learners are producers and are ‘followed’ by individuals that are good at inhibiting prepotent responses that scrounge. We found that females and males with good inhibitory control were more central in most mixed-sex monthly networks. This may suggest that individuals with good inhibitory control behave as scroungers and are more central in the network in order to maximise scrounging opportunities, whereas individuals with poor inhibitory control behave as producers (as was seen in the great tits, Aplin and Morand-Ferron 2017). However, exploratory behaviour and inhibitory control performances were unrelated in black capped chickadees, *Poecile atricapillus* (L. M. Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015), thus it is unclear which aspect of low inhibitory control facilitates foraging ability. Our second potential explanation is that disassortative associations are instead related simply to social preferences. Good inhibitory control may make individuals more desirable social partners due to lower levels of aggression (Strayer 1976). However, crows with good inhibitory control and more social interactions, were also more aggressive themselves (Wascher 2015). It is unknown whether pheasants with poor inhibitory control are more aggressive, nor whether pheasants actively avoid more aggressive conspecifics.

The influence of early life cognitive performances on network structure varied over time. In the mixed-sex networks, there was significant disassortative mixing by inhibitory control performances and visual discrimination performances for the first four and three months, respectively. During the later month/s, random mixing in relation to task performances was observed. This may reflect a loss of statistical power, caused by the diminishing population size. Reared pheasants die of natural causes at high rates following release (Madden et al. in prep). Our monitored population in February comprised 32% of the released population. Alternatively, it may reflect changes in female-male associations, as females are beginning to settle on a single male's territory (Hill & Robertson, 1988; Ridley & Hill, 1987), and hence, different factors may be influencing inter-sexual associations. For example, when choosing which male to join for breeding, females may be motivated to preferentially associate with males based on secondary sexual characteristics (see Mateos, 1998 for review), rather than cognitive performances.

In male-only networks, evidence for mixing by task performances and network centrality based on task performances was much weaker than that seen in mixed-sex networks. These cognitive abilities may be less important in influencing male-male associations. During the winter months, males compete for territories and associations between males at feeding stations may be related to dominance interactions, such as displays and contests (Mateos & Carranza, 1997a) for the acquisition of a territory (Robertson, 1997), rather than indicating shared feeding groups. Their motivation to associate, at least temporarily during a contest with competitors, may be unrelated to cognitive performances.

Our networks were based only on the individuals that we obtained cognitive performance measures for. There were other individuals in the network including both identifiable birds that we had reared but failed to test and unmarked birds that originated from outside our study population. These birds were not included in the analyses. Whether their inclusion would strengthen or weaken the disassortative structure that we observed is unknown, but simulations demonstrate that partial networks with unidentifiable individuals, correlate closely with full networks (M. J. Silk, Jackson, Croft, Colhoun, & Bearhop, 2015), so we believe that the patterns we have observed are representative of population level patterns.

Our results are specific to association networks at feeding stations, we are therefore unable to generalise our findings to other types of network, either directed networks or networks based on specific interaction types. Directed networks of different interaction type are found to be inconsistent. In meerkats, *Suricata suricatta,* grooming, dominance and foraging competition network structures varied (Joah R. Madden, Drewe, Pearce, & Clutton-Brock, 2009). Similarly, in ringtailed lemurs, partner choice in aggressive networks did not correlate with grooming, contact calling or scent marking networks (Kulahci, Ghazanfar, & Rubenstein, 2018). This suggests that network structures vary depending on the network type, but which network types are influenced by individual variation in cognitive abilities may indicate how these abilities may be selected for. For instance, if individual variation in cognitive abilities significantly predicts assortative/disassortative mixing in association networks at feeding stations, but not mixing in aggressive networks based on competition for territories or mates, it may suggest that the particular cognitive abilities in question are not under sexual selection but are important in foraging decisions and may instead be shaped by natural selection.

Social structure has evolutionary implications. Assortment by size is associated with reduced predation risk (Krause, 1994), and increases foraging efficiency (Krause 1994; Utne-Palm and Hart 2000). Associating with individuals of similar behavioural type facilitates cooperation (guppies, Croft et al. 2006). To our knowledge, the evolutionary benefits of disassortative social structure have not been explored directly. We speculate that if individuals poor at learning have a greater number and strength of connections in their social network, compared to good learners, then they have greater access to social information regarding resources (Aplin et al. 2012), and potentially predators (Croft et al., 2006). This amplification in access to social information may benefit individuals unable to gather the information themselves. This alternative behavioural strategy may equalise fitness benefits between individuals of different cognitive abilities, thus maintaining variation in cognitive traits. Frequency-dependent mechanisms have been proposed to explain the maintenance of consistent individual differences in behaviour, in which an individual’s fitness depends on its social environment (Dall, Houston, & McNamara, 2004; Maynard Smith, 1982). Whilst we cannot accurately infer how these early life cognitive abilities manifest in associations at feeding stations in the wild, it is likely that this disassortative social structure has fitness implications for cognitive abilities.

6.5.1 Conclusion

Our findings suggest that individual differences in early life cognitive abilities determine disassortative social structures. Pheasants associate with others who exhibited contrasting abilities in an inhibitory control task and a learning discrimination task. Higher social centrality, in both degree and strength, is seen in individuals with superior inhibitory control, whereas those with higher levels of success on the visual discrimination task had low social centrality, in both degree and strength. This was evident in inter-sexual associations and female-female associations but not in male-male associations. The mechanisms that underpin these relationships between cognitive ability and social network structure remain to be tested. Understanding the ways in which cognitive abilities manifest in the social environment can inform us of their evolution.

Chapter Seven: General Discussion

7.1 Introduction

The social environment has been proposed as a key factor in the evolution of cognition (Social Brain or Intelligence Hypotheses: Dunbar, 1998; Humphrey, 1976; Seyfarth & Cheney, 2002; Relationship Intelligence Hypothesis, Emery, Seed, von Bayern, & Clayton, 2007). Despite the clear link between cognition and the social environment illustrated by comparative species studies (Bond et al., 2007; Lefebvre et al., 2004; MacLean et al., 2013; Reader & Laland, 2002), few studies have explored how the social environment affects the expression of cognitive abilities, how these abilities may influence social structure and potential fitness outcomes for individuals within a species. This is critical to our understanding of how natural selection may drive the evolution of cognitive abilities (Thornton et al., 2014; Thornton & Lukas, 2012). In this thesis, I have used the pheasant, *Phasianus colchicus,* as a model species and explored how past and current social environments affect the expression of cognitive abilities and how differential cognitive abilities may lead to different social environments and (proxy) fitness outcomes for individuals.

Cognitive abilities do not manifest in isolation and cognitive performances are influenced by multiple factors that the social environment contributes to. For instance, both broad and fine-scale social environments influence individual’s stress levels (group size, Markham, Gesquiere, Alberts, & Altmann, 2015; social hierarchy, Abbott et al., 2003; Sapolsky, 2005; social network, Wittig et al., 2008), access to resources (group size, Krause & Ruxton, 2002; social hierarchies, Popp & DeVore, 1979; Wilson, 1975; social networks, Aplin, Farine, Morand-Ferron, & Sheldon, 2012), and access to information (social hiearchy and social network, Jones, Aplin, Devost, & Morand-

Ferron, 2017). Conversely, individual variation in cognitive performances may have consequences for the social environment by shaping individuals’ relationships. This may occur through the effect of cognitive abilities on partner selection and the outcomes of interactions (Reichert & Quinn, 2017; Wascher et al., 2018), or via the influence of cognition on foraging ability (Kulahci et al., 2018b), or foraging strategy (Katsnelson et al., 2011). Both cognitive performances (Ferrari et al., 2014) and the social environment (Silk, Alberts, & Altmann, 2003) have fitness implications for individuals, hence how these two factors interact can inform us of their evolution.

I have explored the relationships between cognitive performances and the social environment, and by carefully considering the order of my observations and experiments I have endeavoured to make the distinction between cause and consequence. My work is some of the first to consider explicitly how individual variation in cognitive performance and the social environment interact. This thesis presents important empirical evidence to further our understanding of why cognition and the social environment are related and allows us to delve into the potential implications of their relationship.

The social environment can be quantified by its broad and fine-scale social structures. I first investigated the broad-scale structure of the social environment, the size of the group that an individual lives in. Group size determines the possible number of relationships. Both females (**Chapter Two)** and males (**Chapter Four**) performed more accurately on cognitive tasks when housed in larger groups. I then investigated more fine-scale social structures, testing the relationship between an individual’s social rank and their cognitive performance. Social rank was inferred from aggressive and submissive interactions between dyads and I showed that more dominant adult males performed more accurately on a cognitive task (**Chapter Three**). The relationship between male social rank and cognitive performance persists even after direct competition with other males has been removed, but I found no support that cognitive performances caused adult social rank (**Chapter Four**). Additionally, there was no relationship between cognitive performances with aggression early in life, in both females and males (**Chapter Five**). Finally, I demonstrated that social structure in the wild is predicted by individual variation in cognitive abilities measured during early life (**Chapter Six**). Individuals associated more with conspecifics that had contrasting cognitive performances to themselves. Those with good inhibitory control abilities were more centrally located in the social network, whereas those with good visual discrimination performances were least central in the social networks. Combined, these results reveal that an individual's cognitive performances are both caused by and have consequences for the social environment (Figure 7.1). Below I first discuss the difficulties researchers face when attempting to measure cognitive abilities and potential limitations of the methods used in this thesis. I then discuss my findings and the potential implications of these results for pheasants, as well as more generally, and explore ideas for future research. Finally, I suggest how the effects of the social environment on variation in cognitive performances further complicates quantifying individual differences in cognitive ability.

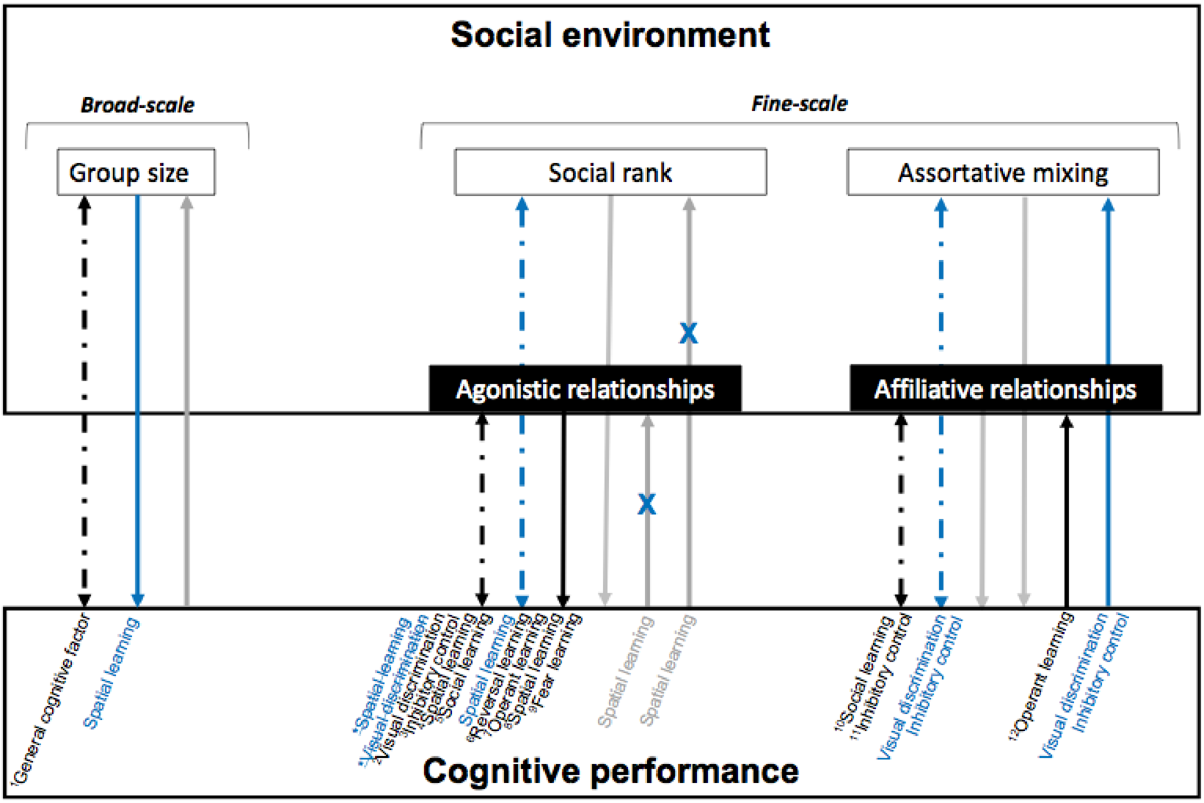

Figure 7.1: Relationships between individual differences in cognitive performances and the social environment. Dashed, double headed arrows represent evidence of a relationship whereby causality was not determined. Single headed arrows indicate the direction of causality in the relationship. Black arrows represent existing evidence, grey arrows represent no existing evidence and blue arrows represent evidence provided by this thesis, and blue X's represent lack of support provided by this thesis. Agonistic relationships indicate investigations into aggressive interactions between dyads. Social rank represents the overall patterns of these agonistic interactions and includes investigations with groups containing >4 individuals in which social rank was inferred. Affiliative relationships indicate affiliative interactions or non-random associations. Assortative mixing indicates social network structure by these affiliative relationships. For clarity, the diagram does not contain other research with non-significant relationships. '*' indicates performances from early life. Superscript number refer to the study reference that can be found in the appendix.

7.2 Factors to consider when measuring cognition

The most appropriate methods to quantify individual variation in cognitive ability is of great interest (Pritchard et al., 2016; Rowe & Healy, 2014; Thornton et al., 2014; Thornton & Lukas, 2012). Throughout this thesis, methods have been adopted that either maximized data collection and or, are a consequence of being part of a larger research project. Below I discuss some potential limitations of the methods used and areas where further investigation is required to fully understand whether these factors may influence our interpretation of individual differences in cognitive performances.

7.2.1 Controlling for extraneous cues

When assessing cognitive performance within a specific domain it is important to control for other external cues that are not of interest but could inform individuals of the reward location. Throughout this thesis, the control of olfactory cues was not described and it is possible that pheasants may have detected the odour of the reward location and not relied solely on spatial (**Chapter Two, Three, Four and Five**) or visual cues (**Chapter Five and Six**). Hence, the respective cognitive ability being targeted may not have been measured accurately. While the control of olfactory cues is not mentioned explicitly, throughout cognitive testing experimenters frequently handled mealworms and a single mealworm was placed on top of the apparatus to standardise each individual’s approach to the apparatus. Hence, the odour of mealworms was not just present on the rewarded well of the apparatus, making it difficult for individuals to use odour as a reliable cue. Furthermore, galliformes have poor olfactory detection, as determined by their small olfactory bulbs (Corfield et al., 2015), so it seems unlikely that olfactory cues confounded task performances. Nonetheless, individuals may vary in their detection of olfactory cues and it is important to exclude this as a possible explanation for inter-individual variation in cognitive performances in future experiments.

7.2.2 Inter-rater reliability

A second confounding factor that is important to consider is inter-rater reliability. Inter-rater reliability is the statistical measurement of the agreement among observers/experimenters in their rating of behaviour. High agreement among observers ensures that the data collected are comparable and there is no ‘observer bias’ in the data. A review of *Animal Behaviour* articles demonstrated that the majority of studies failed to include this statistic (Kaufman & Rosenthal, 2009). In this thesis, inter-rater reliability was not included because prior to each type of cognitive test detailed in this thesis, all observers underwent a briefing and multiple demonstrations on how to score the clear, defined behaviours (e.g. pecking at a location on the apparatus). If there were inconsistencies among observers, I am confident that it would not affect the conclusions of this thesis because observers were rotated across all housing pens/aviaries, therefore the effect of potential bias would be spread across subjects and would merely add noise to the data. Nonetheless, observers may still differ in their recording and the inclusion of this statistic is advisable to improve neutrality on the part of the observer and thus, the validity of the results.

7.2.3 Low sample size and the loss of statistical power

When interpreting results, it is important to consider sample size. Small sample size results in low statistical power and may inhibit our ability to detect relationships. This may have been a problem when assessing repeatability of cognitive performances from early life to adulthood and may explain why we failed to detect intra-individual consistency in cognitive performances of spatial learning performances (**Chapter Four**). Unfortunately, the small sample size (*n* = 8) was unavoidable; pheasant survival into adulthood after release into the wild is low (<30%, see Madden et al., 2018 for review) and low participation is also an issue in cognition studies (<50%, see van Horik et al., 2016). The difficulty in detecting relationships is exacerbated when effect sizes are small and highlights that particular questions may only be satisfactorily answered with large sample sizes or meta-analyses (e.g. Cauchoix et al., 2018). Conclusions made from data with small sample sizes should be interpreted with caution.

7.2.4 Standardisation of cognitive test paradigms

The use of different cognitive tasks to test the same or similar hypotheses is also a reason to interpret results with caution. We still know little about intra-individual consistency in cognitive performances on similar, yet distinct cognitive tasks targeting the same cognitive domain (contextual) (Cauchoix et al., 2018; Griffin, Guillette, & Healy, 2015). When exploring the relationship between social rank/aggression with spatial learning, cognitive performance was assessed using a binary discrimination task (**Chapter Three and Chapter Four**), as well as a four-arm maze task (**Chapter Five**). On the binary discrimination tasks, social rank was positively related to cognitive performances (**Chapter Three and Chapter Four**), whereas aggression was unrelated to cognitive performances on the four-arm maze task (**Chapter Five**). This disparity in findings between the studies may be because of the different task paradigms and suggest that in pheasants, maze task performances are unrelated to aggression, whereas binary spatial task performances are. However, it is worth noting that studies in other taxa have found aggression/social rank was positively related to performances on maze tasks (meadow voles, Spritzer et al. 2004; mice, Fitchett et al. 2005, Barnard & Luo, 2002). The lack of a relationship between aggression and maze task performance in pheasants is more likely due to the age at which individuals were tested (see **Chapter Five**), however, my methods do not allow me to distinguish between these factors. It is important to consider the different task paradigms used as a potential explanation for any differences in findings when testing hypotheses. While it is unclear whether performances on different tasks assessing the same cognitive domain are consistent and thus affect our understanding of relationships between cognitive performances and the social environment, it is also unknown whether variations of the same task (e.g. when the rewarded stimuli is counterbalanced across individuals) may influence our ability to detect relationships between cognitive performances and the social environment.

7.2.5 Counterbalancing the rewarded stimulus

In experimental psychology studies, it is standard practice to counterbalance the rewarded stimulus across individuals (Shettleworth, 2010), as this ensures that the chosen stimulus does not influence population-level performance (Rowe & Healy 2014). In this thesis, generally, the rewarded stimulus was not counterbalanced across individuals. In spite of this, inter-individual variation in cognitive performance was found to be related to a manipulation of group size (**Chapter Two**), captive social rank (**Chapter Four**) and predicted social structure in the wild (**Chapter Six**). Thus, when assessing individual differences it is not clear that this technique is critical. Furthermore, by varying the rewarded stimulus, additional variation is introduced that could contribute to inter-individual variation in cognitive performances. To explore whether counter-balancing or keeping the rewarded stimulus consistent among individuals influences our ability to detect relationships, a population could be subsetted in which one sample receives counterbalanced rewards and the other receives consistent rewards. The relationship between the social environment and cognitive performances in the different population samples can then be compared.

7.2.6 Training to a learning criterion

Training to a learning criterion attempts to remove the effect that preferences/biases may have on cognitive performances by standardising individuals' cognitive performances. For example, subjects may vary in their experience of blue objects and this may influence the subsequent associations that subjects form with blue stimuli on a colour discrimination task. By training to a learning criterion (e.g. 15 consecutive correct choices), individuals are considered to be at the same cognitive starting point, irrespective of their past experiences. After reaching a learning criterion individuals are then tested on a reversal of the task, whereby the task affordances are switched (i.e. the non-rewarded stimuli is now rewarded and vice-versa) and this is considered a reliable measure of cognitive ability. In this thesis, individuals were not trained to a learning criterion because I wanted to standardise the amount of experience that individuals had with the novel test apparatus. Differences in experience with a novel apparatus could potentially confound cognitive performances. For example, if individual A reaches a learning criterion after 30 trials on a novel task, whereas individual B reaches this criterion after 90 trials, their subsequent performance on a reversal of this task is likely to vary again because individual B has more information than individual A regarding the novel apparatus. Instead, I opted for measures of learning in which individuals have had equal experiences, which I argue is more important when studying individual differences using novel apparatus. To ensure that these differences in preference/bias did not influence my conclusions, where possible, I included start performance (performance during first 10 trials) as a covariate in analyses (**Chapter Two**), thereby controlling for this inter-individual variation. I was therefore able to consider the relationship between learning performance and the social environment in light of these inherent differences in preference. Comparing the different approaches within the same population may elucidate whether training to a learning criterion is necessary for our understanding of the relationships between cognitive performances and the social environment.

7.2.7 Implications and future directions

Multiple factors may affect the measurement and interpretation of individual variation in cognitive abilities (see Rowe & Healy 2014). To improve the robustness of findings in future studies and reduce statistical noise, greater consideration should be given to the control of extraneous cues, quantifying inter-rater reliability, investigating the validity of different test paradigms or test standardisation, and increasing sample size. The debates surrounding the most appropriate experimental procedures to use, such as counterbalancing the reward location and training to a learning criterion, may be best assessed by comparing the different methods within the same populations. Contrary to the possible limitations identified, I am confident that these factors did not significantly confound the conclusions from this thesis. In the following sections, I discuss these key findings.

7.3 How does group size affect learning performances?

The relationship between group size and cognitive abilities has long been proposed to explain the evolution of superior cognitive abilities in both humans and non-human animals (corvids, Bond et al., 2007; primates, Dunbar, 1998; MacLean et al., 2013). While most studies have taken a comparative approach, comparing across species, one recent non-human animal study has reported a correlation between group size and cognitive performance within a single species. Stable group size in wild Australian magpies, *Cracticus tibicen dorsalis*, has been shown to correlate positively with cognitive performances across a battery of associative learning tasks (Ashton et al., 2018). The ‘effect’ of group size increased as the magpies aged, and Ashton et al. (2018) suggest that living in a larger group promoted cognitive development. However, in both the magpie study and previous comparative studies, group sizes were not manipulated to explore the direction of causality. In **Chapter two**, by testing the same adult females on two distinct spatial learning tasks while housed in each of two different group sizes, I demonstrate a positive causal effect of group size on the accuracy of spatial learning performances in response to group size. I showed that the effect of the social environment was relatively fast acting, as this improvement in accuracy occurred within one week of housing in each group size. The mechanisms behind this relationship are unclear, and I suggested four non-mutually exclusive mechanisms. Enhanced individual cognitive performances in increasing group size may be related to increased neural plasticity due to cognitive stimulation (Mark R. Rosenzweig et al., 1978), changes in foraging strategy (Belmaker et al., 2012; Morand-Ferron & Giraldeau, 2010) that manifest in learning performances, a change in stress levels (Milinski & Parker, 1991), or a reduction in the duration and, or, the number of vigilance bouts. I discuss this last potential mechanism in more detail because this mechanism is testable using a similar paradigm to the one used in this thesis.

Individuals reduce their own vigilance in response to increasing group size (Beauchamp, 2015). Thus, with less time or fewer occurrences of being vigilant, individuals can invest in attention to stimuli, which facilitates learning (Guilford & Dawkins, 1987). In support of this, female pheasants decrease their vigilance when in larger groups (Whiteside, Langley, & Madden, 2016). However, I also showed that inter-individual differences in male performances on a single spatial task was associated with elevated accuracy in task performances in response to female group size (**Chapter Four**), yet males increase their vigilance when housed with larger group sizes (Whiteside et al., 2016). This may suggest that the mechanism underpinning the relationship between group size and cognitive performances, at least in pheasants, is unrelated to vigilance, and, or, may be sex-specific.

7.3.1 Implications and future directions

If larger group size influences learning performances on foraging tasks, learning performance may influence pheasants' foraging efficiency in different harem sizes in the wild. This potential benefit of living in a larger harem has not previously been addressed. To assess whether individuals in larger harems are more efficient foragers, crop samples could be analysed, dietary breadth assessed or growth rates recorded (Whiteside, Sage, & Madden, 2015). This would indicate whether the enhanced learning abilities of living in a larger harem translates into real world foraging abilities. If these beneficial effects on learning influence foraging efficiency, we may expect individuals to be part of larger harems. However, this is not what we see in the wild, in which the average harem size observed was a single male with 2.07 females (Whiteside et al., 2016). Perhaps, the slight reduction in predator detection found in larger harems (Whiteside et al. 2016), or other costs of increasing group size, such as increased competition (Krause & Ruxton, 2002), outweighs the learning benefits that could be gained from living in a larger harem size. This requires further investigation. Similar patterns may be seen in other species in which group living facilitates more efficient foraging behaviour mediated by improved cognition and consequent fitness gains.

Understanding the mechanism behind this relationship could help elucidate which factors of group living are important in influencing cognition. To determine whether reduced individual vigilance behaviour may be the mediating factor in the relationship between larger group size and enhanced cognitive performance, a similar paradigm to the one used in this thesis could be adopted, and in addition, activity budgets and cognitive performances could be measured simultaneously. The prediction being that individuals in larger groups would exhibit fewer or shorter vigilance bouts while completing cognitive testing and would consequently have greater accuracy on learning tasks because they have spent longer paying attention to the task (Guilford & Dawkins, 1987).

This thesis demonstrated the first experimental study of the effect of group size on cognitive performance, hence further investigation into whether these positive effects continue with increasing group size, whether they are linear, or at what point this positive effect plateaus, and whether similar patterns exist within other species, would help us to understand this effect more fully. For instance, the point at which the enhancement on learning performance ceases, may indicate the number of conspecifics that are ‘important’ in influencing individual cognitive performances.

7.4 Aggression, social rank and spatial learning: evidence of co-development?

The more aggressive individual of a dyad is reported as exhibiting superior spatial learning performance compared to the less aggressive individual (mice, Fitchett, Collins, Barnard, & Cassaday, 2005; Francia et al., 2006; rats, Spritzer, Meikle, & Solomon, 2004). I investigated this relationship in the social hierarchy of a group of male pheasants and thus considered how dyadic relationships manifest in a group (**Chapter Three**). Social rank was inferred from aggressive and submissive behaviours and generally, higher ranking individuals were more aggressive and received more submissive behaviour. I found a positive relationship between social rank and spatial discrimination performances. Due to the correlational nature of this investigation, I was unable to determine whether the current social rank caused the differences in learning performances or whether a difference in learning performances pre-determined social rank. Therefore, as a follow up to this, I demonstrated that the relationship between aggression and spatial learning performance is not present during early life (**Chapter Five**). Similarly, early life spatial learning performances were unrelated to adult aggression, reflected in social rank (**Chapter Four**). Hence, I found no evidence that spatial learning performance was inherently linked to aggression and subsequently determined social rank (Figure 7.1). These results suggest that aggression and spatial learning performances become associated over an individual’s life. When attempting to determine whether aggression directly affected the expression of cognitive ability, I tested adult males in an artificial dominance condition, in which they were housed with a group of females and received no direct aggression from other males. This manipulation revealed increases in dominance behaviours, crowing and lateral struts, yet cognitive performances were predicted by males’ group social rank even though they were not subject to the direct aggression associated with that social rank during this particular phase of cognitive testing. These results suggest that it is not solely the direct aggression, or the risk of aggression, that causes social-rank related variation in cognitive performances.

7.4.1 Implications and future directions

The results from this thesis may suggest that the relationship between aggression and spatial learning developed over time and the effects of past social rank and, or, past aggression may have a long-lasting influence on cognitive performance. This potential co-development of aggression and cognitive performance could indicate that the relationship is flexible and dependent on experiences. This raises many further questions. How and when does the relationship between social rank and spatial learning performance emerge? Is one factor stronger than the other in driving this relationship? How long do the effects of social success or social defeat last? Does social rank relate to performances in other cognitive domains? Are these patterns specific to pheasants or are they more general patterns? Attempting to answer these questions would further our understanding of how and why these factors come to be related.

To investigate when the relationship between social rank and spatial learning performances emerges, ideally, long-term studies of individuals from early in life through to adulthood, and their changes in social interactions and the associated changes in learning performances would be beneficial. To separate cause and consequence, captive studies using the same individuals for which social interactions or learning performance could be manipulated, and the changes in the other factor observed, could be compared to controls. Aggressive interactions could be staged, so that winners could be determined experimentally (see Hsu, Earley, & Wolf, 2006). Learning performances could be manipulated by allowing some individuals the opportunity to learn which cues predict reward and providing the remaining individuals with rewards ‘predicted’ by random cues.

To examine how long-lasting the relationship between aggression and spatial learning performance is, long term studies of individuals that have had their social rank manipulated may indicate how long it takes for the effects of aggression on cognition to subside. Such studies would also indicate if this duration differs between individuals of different social ranks, i.e. do lower ranking individuals have their learning performances ‘impaired’ for longer than higher ranking individuals have their learning ‘enhanced’.

Repeating experiments but with tasks aimed at testing different cognitive domains will indicate whether aggression is linked specifically to cognitive processes involved in spatial learning or whether there are more general mechanisms between the link between cognition and aggression. Finally, exploring these ideas in other systems will indicate whether these are common patterns relevant to many systems, or are specific to particular systems, such as polygynous species that locate and defend resources. Understanding these general patterns will give further indication of their function and evolution.

7.5 Cognitive performances, foraging strategy and social structure

The structure of associations and interactions of a species may arise from the attributes of the group members. Fine-scale structure within groups may arise because of non-random assortment between individuals and one factor that may determine this assortativity is the cognitive performances and associated behaviour of such individuals. Previously, this has been inferred indirectly. Individual learning performances have previously been shown to predict foraging strategy in house sparrows, *Passer domesticus* (Katsnelson et al., 2011). Foraging strategy has been linked to disassortative social structure in barnacle geese, *Branta leucopsis* (Kurvers et al., 2010) and individual-level social structure in wild great tits, *Parus major,* with those that adopt the scrounging foraging role being more central in the social network, presumably to maximise their access to resources (Aplin & Morand-Ferron, 2017). It is unclear whether individual differences in cognitive performances cause the emergent social network structure, or such differences arise because of an individual's position within the social network facilitates or constrains their opportunity to develop such cognitive abilities. In **Chapter Six** I demonstrated that in the wild, adult pheasants disassort by their early life inhibitory control and visual discrimination performances. Additionally, network centrality was predicted by early life cognitive performances;

individuals with superior inhibitory control and poor visual discrimination performances were more centrally located. I suggested that cognitive performances may influence foraging strategy, which in turn influenced social structure. Potentially, individuals that possessed particular abilities that negatively impacted their independent foraging ability compensated by increasing their social connections.

7.5.1 Implications and future directions

The relationships between cognitive performances, foraging strategy and social network structure described in previous research (Aplin & Morand-Ferron, 2017; Katsnelson et al., 2011; Kurvers et al., 2010), and in this thesis, suggest that cognitive abilities may influence foraging decisions or foraging efficiency. This remains to be tested directly but would further our understanding of the reasons for a relationship between cognitive performances and social structure. Furthermore, we lack a single study system in which each of these relationships has been demonstrated, as well as determining cause and consequence in each of these relationships. If cognitive abilities translate into producer-scrounger dynamics that influence social structure, this may have implications for selection on cognitive abilities. For instance, if cognitive abilities manifest in producer-scrounger games, this may suggest that frequency-dependent selection (Barnard & Sibly, 1981) operates on cognitive abilities. Thus, the fitness outcomes of an individual's cognitive ability will depend on their social environment. Potentially, individuals could construct their own social niche (Saltz, Geiger, Anderson, Johnson, & Marren, 2016), dependent on their cognitive ability. If particular cognitive abilities are characterised by particular relationships or 'positions' in a social environment, then we can begin to formulate hypotheses for how the social environment may influence an individual's fitness, further our understanding of how cognitive-social phenotypes arise and what this may mean for the evolution of cognitive abilities.

7.6 Reliably measuring cognitive ‘ability’

Quantifying individual differences in cognitive abilities, upon which selection can act is confounded by many variables, such as hunger, motivation, previous experience, salience of cues (Rowe & Healy, 2014), neophobia (Tebbich et al., 2012), and stress (de Kloet et al., 1999; Mendl, 1999). To add further complexity to how cognitive abilities may be expressed, each of these factors likely interact. This thesis highlights that the current (**Chapter Two** and **Chapter Four**) and past (**Chapter Four**) social environment impacts cognitive performances, further complicating the measurement of cognitive abilities. Furthermore, I have demonstrated that individual cognitive performance is affected by changes in some social structure and not others. For instance, in pheasants, if living in a harem with two extra females enhances both female (**Chapter Two**) and male cognitive performances (**Chapter Three**), but the removal of direct social pressure from male competitors does not reduce impairment in lower ranking males’ cognitive ability (**Chapter Three**), this may mean that some relationships influence cognitive performances more than others, and/or, the effects of agonistic relationships are long lasting.

7.6.1 Implications and future directions

The effect of the social environment on the expression of cognitive abilities has great implications for quantifying individual differences. It may also hinder our ability to obtain repeatability estimates for learning performances (Cauchoix et al., 2018) and understanding factors like general cognitive ability (Burkart et al., 2016). The evidence provided by this thesis suggests that incorporating the social environment is necessary when attempting to reliably quantify individual variation in cognitive abilities. In captivity, group sizes can be held constant to make broad-scale social structure comparable; sex ratios can be skewed to reduce aggression and fine-scale social structures such as social rank or affiliative relationships (e.g. non-random associations) can be measured and included in analyses.

With focus shifting towards testing cognition in the wild (Pritchard et al., 2016; Thornton et al., 2014), quantifying recent or past social interactions and how they may influence cognitive performances, is more difficult. Recent technological advances permit the detailed study of associative social structure and social learning abilities in wild birds (Aplin & Morand-Ferron, 2017; Aplin et al., 2013, 2012; Aplin et al., 2015; Aplin, Sheldon, & Morand-Ferron, 2013; Aplin, Farine, Morand-Ferron, et al., 2014; Aplin, Farine, Mann, & Sheldon, 2014; Farine, Aplin, Garroway, Mann, & Sheldon, 2014; Jones, Aplin, Devost, & Morand-Ferron, 2017; Psorakis et al., 2015). Information on individual cognitive performances, independent of social learning (asocial), may be more difficult to obtain as this requires testing individuals out of view of conspecifics. Furthermore, information on agonistic and other affiliative relationships (not simply associative), as well as those social interactions that do not occur at feeding sites, are not trivial to collect. A system is needed which combines the measurement of fine-scale social structures and detailed learning performances in the wild.

7.7 Final summary

This thesis has shown that the relationship between cognitive performances and the social environment is complex and bi-directional (Figure 7.1). In pheasants, cognitive performances and agonistic social relationships are unrelated early in life. Yet, cognitive abilities assayed during early life predict adult affiliative relationships. Adult cognitive performances are responsive to changes in group size, are related to agonistic social relationships in adulthood and demonstrate social rank-related variation, even after the removal of agonistic relationships. Hence, the relationship between cognitive performances and the social environment depends on the cognitive domain, the age at which these factors are measured and the type of social relationship or social structure. The complex picture of how performances in various cognitive domains may or may not be related to different forms of social structure, is just emerging. Efforts to distinguish between cause and consequence in the relationship between cognition and the social environment is critical if we are to understand how selection may have shaped these two factors so pertinent to an individual's life.

7.8 Appendix

Figure 7.1 references

[1] Ashton et al. 2018

[2] Kitaysky et al. 2003

[3] Wascher 2015

[4] Spritzer et al. 2004; Francia et al. 2006; Fitchett et al. 2005

[5] Nicol & Pope 1999

[6] Bunnell, Gore & Perkins 1980

[7] Boogert et al. 2006

[8] Barnard & Luo 2002

[9] Kaczer et al. 2006

[10] Aplin & Morand-Ferron 2017

[11] Wascher 2015

[12] Kulachi et al. 2018

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