ASSESSING FLEXIBILITY IN SHOALING AND LEARNING IN THE TRINIDADIAN GUPPY

Ivon Vassileva

Department of Biology
McGill University, Montreal
July 2019

A thesis submitted to McGill University in partial fulfillment of the requirements of the degree of Master of Biology

Table of Contents

Abstract

The study of social behaviour patterns, including grouping and social learning, have gathered much and continuing scientific interest due to the benefits they provide to individual fitness such as predator protection and increased foraging efficiency. In this thesis, I examined the flexibility of social grouping and social learning behaviours in the Trinidadian guppy, *Poecilia reticulata*. In the wild, guppies display varied grouping tendencies depending on predation and competition levels in their environment. In general, high predation environments lead to stronger grouping tendencies while low predation environments lead to weaker, more transient grouping tendencies. In Chapter 2, I investigated the flexibility of grouping propensities in the absence of changes in predation or competition but with direct manipulation of foraging rewards. I found that guppies can be trained to selectively group with groups of different sizes. As selective grouping can have an impact on access to information, one of the potential benefits of grouping, in Chapter 3 I investigated the flexibility of learning in the guppy. Information can be acquired socially, for example from group members, or asocially, for example through trial and error. Recently, the consensus view of the mechanisms underlying social and asocial learning has shifted. The view that independent, derived mechanisms underlie social learning has shifted to the view that a single unifying mechanism underlies social learning: associative learning. However, few studies have directly investigated this. Thus, in Chapter 3, I attempt to address questions about the independence of social and asocial learning through direct behavioural manipulations. Domesticated guppies were not able to learn a foraging location through either social or asocial cues, suggesting that our training paradigm was not effective in these conditions. These results highlight the importance of establishing a robust and repeatable learning measure. Surprisingly, I found evidence for learning of group size, but not of foraging location, using the same population of fish and very similar training paradigms. Together, these two Chapters suggest that there may be many factors affecting learning, such as previous experience, specifics of the learning task, and stress. Investigating the flexibility of social grouping and learning tendencies can shed light on broader evolutionary questions, such as how sociality evolves and how species can adapt to changing environmental conditions, both natural and human induced.

Résumé

L’étude des modèles de comportement social, y compris le groupement et l’apprentissage sociaux, ont suscité un intérêt scientifique considérable et persistant, dû aux avantages qu’ils ajoutent à la valeur adaptive individuelle comme la protection contre les prédateurs et l’augmentation de l’efficacité de l’approvisionnement. Dans ma thèse j’ai étudié la flexibilité du groupement social et de l’apprentissage social chez les guppies Trinidadien, *Poecilia reticulata*. Dans la nature sauvage, les guppies affichent des tendances de groupement variées selon le niveau de prédation et de compétition de leur environnement. Les environnements à prédation élevée mènent en général à de plus fortes tendances de groupement tandis que les environnements à basse prédation mènent à des tendances de groupement plus faibles et transitoires. Au chapitre 2 j’ai étudié la flexibilité des tendances naturelles de groupement en l’absence de changements dans les niveaux de prédation ou de compétition, mais avec une manipulation directe de récompenses alimentaires. J’ai constaté que les guppies peuvent être entraînés à se grouper de manière sélective avec des groupes comptant un nombre de spécimens différent. Étant donné que le groupement sélectif peut avoir un impact sur l’accès à l’information, ce qui constitue un des avantages potentiels du groupement, j’ai décidé d’étudier au Chapitre 3 la flexibilité de l’apprentissage chez le guppy. L’information peut être obtenue socialement- procurée par exemple par d’autres membres du groupe, ou de manière asociale- par essais et erreurs. La vision consensuelle des mécanismes étant à la base de l’apprentissage social et l’apprentissage asocial a récemment changé. L’opinion que les mécanismes indépendants, dérivés sont à la base de l’apprentissage social a été remplacée par l’opinion qu’il n’y a qu’un seul mécanisme unificateur qui est à la base de l’apprentissage social : apprentissage associatif. Toutefois peu d’études ont examiné directement ce fait. Cela dit, j’ai essayé de soulever au Chapitre 3 des questions sur l’indépendance des apprentissages social et asocial en utilisant des manipulations du comportement directes. Les guppies domestiques n’arrivaient pas à apprendre l’emplacement de la nourriture ni à l’aide d’indices sociaux ni d’indices asociaux, nous suggérant ainsi que notre paradigme d’entraînement n’était pas efficace dans ces conditions. Ces résultats soulignent l’importance de la mise en place de mesures d’apprentissage fortes et répétitives. Étonnamment j’ai trouvé un témoignage du succès de l’apprentissage à choisir un groupe par rapport au nombre de ses spécimens mais non pas du

succès par rapport à l'emplacement de la nourriture malgré l'utilisation de la même population de poisons et des paradigmes d'entraînement très similaires. Ces deux chapitres ensemble suggèrent qu'il pourrait y avoir beaucoup de facteurs affectant l'apprentissage tels que les expériences passées, les spécificités de la tâche à apprendre et le stress. Examiner la flexibilité des tendances du groupement et de l'apprentissage social peut jeter de la lumière sur des questions évolutionnaires plus vastes telles que la manière dont la sociabilité évolue et comment les espèces peuvent s'adapter aux changements des conditions environnementales, provoqués tant par la nature que par les humains.

Acknowledgements

I would like to start off by thanking my wonderful supervisors, Simon M. Reader and Rachel A. Page for their guidance, support and encouragement in taking on and completing my thesis. Simon, thank you for helping me navigate the unexpected twists and turns of research, and for helping me successfully come out on the other end. Your feedback and advice have pushed me to think more critically, to develop my thoughts thoroughly and express myself clearly. Rachel, thank you for allowing me to briefly join your neotropical lab and providing me with the opportunity to explore the world of bat behaviour! Your advice and positivity helped me do great science and be confident in my abilities. I also want to acknowledge my other supervisory committee members, Jon Sakata and Louis Lefebvre for helping guide my thesis and providing valuable comments and suggestions that have greatly improved my work. A special thanks to Julia Horrocks, Carla Daniel and the Barbados Sea Turtle Project, for allowing me to intern at such a great organization and learn so much about applied conservation and sea turtles. Your passion and dedication to your work are a true inspiration.

A huge thank you to all the Reader lab members, your support, encouragement and friendly chatter have made my time here memorable and enjoyable. Pierre-Olivier Montiglio, Melanie Guigueno, Raina Fan, Maria Creighton, Wyatt Toure, Mathilde Colinet, Sarah Turner and Adam Reddon, your friendship and support helped guide my work and make me a better scientist. Your advice and comments were invaluable in the design and analysis of my thesis chapters and other projects. Special thanks to Paul Q. Sims and Laura Chouinard Thuly for their statistics help, and Maria Cabrera for all the fish knowledge! Frederique Truchon, thank you for being such a good friend and an awesome collaborator, you made setting up a new lab space as fun as it could be. To the amazing animal care team throughout the years, thank you for taking such good care of our fish and keeping them healthy and happy for our experiments. Alexandra Berger, Aiman Hadif, Alice Zhang, Beatriz Quineche, Saksham Mungroo, Yi Zhao, Alexandra McCallum and Anya Sivajothy, your help is vital to our lab.

Thank you to the Neotropical Environment Option (NEO) and the Biodiversity Ecosystem Services and Sustainability (BESS) groups for the amazing sense of community provided and for

their financial support. Thank you to the Biology Department support and administration staff, who facilitated various aspects of my projects and my thesis and provided funding for my travels.

Last but not least, I'd like to thank my amazing friends and family for their love and support throughout my every journey. Gabriela, Irida, Diliana and Sara, thank you for being there to listen and encourage me, to help me through the hard times and to celebrate the good. To mom, dad, Stefany, Boris and Meme, without your love and never ending support, I would have never been able to start or complete my Masters. Thank you for pushing me to become the best version of myself and for always believing in me. To my amazing and supportive partner Elias (and his incredible family!), thank you for encouraging me to pursue my dreams, regardless of the distance or time we had to spend apart, and for being so patient and listening to all my fish and animal stories. I love you all.

Contribution to original knowledge

This thesis is manuscript based, with all Chapters containing original scholarship and contributions to knowledge. In Chapter 2, I provide experimental evidence for selective group-size choice in guppies, without changes in predation or competition, drivers of group size in the wild. In Chapter 3, I use a new experimental design inspired by approaches in experimental evolution with the objective of identifying carryovers or trade-offs between social and asocial learning, with the aim of helping to address debates on the specialization of social learning mechanisms. Both Chapters address topics of current interest, in new and promising ways. To the best of my knowledge, I provide the first evidence for experimentally shaping group size preferences, and offer a new experimental approach that can be used to address the independence of social and asocial learning.

Contribution of authors

Chapter 1: General Introduction

Ivon Vassileva wrote the chapter with guidance and input from Simon M. Reader

Chapter 2: Experimental manipulation of grouping tendencies in fish using food reinforcement

Ivon Vassileva and Simon M. Reader designed the study, and Ivon Vassileva conducted the experiment and collected data. Ivon Vassileva, Simon M. Reader and Paul Q. Sims analyzed data. Ivon Vassileva wrote the manuscript with input from Paul Q. Sims and Simon M. Reader. Manuscript to be submitted to Biology Letters. All authors approve submission as part of the present thesis.

Chapter 3: Examining the independence of social and asocial learning in the Trinidadian guppy using reinforcement training

Ivon Vassileva and Simon M. Reader designed the study, Ivon Vassileva piloted and conducted the experiment, collected and analyzed data and wrote the manuscript with input from Simon M. Reader.

Chapter 4: General Discussion

Ivon Vassileva wrote the chapter with guidance and input from Simon M. Reader

CHAPTER 1: GENERAL INTRODUCTION

Group living and social learning:

Group living is a common phenomenon found across species, habitats and geographic locations. Social attraction, which maintains close proximity with others in space and time, is the unifying mechanism of social groups, and group living involves a gradient from temporary aggregations to stable groups with non-random structures (Ward and Webster 2016). Throughout their lifetimes, even solitary living animals may form groups for short periods of time, for example the formation of family groups. Within these groups, individuals will engage in many social interactions which shape their social relationships and fitness (Kutsukake 2009). However, variation in social attraction and social grouping is seen between species, populations and between individuals themselves (Wright et al. 2006; Kappeler et al. 2013). Sociality and social grouping confer various adaptive advantages to members, including antipredator benefits and access to information. In foraging contexts, for example, information from others about resource location and quality can increase foraging efficiency (Ward and Webster 2016). In this thesis, I focus on the Trinidadian guppy, *Poecilia reticulata* to investigate the flexibility of grouping behaviours (Chapter 2), and one of the main proposed advantages of grouping, gaining social information (Chapter 3).

Group living can provide numerous benefits, such as protection from predators, increased foraging efficiency, proximity to potential mates, conservation of heat and water, increased access to information and reduction of energetic costs of movement (Krause and Ruxton 2002). Group living can also incur costs, including increased predator attack rates on larger groups, competition for food and for mates, increased parasite transmission, and misdirected parental care (Krause and Ruxton 2002). Many of these costs and benefits have been demonstrated empirically (Ruxton and Sherratt 2006; Curley et al. 2015). Depending on the perceived costs and benefits, individuals can make choices on whether to engage in grouping behaviours or not, as well as whom to group with. Studies investigating grouping preferences have focused on various aspects, such as species, with a preference for conspecifics over heterospecifics; body length and colour, with a preference for size-matched companions; familiarity, generally with a preference for familiars; and kinship, with kin preferences in some species, all suggesting that groups are non-random assemblages (Krause and Godin 1994; Griffiths and Magurran 1998; Lachlan et al. 1998; Krause and Ruxton 2002; Hoare and Krause 2003; Jones et al. 2010). Further investigations focused on the flexibility of grouping have principally examined how contextual factors (e.g. predation, competition, group composition, etc.) influence grouping decisions (Krause and Ruxton 2002), with very few involving direct manipulations of the costs and benefits experienced. In contrast with varying contextual cues to measure changes in behaviour such as grouping, here I attempt to manipulate the behaviour directly using positive reinforcement training. Thus, in Chapter 2, I investigate the flexibility of shoaling tendencies in the Trinidadian guppy, using this direct reinforcement training, to see if guppy grouping can be manipulated without changes in other factors (such as predation and competition). Understanding the mechanisms of shoaling behaviours and group formation can help in our understating of the evolution of sociality and grouping, and in making predictions about the possibility of information transfer in groups (Hoare and Krause 2003).

Information sharing and social learning are common and important correlates of grouping (but see Reader & Lefebvre 2001). For example, antipredator reactions in banded killifish (*Fundulus diaphanous*) spread faster through a group than if a predator itself is approaching, highlighting the adaptive importance of information transfer through groups (Godin and Morgan 1985). Some researchers note that social learning can emerge as a by-product of forming groups (van der Post and Hogeweg 2008). For example, shoaling fish have been shown to learn about their environment simply as a result of their tendency to group with and follow others and their social learning performance has been shown to be intertwined with grouping behaviour (Brown and Laland 2002; Reader et al. 2003; Chapman et al. 2008; Lindeyer and Reader 2010). Because of grouping tendencies, social learning has been shown to allow for the rapid propagation of behaviours throughout groups, such as route preferences within guppy shoals (Laland and Williams 1997). Furthermore, group size has been implicated in learning speed, with larger groups positively associated with increased foraging efficiency and increased decision-making speed (Pitcher et al. 1982; Day et al. 2001; Ward et al. 2011). Group composition is also an important factor affecting learning performance, with studies finding that guppy shoals containing a mix of bold and shy individuals are most successful in approaching a novel feeder and provide the most benefits for the individuals involved, compared to groups of only bold individuals and groups of only shy individuals (Dyer et al. 2009). If individuals group selectively, this could result in directed social learning, whereby the flow of information is not random, but directed to certain individuals depending on association patterns (Coussi-Korbel and Fragaszy 1995; Lachlan et al. 1998; Duffy et al. 2009). It is important to note that social learning has also been observed in typically solitary species (Lefebvre and Giraldeau 1996; Wilkinson et al. 2010; Webster and Laland 2018). However, group living could possibly facilitate the propensity to acquire social information and learn, because of the proximity with others and abundance of socially available information. As such, when considering the factors underlying variation in social learning it is pertinent to consider group living and flexibility of grouping behaviours as well as learning propensities.

Social learning versus asocial learning:

Acquiring information

There are two main information sources animals can use within their lifetime: personal information and social information. Personal (also called individual or private) information, henceforth called asocial information (following Heyes 1994), is information acquired through an individual's own actions and interactions with the environment. Anything learned from trial and error experiences, habituation and sensitization is termed asocial learning (Kendal et al. 2018). Social information, on the other hand, is information acquired from other individuals, for example through social learning, which has been defined as learning facilitated "by observation of, or interaction with, another individual (typically a conspecific) or its products" (Heyes 1994 p. 207, Hoppitt and Laland 2013; Kendal et al. 2018). Social and asocial information use and learning vary in their costs and benefits. Social learning allows animals to benefit from learning about their environment without the costs of asocial learning, such as the time and energy needed for individual exploration or increased exposure to predators (Brown and Laland 2003). Social learning is particularly advantageous in fairly rapidly changing environments, where the environment is not predictable enough to promote genetic adaptations, but not so unpredictable that learned information becomes inaccurate right away (Hoppitt and Laland 2013). However, there are also costs proposed to be associated with social learning, including increased competition for shared resources and the possibility of acquiring outdated or inaccurate information (Rendell et al. 2011). Conflicting information from social and asocial sources is most likely to occur in temporally or spatially variable environments, and so, making informed decisions is important as it will have a direct effect on an individual's fitness (Dall et al. 2005; Trompf and Brown 2014).

Social learning is widespread across taxa, has been demonstrated in the wild and in the laboratory, and has been found in many contexts, including anti-predator behaviour, learning escape routes or migration paths, foraging locations and novel foods, mate choice copying and nest sites (Brown and Laland 2003; Laland and Hoppitt 2003; Chittka and Leadbeater 2005; Reader and Biro 2010; Grüter and Leadbeater 2014). Well-known examples of social learning include the spread of novel foraging techniques in a wild population of great tits (*Parus major*), and acquisition of novel food preferences in Norway rats (*Rattus norvegicus*) in the laboratory (Galef and Wigmore 1983; Aplin et al. 2014). Social learning has important consequences: it can allow for the spread of novel behaviour patterns (innovations) which can then underlie the spread of behavioural patterns within animal groups, it can shape group structure, affect processes like speciation, and has also been implicated in explanations of the advance of human culture (Boyd and Richerson 1985; Lachlan and Servedio 2004; Cantor et al. 2015).

Social learning strategies

Based on the different pay-offs associated with social and asocial learning, it has been suggested that animals will employ various "social learning strategies" or "biases", to selectively determine when and who to learn from (Laland 2004; Rendell et al. 2011). Social learning strategies are a set of rules that explain in which situations animals will use either social or asocial information, and how they will use social information: the way social learning is employed is what makes it valuable (Heyes 2016a). These rules do not require the animals to understand that they are employing a particular rule or to be able to understand the outcome of their choice (Laland 2004, Shettleworth 2010). Social learning strategies are important as they may influence evolutionary processes on a population level (Kendal et al. 2009). This can lead both to innovations and spread of cultural traditions, but it can also lead to spread of maladaptive information (Kendal et al. 2009).

Several of the proposed social learning strategies suggest when animals should use social over asocial information. An example is the hypothesis that social learning will be used when asocial learning is costly (Laland 2004, Kendal et al. 2005). Use of social information when asocial information is costly has been seen in guppies (Kendal et al. 2004), nine-spined sticklebacks (*Pungitius pungitius*) (but not three-spined sticklebacks (*Gasterosteus aculeatus*)) (Coolen et al.

2003), starlings (*Sturnus vulgaris*) (Templeton and Giraldeau 1996), and three species of monkeys (Day et al. 2003). Other commonly employed strategies include the use of social learning when asocial information is uncertain, unreliable or outdated (Laland 2004, Kendal et al. 2005). These strategies have all been experimentally demonstrated in a range of species (Coolen et al. 2003; Kendal et al. 2004; Nicol 2004; van Bergen et al. 2004). Moreover, several social learning strategies can be employed at simultaneously (Kendal et al. 2018).

Debates on social learning

One major issue researchers have raised regarding social learning strategies and research in the social learning domain is that these strategies are mechanism neutral, meaning they simply provide a functional account of behaviour without considering the underlying mechanisms (Heyes 2012; Kendal et al. 2018). This "blackboxing" of the mechanism has been argued to "no longer be a tenable scientific strategy" (Heyes 2016b p. 2). Instead, research on how, why and when social learning has evolved and the mechanisms underlying its evolution would be valuable (Leadbeater 2015; Reader 2016). In the past, some had argued that social learning strategies must be complex, domain specific and genetically inherited mechanisms of decision-making, however recently this view has been questioned ('complex and domain specific' view: Templeton et al. 1999; 'general and associative view': Heyes 1994, 2012; Heyes and Pearce 2015). Instead, it has been suggested that social learning is domain general, involves taxonomically general psychological mechanisms (like associative learning), and that social and asocial learning both share the same mechanisms (Heyes 1994; Heyes and Pearce 2015). Associative learning can be defined as learning resulting from experiencing predictive relationships either between two stimuli or a behaviour and a stimulus (Shettleworth 2010; Kendal et al. 2018). If a process were completely domain general, that would mean that the same computations are applied to information from social and asocial sources (Heyes 2016a). For Heyes and Pearce (2015), social and asocial learning vary at the level of the cues, not at the level of processing, and learning is simply modulated by the salience of events or cues, the attention paid to them, and the time between events. Furthermore, considering social learning strategies as biases shaping behaviour has been suggested to be a more accurate representation than hard, fixed rules that are blindly applied between individuals and contexts (Kendal et al. 2018). Understanding when and how social learning is used can help us understand what has influenced the evolution of cultural transmission and to avoid "misleading generalizations" about when and how animals use social or asocial learning (Heyes and Pearce 2015, p. 7).

Heyes (2016a) lists four lines of evidence that suggest that social and asocial learning are domain general learning process. Firstly, she presents research in birds and primates finding that social and asocial learning performance co-vary positively (Lefebvre and Giraldeau 1996; Reader and Laland 2002, Reader et al. 2011). Secondly, she argues that since social learning is seen in non-social species, such as tortoises and octopuses (Fiorito and Scotto 1992; Wilkinson et al. 2010), it cannot be a specialized adaptation in social species. Thirdly, the same associations can be learned through both social and asocial learning, as individuals can socially and asocially learn about a single stimulus, the relationship between stimuli or the relationship between stimuli and their outcomes (Heyes 2012). Lastly, she argues that social value can be learned through associative processes, as demonstrated in human studies on decision-making, where the same computations are involved in the processing of information from a social partner and personal experiences (Behrens et al. 2007).

Though consensus seems to be shifting toward a more associative learning view (e.g. Leadbeater and Chittka 2007a, 2007b; Dawson et al. 2013), the degree to which social learning is only due to this general mechanism is still debated. Kendal et al. (2018) suggested that social learning strategies and associative learning theory are not alternatives, but rather that social learning strategies involve associative learning processes combined with specific social learning mechanisms. Kendal et al. (2018) argue that attributing social learning to only associative learning processes is overly restrictive. They note that positive correlations between social and asocial learning in birds and primate do not negate the possibility of separate underlying mechanisms for each, especially when considering a wider range of studies within species showing both positive and negative correlations between the two types of learning (Burkart et al. 2009; Katsnelson et al. 2011; Aplin et al. 2013 see also table 1.1, below). Further experiments show that animals respond differently to social and asocial information, with bumblebees relying more on social than asocial learning when tasks are complex or when the environment is variable (Smolla et al. 2016; Baracchi et al. 2018). This suggests that if animals respond differently to social and asocial information, this can allow for the possibility of the enhancement of one mechanism over the other through e.g. evolved adaptive specializations or developmental specializations (Heyes 2016a; Kendal et al. 2018). When considering the argument that solitary animals are seen to socially learn and thus social learning must be associative, it can be argued that even solitary animals are still exposed to social information. Solitary animals can still learn from mates, broodmates and neighbours (Webster and Laland 2018). As it is currently not known if group living species have special adaptations for social learning, it is important to not completely dismiss the possibility of specializations (Reader & Lefebvre 2001; Webster and Laland 2018; Kendal et al. 2018). However, on both sides of the debate there seems to be agreement that social learning processes in humans and those promoting human culture are based on a special "metacognition" and thus may be more specialized (Heyes 2016b). As can be seen, there is a lot of overlap between social and asocial learning, and conclusions about whether they are governed by the same mechanisms remain inconclusive. This is a topic of rich debate, which I address through the studies that comprise my thesis.

To shed light on this debate, researchers have compared social and asocial learning performance both across and within species on various social and asocial tasks. In these experiments, correlations between social and asocial learning tasks have been taken to support the idea that the two process are not independent, while the absence of correlations suggests the processes may be independent – although no definitive conclusion can be drawn from such correlative evidence (Reader 2003; Reader 2016). Both across and within species, positive, negative and no correlations are seen between measures of social and asocial learning performance (table 1.1). Thus, a definitive, broad conclusion on the relationship between social and asocial learning is hard to make. One possibility to avoid correlational data is to use behavioural manipulations to investigate social and asocial learning performance within individuals. In Chapter 3, I use a reinforcement training paradigm to manipulate the pay-offs associated to social and asocial cues, and thus examine how this influences the resulting learning of foraging locations.

Table 1.1: Correlational studies across and within species comparing social and asocial learning performance in non-human animals.

Across species				
Species	**Social task**	**Asocial task**	**Results**	**Citation**
Pinyon jay (*Gymnorhinus cyanocephalus*; highly social) Clark's nutcracker (*Nucifraga columbiana*; less social)	Motor task or discrimination task learned socially in group	Motor task or discrimination task learned asocially in isolation	Jays: learned faster through social learning than asocial, only in motor task and not discrimination Nutcrackers: learned equally under both conditions	Templeton et al. 1999
Great tit (*Parus major*) Blue tit (*Parus caeruleus*) Marsh tit (*Parus palustris*) Blackbird (*Turdus merula*) Songthrush (*Turdus philomelos*)	Observing foraging task done by conspecifics	Asocial foraging task	Positive correlation between social and asocial task	Lefebvre and Giraldeau 1996 (using data from Sasvari 1979, 1985, 1985)
116 species of primates (2002), 62 species of primates (2011)	Social learning frequency	Innovation frequency	Positive correlation between social learning and innovation	Reader and Laland 2002 and Reader et al. 2011
Human infants 2.5 years old (*Homo sapiens*) Chimpanzees (*Pan troglodytes*) Orangutans (*Pongo pygmaeus*)	Social cognition: Social learning and communication tasks	Physical cognition: spatial memory, object manipulation and tool use tasks	Humans outperformed chimps and orangutans in social cognition tasks. No difference between humans and chimps in physical cognition tasks	Herrmann et al. 2007
Within species				
Species	**Social task**	**Asocial task**	**Results**	**Citation**
Pigeons (*Columba livia*)	Social learning foraging task in group	Novel foraging innovation task in isolation	Positive correlation between social learning and innovativeness	Bouchard et al. 2007
Starlings (*Sturnus vulgaris*)	Novel foraging task in group and diffusion of task	Asocial learning task in isolation	Positive correlation between social and asocial learning	Boogert et al. 2008
Great tits (*Parus major*)	Learning of foraging location (white feeder) from tutor	Learning of foraging location (green feeder) from asocial training	Difference based on personality. Fast exploring birds learned quickly from tutor, switching to white feeder when tutor present. Slow exploring birds did not	Marchetti and Drent 2000
Zebra finches (*Taeniopygia guttata*)	Latency to solve novel foraging tasks in group	Male song complexity	No correlation between song complexity and social foraging task	Templeton et al. 2014
Common marmosets (*Callithrix jacchus*)	Social learning of complex foraging task through video	Goal directed type I innovation and incidental type II innovation in isolation	Negative correlation between social learning and type II (incidental), no correlation with type I (goal directed)	Burkart et al. 2009

Others have attempted to address the same question using conditioning experiments (an associative mechanism), especially in insects, as they have been observed to use social information use and social learning (Grüter and Leadbeater 2014; Leadbeater and Dawson 2017). Bumblebees (*Bombus* spp.) in particular have been shown to be able to learn foraging cues, such as location, colour and smell, through a combination of general social mechanisms and associative learning (Leadbeater and Chittka 2007a, 2007b). Knowing that bees in general have a preference for occupied flowers, this preference has been shown to be strengthened through positive associations with food reward at occupied flowers, and weakened with negative associations of no food reward at occupied flowers (Leadbeater and Chittka 2009). Further, studies have shown that classical conditioning of two learned associations, the conspecific and a colour, and the conspecific and food reward, can lead to learning of a colour and food reward that can be explained without needing an adaptively specialized social learning mechanism (Dawson et al. 2013). In this case, a response to a social stimulus (conspecific feeding) becomes conditioned to an asocial stimulus (flower colour). Similarly, other work has found that response to alarm pheromones (social cue) can lead to learning about asocial stimuli, such that bees were deterred from approaching a certain colour light, if it had been previously paired with conspecific alarm cue (Dawson et al. 2016; Leadbeater and Dawson 2017). These findings demonstrate that what seems like a complex phenomenon may be based on relatively general associative processes. However, differences in the salience of social and asocial cues are also observed. Bumblebees who watched and foraged alongside other conspecifics learned a flower colour preference that they continued to display when foraging with others and alone. However, bumblebees who watched and foraged alongside immobile model bees and bee sized white blocks only displayed the learned the flower colour preference when stimuli were present, not when they were foraging alone (Avarguès-Weber and Chittka 2014). This could suggest a special salience of social cues resulting in different patterns of associative learning compared to non-social static cues (Avarguès-Weber and Chittka 2014). Similarly, when resources were unreliable, bumblebees copied flower choices of realistic looking bumblebee models and not those of rectangular blocks (Smolla et al. 2016). This seems to support the idea of a social learning specialization, potentially a specialized input mechanism, that results in social cues having a specific associated salience to them which induces a certain response, but do not negate that general associative processes are still the underlying driving force. These studies provide evidence that social learning can be shaped, but they have not looked at carryovers with asocial learning. Thus, in my thesis, I attempt to build on this work, adding an asocial component, to test whether general associative processes are sufficient to explain variation in learning of social and asocial cues.

Other factors influencing learning

Social learning is highly variable, with differences in learning tendencies varying across populations and individuals. Decisions on when to use social learning are affected by factors such as age, social rank and reproductive state, and in some cases, individual characteristics have been shown to override social learning strategies (Kendal et al. 2004; Webster and Laland 2011; Mesoudi et al. 2016). Two particularly important factors affecting individual variation in social information use and social learning are within lifetime experiences and personality traits of the individuals. Current, recent (Swaney et al. 2001; Katsnelson et al. 2008; Webster and Laland 2018) and early life experience (Leris and Reader 2016) can affect reliance on social information. It has been suggested that experiential effects rather than evolved differences explain much variation in social learning (Kendal et al. 2009; Reader 2016). Further research has also looked at other personality traits, including sociality, neophobia (fear of novel objects) and aggressiveness, and correlated these traits with measures of social and asocial learning, further highlighting the importance of considering personality within learning tests (Boogert et al. 2006; Lindeyer et al. 2013; Trompf and Brown 2014; Udino et al. 2017). Thus, both social and asocial information is important to individuals and can vary in the degree of use based on the experiences the individuals have had in their lifetimes, as well as on their personality traits. To account for these effects, I tried to provide all subjects with the same recent life experience. In addition, I measured boldness and exploration prior to my tests of social learning.

Across populations of the same species, differences in social learning and social information use have been seen, although this is not widely studied. In doves (*Zenaida aurita*), differences in the way different populations learn from grackles (*Quiscalus lugubris*) have been found, suggesting that population differences in foraging behaviours shape differences in their social behaviours (Carlier and Lefebvre 1997). In guppies, the propensity to use social information and social learning in a foraging context differs across populations (Chouinard-Thuly 2018). Finally, in humans, varying cultural traditions appears to lead to differences in social learning observed across populations (Mesoudi et al. 2016). Taken together, results from experiments on social learning strategies, individual's experiences and personality and population differences, suggest that social and asocial learning are variable. As such, investigations of what underlies this variation are needed. In my thesis, I designed experiments that varied the cost, reliability and certainty of information to provide insight into the mechanisms underlying social and asocial learning.

Study species:

The Trinidadian guppy is an excellent study species to investigate questions on grouping and social learning, because of their highly social behaviour, ability to socially learn, and their tractability in laboratory tests (Brown and Laland 2003; Reader et al. 2003; Magurran 2005). The guppy is a small, tropical freshwater fish native to Trinidad and Tobago, Venezuela, Guyana and Surinam, although they have been found invading waterways across the world (Magurran 2005). In Northern Trinidad, guppies have been found in various distinct rivers with little or no connection between them, providing distinct habitats for different guppy populations (Magurran 2005). Within each river, upstream and downstream sections are often separated by waterfall systems, which limit the dispersal of both guppies and their predators, with upstream sections generally containing no predators, high biomass and low primary productivity, while downstream sections generally contain large numbers of predators, low biomass and high primary productivity (Reznick et al. 2001). Of specific importance to guppies is the variation in predation and competition across sections, with upstream sections having low predation but high competition levels, and downstream sections having high predation and low competition levels (Magurran 2005). Thus, in high predation areas, guppies tend to have high reproductive investment, high shoaling tendencies and low risk-taking tendencies, compared to conspecifics from low predation areas (Seghers 1974; Magurran and Seghers 1994; Song et al. 2011; Herbert-Read et al. 2017; Heathcote et al. 2017). Different behavioural adaptations have been suggested for high and low predation populations, with high predation populations selected for strong shoaling propensities, while low predation populations are selected for aggressiveness and territoriality (Magurran and Seghers 1991). It has been assumed that these environmental conditions are responsible for shaping differences in guppy phenotype and behaviour (Seghers 1974; Rodd and Reznick 1991; Magurran et al. 1992; Magurran 2005).

The guppy has been widely studied, with descriptions of its life history and behaviour investigated both in the wild and in the laboratory, across various contexts (Magurran 2005). Specifically, guppies have been shown to socially learn foraging sites, mate choice, escape routes and anti-predator behaviour (Dugatkin and Godin 1992; Lachlan et al. 1998; Brown and Laland 2002; Reader et al. 2003; Kelley et al. 2003). The propensity to use social information has been found to differ across populations: in one river, the Aripo, guppies from the downstream population copied conspecific foraging location, whereas guppies from the upstream population avoided conspecific foraging location (Chouinard-Thuly 2018). This trend can be attributed to high risk of foraging alone in high predation streams, and to high rates of competition in low predation streams (Chouinard-Thuly 2018). Guppies also display striking grouping preferences, with marked preferences for shoaling with larger groups, familiar individuals and poor competitors (Krause and Godin 1994; Metcalfe and Thomson 1995; Griffiths and Magurran 1998; Lachlan et al. 1998). Factors affecting shoal composition, such as predation and familiarity, are known to impact the diffusion of social information (Hasenjager and Dugatkin 2016, 2017). Furthermore, fish have been found to be particularly suitable for cognition and behaviour experiments as they are not only easy to work with, but they also share a conserved brain structure and physiology with other vertebrates, facilitating potential generalization of results (Bshary et al. 2014).

Male and female guppies are sexually and behaviourally dimorphic, with differences in body shape, size and colouration, as well as differences in grouping, foraging and sexual behaviours (Magurran 2005). Physically, females have larger bodies and are less colourful than males, and behaviourally have been shown to group more often and for longer periods of time, forage for a longer time and spend less time engaging in sexual activities than do males (Magurran 2005). Female guppies having been shown to have more shoal fidelity, be more exploratory and innovative, and to be more likely to use social information in general (Lindstrom and Ranta 1993; Reader and Laland 2000; Magurran 2005; Lucon-Xiccato et al. 2016). To avoid confounding the results with possible effects of sexual interactions, I chose to use only females in my thesis work.

Due to the female guppy's diverse repertoire of social behaviours, including selective shoaling and selective use of social information across contexts, as well as the large amount of knowledge about the species and general ease of manipulation, this is a valuable system to use to address my research questions. Knowing that natural guppy populations vary in their shoaling and social information use propensities, likely driven by differences in levels of predation and competition, further indicates they are a useful system that can be used to address the flexibility of these processes. Thus, my goal was to manipulate shoaling and social learning tendencies, without changes in predation and competition, to investigate how flexible they are without their natural drivers in the wild.

Thesis overview:

The previous sections discuss the importance of grouping and social information use and social learning on individuals and populations across species, as well as the importance in addressing the underlying mechanisms of social and asocial learning. In this thesis, I will investigate the flexibility of shoaling and learning tendencies in the Trinidadian guppy. Binary choice designs are ideal for investigations of cue attractiveness as in my studies, by allowing for the manipulation of pay-offs associated with the cues in a directed way (Ward and Webster 2016). Highlighting the importance of grouping to both individual fitness and social learning, I investigate the flexibility of grouping behaviours of female guppies in Chapter 2, by manipulating the pay-offs associated with grouping with shoals of different sizes. Small fishes, such as the guppy, have been said to be an ideal study species for experimental studies of grouping behavior (Ward and Webster 2016). Knowing their wide range of natural variation in shoaling propensities in the wild, I asked whether I could experimentally shape their preferences without the effects of predation and competition. I show that female guppies are capable of selectively grouping with a shoal of a particular size, suggesting that grouping behaviours are flexible and can rapidly be trained. Group living has been implicated in the evolution of more complex social behaviours such as increased communication, cooperation and cheating, and as such is an important area of investigation (Curley et al. 2015). The costs and benefits associated with grouping further affect the fitness of members and have far reaching implications in the success and survival of group members and populations.

In Chapter 3, I experimentally tested for the carryover and trade-off effects of social and asocial learning by creating a design to tease apart social and asocial learning tendencies in individuals. The idea behind this design stems from research that explores evolutionary constraints, using experimental evolution in an attempt to create specific phenotypes (Brakefield and Roskam 2006; Dunlap and Stephens 2014), combined with ideas from the comparative studies of social and asocial learning outlined above. Specifically, work in experimental evolution has created and tested models that modify cue reliability along two continuums to test if different learning phenotypes can be created over evolutionary time (Dunlap and Stephens 2014). I developed a similar design for within lifetime learning of social and asocial cues, incorporating and controlling for factors shown to influence learning such as prior and current experiences, cue reliability and personality. While the results did not provide support for either of the expected outcomes, my study showed that learning may not be as robust as expected. In my experiments, guppies did not learn foraging location from social or asocial cues. Overall, I found that guppies show flexibility in their grouping tendencies and can learn to group with certain size groups.

CHAPTER 2: EXPERIMENTAL MANIPULATION OF GROUPING TENDENCIES IN FISH USING FOOD REINFORCEMENT

Vassileva, I., Sims, P.Q. & Reader, S.M

To be submitted to Biology Letters

Abstract:

Many animals form groups, with multiple benefits to group living such as protection from predation and access to social information. However, costs are also associated with grouping, including increased competition with conspecifics. Here, we address how experience shapes grouping tendencies. The Trinidadian guppy, *Poecilia reticulata,* is a social fish species that is often seen to shoal (group) with conspecifics, but with marked variation in grouping tendencies among wild populations. In general, guppies, like many fish, prefer larger groups. However, guppies form smaller groups under low predation conditions, likely the result of intraspecific competition. We examined flexibility in shoaling tendencies in female guppies by experimentally shaping shoaling preferences through reinforcement training. Fish were rewarded with food for 20 trials when joining either large (six-fish) or small (two-fish) shoals, followed by a preference test. Before training, subjects preferred the large shoal. Reinforcement training altered this prior preference, with fish trained to the small shoal increasing their relative preference for this shoal. Thus, guppy shoaling tendencies are flexible, can adjust rapidly to recent experience, and fish can be trained to selectively approach and group with differently sized shoals, even without changes in predation or competition.

Introduction:

Social grouping confers many benefits to group members, such as increased predator protection, foraging success, mating opportunities and access to social information (Krause and Ruxton 2002; Hoare and Krause 2003). However, group living can also increase competition for mates or resources and the risk of disease transmission (Pitcher and Parrish 1993; Altizer et al. 2003). Thus, individuals often make decisions about whether to join or leave a group. Grouping behaviours have been widely investigated by numerous scientific fields, including work in insects, fish, birds and mammals, including humans, showing variations in the costs and benefits of grouping between individuals and contexts (da Silva et al. 1994; King et al. 2011; Ward and Webster 2016; Markham and Gesquiere 2017; Couzin 2018; Ohkubo et al. 2018; Hintz and Lonzarich 2018). Group size and composition vary considerably, and have been shown to be shaped by evolution, early-life experiences and current conditions (Ward and Webster 2016).

Grouping has been extensively studied in fish, and a common finding is that fish prefer to shoal (group) with larger over smaller groups of conspecifics (Krause and Godin 1994; Lachlan et al. 1998; Cabrera-Alvarez et al. 2017). Compared to smaller groups, larger groups show increased foraging efficiency, increased speed and accuracy of decision making about predators, and reduced predation rates (e.g. Pitcher et al. 1982; Day et al. 2001; Ward et al. 2011; Ioannou et al. 2012). However, fish grouping tendencies vary. For example, in the Trinidadian guppy, *Poecilia reticulata,* a well-studied small tropical fish, populations vary extensively in grouping behaviour, making them a valuable system for the study of the factors shaping grouping tendencies (Magurran 2005). Females form groups of 2-40 individuals, shoaling more than males (Magurran 2005). Guppies are particularly well studied in the Northern Trinidad mountain range, where the upstream and downstream sections of the rivers they inhabit are characterised by differences in predation, biomass and productivity (Reznick et al. 2001; Magurran 2005). These characteristics have been found to affect guppy shoals, with guppies in high predation, downstream sites typically forming larger, more cohesive shoals than guppies in low predation, upstream sites (Seghers 1974; Magurran 2005; Huizinga et al. 2009). This pattern is also seen in laboratory reared fish, suggesting a genetic basis to this behaviour (Magurran and Seghers 1994; Huizinga et al. 2009).

Like many animals, guppies use numerous factors and cues in grouping decisions, including individual phenotype, the characteristics of potential shoals and shoalmates, the costs of alternative options, and local predation risk (Griffiths and Magurran 1998; Lachlan et al. 1998; Magurran 2005; Jones et al. 2010; Mühlhoff et al. 2011; Cabrera-Alvarez et al. 2017). An open question is the extent to which group size preferences can be shaped by direct experience with the benefits of grouping, rather than by external factors such as predation risk, potentially indicating the ability to adjust to changing conditions. Firth and Sheldon (2015) note the necessity and novelty of direct experimental manipulations of social associations in order to identify causal impacts of grouping decisions. To address this, they manipulated food access in wild songbirds over 90 days and found impacts on the social network as well as on other traits (Firth and Sheldon 2015; Firth et al. 2015, 2016). Similarly here, we use food reinforcement training in guppies to vary the benefits of joining a large or small group and to investigate plasticity in grouping preferences. We deliberately used a limited training regime in order to examine whether short-term changes in grouping benefits can impact later shoal choice. We tested shoaling preferences of adult female guppies before and after a 10-day, 20-trial, food reinforcement training period, which trained fish to selectively approach shoals of different sizes. Training treatments were counterbalanced, with half of the fish rewarded for the small shoal (small-shoal-rewarded treatment) and half for the large shoal (large-shoal-rewarded treatment). We expected high levels of shoaling with the large shoal before training (Lachlan et al. 1998; Mühlhoff et al. 2011; Cabrera-Alvarez et al. 2017). We predicted that the large-shoal-rewarded treatment would increase subjects' relative preference for the large shoal, with the opposite effect in the small-shoal-rewarded treatment. We were particularly interested in whether a prior shoaling preference could be reversed, suggesting an even stronger influence of experience on grouping tendencies.

Methods:

We placed 36 female guppies, previously reared in common garden housing (see electronic supplementary material), in pairs in 'home' tanks (*l* 40 x *w* 20 x *h* 25 cm; water depth 20 cm). We paired fish to avoid any isolation stress, and given that the repeated measures design required individuals to be identified, we placed a larger and a smaller female in each tank. An additional 20 female shoal fish, taken from a separate common garden tank to avoid prior familiarization between subjects and shoal fish, were placed into two home tanks of 10 guppies each. Shoal fish tanks were divided in two sections using plastic white opaque dividers with guillotine trap doors (figure 2.1a). The trap doors were always open except during training when an assemblage of either two ('small shoal') or six ('large shoal') fish, haphazardly selected for body size, were guided into the front compartment and the guillotine door closed. We ensured that fish of various body sizes were in each shoal. We measured subjects' shoaling preferences before and after training.

Training:

Subjects remained in home tanks throughout training to avoid any stress related to tank transfers. One week prior to training, we pre-trained fish twice daily to feed only from previously unfamiliar feeders (see electronic supplementary material). All fish fed from the feeders. During training, the subjects' tank was placed between the two shoal fish tanks (figure 2.1a). Shoals of two or six fish were revealed on each side, with subjects (*n* = 18 per treatment) rewarded for approaching either the large or small shoal depending on their randomly-assigned training treatment. The feeders were removed after 5-min and the subject tank was returned to its housing location. Training was conducted twice daily, in the morning between 08:00 and 12:00 and in the afternoon between 13:00 and 17:00, for 10 days. The location of the different sized shoals was randomly assigned daily.

Preference test:

Tests were conducted in a testing tank (*l* 77 x *w* 32 x *h* 32 cm; water level 27 cm) with a white plastic bottom that was visually divided into five sections (figure 2.1b): two outermost 'tight' shoaling zones measuring 5 cm from the shoal (i.e. 2-3 fish body lengths), two 'loose' shoaling zones a further 5 cm from the shoal, and the central 'neutral' zone measuring 35 cm. Two 2L plastic bottles (10 cm *d*) were suspended into the water from a vertical bar. To simulate shoals moving apart, each bottle could be pulled to opposite ends of the tank (modified from Keenlyside 1955). Each bottle contained either two or six fish haphazardly selected from the shoal fish, representing the small and large shoal. A single subject was placed into a transparent plastic cylinder at the starting point, with both bottles in the centre of the tank. Following a 5-min acclimation, the subject was released and the shoals were slowly pulled apart at a constant speed to opposite ends of the tank. Once the subject swam into either of the loose shoaling zones, a 5-min observation period began.

Behavioural measures and data analysis:

Subjects locations were recorded live by eye and by a webcam (C920 HD Pro Webcam, Logitech, USA) filming from above. Fish within two or four body lengths have been classified as shoaling, with both criteria in use (Pitcher and Parrish 1993; Chapman et al. 2008; Morell et al. 2008; Jones et al. 2010). We thus recorded both tight shoaling (within two body lengths) and loose shoaling (within four body lengths) to check the robustness of our measures. The tight and loose shoaling measures gave a very similar pattern of results (see electronic supplementary material tables S2.1 and S2.2). For conciseness, we present the tight shoaling results below.

We calculated the 'large shoal preference' (LSP), a measure of the preference for the large relative to the small shoal, by subtracting the time spent with the small shoal from that spent with the large shoal. We prefer this value over a proportional score, as it provides an intuitive measure that accounts for the magnitude of the shoal preference (for discussion, see electronic supplementary material). We examined the effect of training treatment by calculating the change in LSP from before to after training. We then ran a linear model (LM) on the LSP change, with training treatment and body mass (mean centred and standardized to 1 SD) as predictors. We then tested if the LSP change differed from chance by analysing the large-shoal-rewarded and small-shoal-rewarded treatments separately with further linear models, with body mass as a fixed effect. As our linear models cannot determine the preference for one shoal or another, to examine whether fish preferred the large over small shoal, we used Wilcoxon sign rank tests to examine if LSP differed from chance in each of the four possible combinations of time (before/after training) and treatment (large/small-shoal-rewarded).

Results:

Subjects spent most of the 300-sec trial tightly grouping with one of the two shoals, both before (91% and 96% of the trial on average in fish assigned to the large vs. small shoal rewarded treatment, respectively) and after training (92% and 89%, respectively). Before training, subjects spent significantly more time with the large versus the small shoal in both treatments (Wilcoxon: large-shoal-rewarded treatment: $t_{17}= 45.50$, $p = 0.047$; small-shoal-rewarded treatment: $t_{17}= 77.50$ $p= 0.002$). However, the strength of this initial preference was greater in the large-shoal-rewarded treatment compared to the small-shoal-rewarded treatment (see electronic supplementary material, figure S2.1), making it particularly important to address the change in preference due to training.

There was a significant effect of treatment on the change in large shoal preference over training (LM: $t_{33}= -2.78$, $p = 0.009$; figure 2.1, electronic supplementary material table S2.1). Subjects rewarded for approaching small shoals decreased their time spent with the large shoal relative to the small shoal (*LM:* $t_{16}= -2.19$, *p (compared to 0)*= 0.044, electronic supplementary material table S2.2), while subjects rewarded for approaching large shoals increased their relative preference for the large shoal, although not significantly so (*LM:* $t_{16}= 1.68$, *p (compared to 0)*= 0.11, electronic supplementary material table S2.2). After training, large-shoal-rewarded subjects maintained a significant preference for the large shoal (Wilcoxon t_{17}= 85.50*,* p <0.001), while this effect was not significant in small-shoal-rewarded subjects (Wilcoxon t_{17}= 43.50*,* p= 0.059).

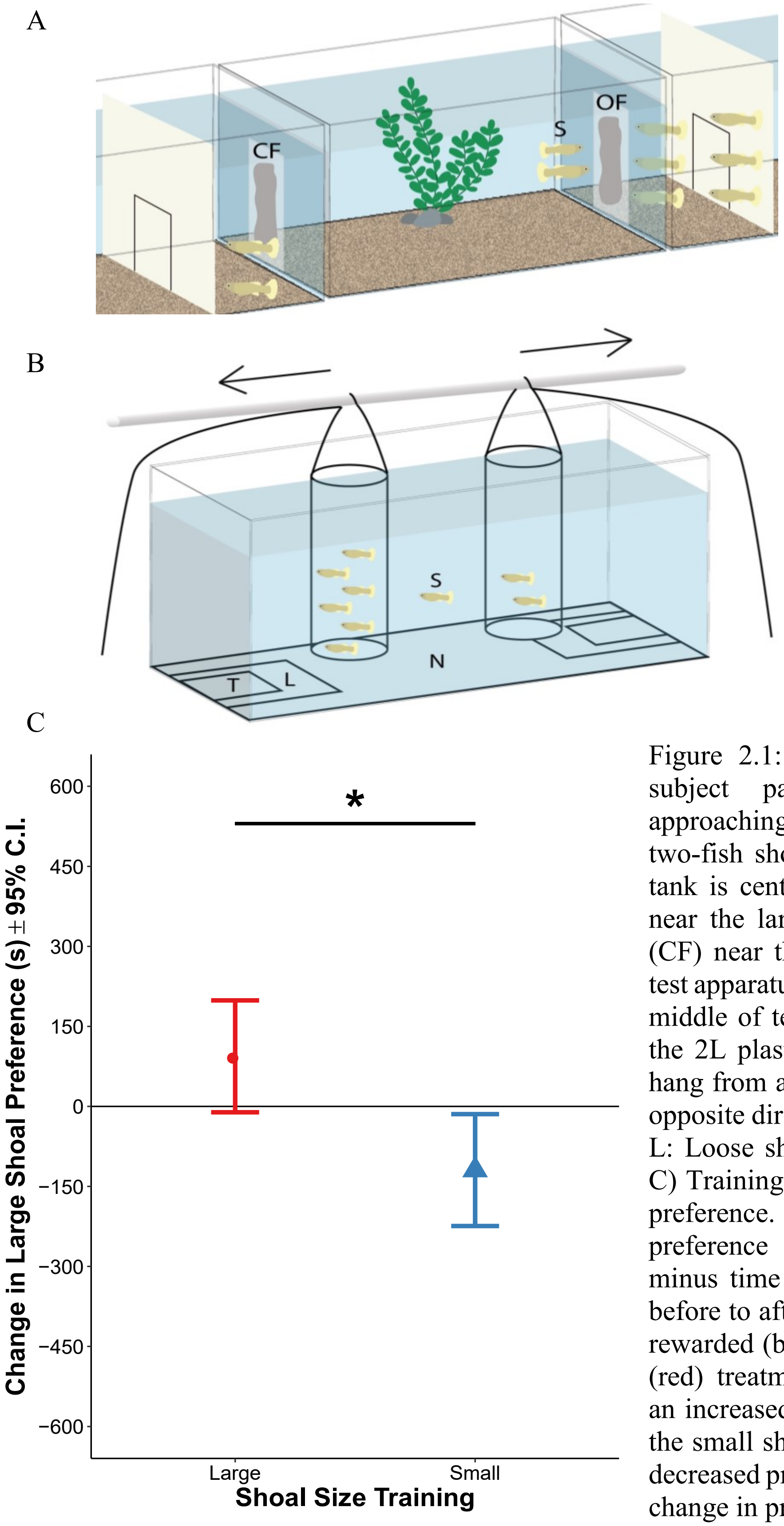

Figure 2.1: A) Training apparatus. The subject pair (S) is rewarded for approaching the large six-fish shoal. A two-fish shoal is on the left. The subject tank is central with an open feeder (OF) near the large shoal and a closed feeder (CF) near the small shoal. B) Preference test apparatus. Individual subject fish (S) in middle of testing tank with two shoals in the 2L plastic bottles. The plastic bottles hang from a vertical bar and are moved in opposite directions. T: Tight shoaling area; L: Loose shoaling area; N: Neutral zone. C) Training shapes changes in large shoal preference. Change in the large shoal preference (time spent with large shoal minus time spent with small shoal) from before to after training for the large-shoal-rewarded (blue) and small-shoal-rewarded (red) treatments. Positive scores indicate an increased preference for the large over the small shoal, negative scores indicate a decreased preference, and zero indicates no change in preference. * :$p < 0.05$.

Discussion:

We show that female guppy shoaling tendencies are flexible and that fish can be trained to selectively approach and group with shoals of different sizes. Strikingly, training for the small-shoal-rewarded condition reduced an initial prior preference for the large shoal in only twenty 5-min training trials. In the large-shoal-rewarded treatment, fish increased their preference for the large shoal as predicted, but this was not statistically significant, perhaps due to a ceiling effect: there was a high initial preference for the large shoal. Previous work has demonstrated that group size choice depends on context, internal state, and shoal characteristics (e.g. Krause and Godin 1994; Hoare et al. 2004; Hellstrom et al. 2016). Here we show that rapid learning through reinforcement training affects shoaling propensities in a directed manner.

Our methodology provides a useful route to investigate the costs and benefits of grouping, by allowing for the direct manipulation of behavioural phenotype (here, group size preference). Depending on the longevity of the trained preference, this training approach provides a route to test adaptive hypotheses about shoaling. Furthermore, effects on the brain such as changes in neurochemistry, as well as carryovers to other behaviours can be assessed. Our approach allows grouping propensities to be changed and their consequences measured without changing prevailing conditions such as predation risk or feeding motivation that could cloud assessment of the causal contribution of association preference. A particularly interesting area is the impact of selective grouping, as is seen in our experiment, on the social transmission of information, potentially directing what is learned based on the shoal preferences of individuals (Laland and Williams 1997; Lachlan et al. 1998; Chapman et al. 2008; Duffy et al. 2009).

Differences in preferred group size can be explained by benefits that both large and small groups confer to individual members. Large groups can provide increased protection from predators and increased foraging success due to shared information or joint action (Pitcher and Parrish 1993; Day et al. 2001; Liker and Bokony 2009; Ioannou et al. 2011). However, small groups may provide advantages such as reduced conspicuousness to predators, reduced competition over limited resources, and even informational advantages under certain circumstances (Chapman et al. 2008; Ford and Swearer 2013; Kao and Couzin 2014). In our study, reinforcement training overrode a prior preference. Thus shoal-size preference in guppies is not fully constrained by genetics, predation or competition effects. This malleability could allow for very fast adaptive changes under varying conditions. An open question is how widespread this flexibility and rapid learning is. Conceivably, temporal and spatial changes in the costs and benefits of grouping in guppies (Magurran 2005) may have shaped an unusually flexible system. Alternatively, similar flexibility under direct reinforcement may be extremely widespread, even in species where the benefits of group size are relatively fixed. In conclusion, our study supports the idea that guppies are flexible in their grouping behaviours, and will base their decisions on the relative costs and benefits associated with their options.

Acknowledgements: We thank our work-study students for caring for our experimental fish, the Reader laboratory members and Rachel Page for their support and helpful comments, and Helen Rodd for donating fish.

Funding: This research was funded by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC; grants #418342-2012, #429385-2012) and the Canadian Foundation for Innovation (grant #29433), awarded to SMR, and NSERC-CREATE Biodiversity, Ecosystem Services and Sustainability and NEO-STRI-McGill fellowships to IV.

Ethics: Methods were approved by the Animal Care Committee of McGill University (Protocol 2015-7708) and were conducted in accordance with the ethical guidelines of the Canadian Council on Animal Care and ABS/ASAB.

References:

Altizer, S., Nunn, C. L., Thrall, P. H., Gittleman, J. L., Antonovics, J., Cunningham, A. A., Dobson, A.P., Ezenwa, V., Jones, K.E., Pedersen, A.B., Poss, M., & Pulliam, J. R. C. 2003. Social organization and parasite risk in mammals: Integrating theory and empirical studies. *Annual Review of Ecology, Evolution and Systematics*, 34, 517-547.

Cabrera-Álvarez, M. J., Swaney, W. T., & Reader, S. M. 2017. Forebrain activation during social exposure in wild-type guppies. *Physiology & Behavior*, 182, 107-113.

Chapman, B. B., Ward, A. J. W., & Krause, J. 2008. Schooling and learning: early social environment predicts social learning ability in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 76, 923-929.

Couzin, I. D. 2018. Synchronization: The key to effective communication in animal collectives. *Trends in Cognitive Sciences*, 22, 844-846.

da Silva, J., Macdonald, D. W., & Evans, P. G. H. 1994. Net costs of group living in a solitary forager, the Eurasian badger (*Meles meles*). *Behavioral Ecology*, 5, 151-158.

Day, R. L., MacDonald, T., Brown, C., Laland, K. N., & Reader, S. M. 2001. Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour*, 62, 917-925.

Duffy, G. A., Pike, T. W., & Laland, K. N. 2009. Size-dependent directed social learning in nine-spined sticklebacks. *Animal Behaviour*, 78, 371-375.

Firth, J. A., & Sheldon, B. C. 2015. Experimental manipulation of avian social structure reveals segregation is carried over across contexts. *Proceedings of the Royal Society B: Biological Sciences*, 282.

Firth, J. A., Sheldon, B. C., & Farine, D. R. 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. *Biology Letters*, 12.

Firth, J. A., Voelkl, B., Farine, D. R., & Sheldon, B. C. 2015. Experimental evidence that social relationships determine individual foraging behavior. *Current Biology*, 25, 3138-3143.

Ford, J. R., & Swearer, S. E. 2013. Two's company, three's a crowd: Food and shelter limitation outweigh the benefits of group living in a shoaling fish. *Ecology,* 94, 1069-1077.

Griffiths, S., & Magurran, A. 1998. Sex and schooling behaviour in the Trinidadian guppy. *Animal Behaviour*, 56, 689-693.

Hellström, G., Heynen, M., Borcherding, J., & Magnhagen, C. 2016. Individual consistency and context dependence in group-size preference of Eurasian perch. *Behavioural Processes*, 133, 6-11.

Hintz, W. D., & Lonzarich, D. G. 2018. Maximizing foraging success: the roles of group size, predation risk, competition, and ontogeny. *Ecosphere*, 9.

Hoare, D. J., Couzin, I. D., Godin, J. G. J., & Krause, J. 2004. Context-dependent group size choice in fish. *Animal Behaviour*, 67, 155-164.

Hoare, D. J., & Krause, J. 2003. Social organisation, shoal structure and information transfer. *Fish and Fisheries*, 4, 269-279.

Huizinga, M., Ghalambor, C.K., & Reznick, D.N. 2009. The genetic and environmental basis of adaptive differences in shoaling behaviour among populations of Trinidadian guppies, *Poecilia reticulata. Journal of Evolutionary Biology*, 22, 1860-1866.

Ioannou, C. C., Bartumeus, F., Krause, J., & Ruxton, G. D. 2011. Unified effects of aggregation reveal larger prey groups take longer to find. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2985-2990.

Ioannou, C. C., Guttal, V., & Couzin, I. D. 2012. Predatory fish select for coordinated collective motion in virtual prey. *Science*, 337, 1212-1215.

Jones, K. A., Croft, D. P., Ramnarine, I. W., & Godin, J.-G. J. 2010. Size-assortative shoaling in the guppy (*Poecilia reticulata*): The role of active choice. *Ethology*, 116, 147-154.

Kao, A. B., & Couzin, I. D. 2014. Decision accuracy in complex environments is often maximized by small group sizes. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133305.

Keenleyside, M. H. A. 1955. Some aspects of the schooling behaviour of fish. *Behaviour*, 8, 183-247.

King, A. J., Narraway, C., Hodgson, L., Weatherill, A., Sommer, V., & Sumner, S. 2011. Performance of human groups in social foraging: the role of communication in consensus decision making. *Biology Letters*, 7, 237-240.

Krause, J., & Godin, J.-G. J. 1994. Shoal choice in the banded killifish (*Fundulus diaphanus, Teleostei, Cyprinodontidae*): Effects of predation risk, fish size, species composition and size of shoals. *Ethology*, 98, 128-136.

Krause, J. D., & Ruxton, G. D. 2002. Living in Groups. Oxford; Oxford University Press.

Lachlan, R. F., Crooks, L., & Laland, K. N. 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, 56, 181-190.

Laland, K. N., & Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, 53, 1161-1169. d

Liker, A. S., Bókony, V., & Brown, J. H. 2009. Larger groups are more successful in innovative problem solving in house sparrows. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 7893-7898.

Magurran, A. E. 2005. Evolutionary Ecology: the Trinidadian Guppy. Oxford; Oxford University Press.

Magurran, A. E., & Seghers, B. H. 1994. Predator inspection behaviour covaries with schooling tendency amongst wild guppy, *Poecilia reticulata*, populations in Trinidad. *Behaviour*, 128, 121.

Markham, A. C., & Gesquiere, L. R. 2017. Costs and benefits of group living in primates: an energetic perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160239.

Morrell, L. J., Croft, D. P., Dyer, J. R. G., Chapman, B. B., Kelley, J. L., Laland, K. N., & Krause, J. 2008. Association patterns and foraging behaviour in natural and artificial guppy shoals. *Animal Behaviour,* 76, 855-864.

Mühlhoff, N., Stevens, J. R., & Reader, S. M. 2011. Spatial discounting of food and social rewards in guppies (*Poecilia reticulata*). *Frontiers in Psychology*, 2, 68-68.

Ohkubo, Y., Yamamoto, T., Ogusu, N., Watanabe, S., Murakami, Y., Yagi, N., & Hasegawa, E. 2018. The benefits of grouping as a main driver of social evolution in a halictine bee. *Science Advances*, 4, 1700741.

Pitcher, T. J., Magurran, A. E., & Winfield, I. J. 1982. Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology*, 10, 149-151.

Pitcher, T. J. Parrish, J. K. 1993. Functions of Shoaling Behaviour in Teleosts. In T. J. Pitcher (Ed.), The Behaviour of Teleost Fishes (pp. 294-337). Boston, MA: Springer US.

Reznick, D., Butler Iv, M. J., Rodd, H., & Dolph, S. 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *The American Naturalist*, 157, 126-140.

Seghers, B. H. 1974. Schooling behavior in the guppy (*Poecilia reticulata*): An evolutionary response to predation. *Evolution*, 28, 486.

Ward, A., & Webster, M. 2016. Sociality: The Behaviour of Group-Living Animals. Switzerland: Springer

Ward, A. J. W., Herbert-Read, J. E., Sumpter, D. J. T., & Krause, J. 2011. Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America*. 108, 6.

Supplementary materials:

Methods:

Housing conditions and subjects

Subjects and demonstrators were taken from a domestic strain of guppies, gifted to us by the Rodd laboratory at the University of Toronto. Fish stocks were obtained from a mix of commercial suppliers and subsequently bred in both the Rodd and Reader laboratories. In the Reader laboratory, subjects and demonstrators were reared and housed in two 115 l tanks (*l* 91 x *w* 45 x *h* 30 cm, water height 20 cm) in mixed-sex and mixed-age conditions. Fish were housed before and throughout the experiment in 12-hour light:dark cycles. All tanks were equipped with an air-driven sponge filter, thermostat controlled heaters and enriched with gravel and artificial plants. Water temperature was maintained at 26.0 ± 1.0 °C. Before the experiment began, fish were fed once a day with crushed vegetable flake food (Tetramin, Tetra, Germany) and rehydrated decapsulated brine shrimp (Brine Shrimp Direct Inc., Utah, USA). Throughout the experiment fish were fed from feeders described below. Two pairs of subjects died during the experiment (final $n = 36$).

Experimental design:

Subjects were randomly assigned to one of two treatments: the large-shoal-rewarded and small-shoal-rewarded treatments, which trained fish to approach and feed at an unfamiliar six fish or two fish shoal, respectively. The shoaling test, conducted before and after the training, consisted of a choice test, where the small and large shoals were placed in two clear containers that were slowly moved away from the subject to opposite ends of the tank. Testing and training were thus conducted in slightly different contexts.

Training:

During training, the subject housing tank was placed in between the two shoal fish tanks, as described in the paper (figure 2.1a). Following a 5-min acclimation period, shoals of two and six fish were made visible on each side. The location of the different size shoals was randomly assigned daily. Thirty seconds after the reveal, two gelatin strip feeders (described below, figure 2.1a) were placed vertically in the subject's tank, leaned against the side of the tank wall where the shoals were visible. The open gelatin strip was placed at the location of the shoal for which they were being trained (small or large) while the closed strip was placed at the untrained shoal. Subjects in the large-shoal-rewarded treatment were fed at the six-fish shoal, while subjects in the small-shoal-rewarded treatment were fed at the two-fish shoal. Subjects were given 5 min to feed, after which the feeders were removed and the subject tank was placed back in the housing location.

Feeders

Feeders were made of a thick transparent plastic sheet, cut into a 3x9 cm strip. Unflavoured gelatin (Knox, E.D. Smith Foods Ltd., Canada) was prepared and mixed with crushed flake food (Tetramin, Tetra, Germany) and freeze dried bloodworms (*Glycera* spp., Omega One, OmegaSea, USA). The mixture was then poured onto the strips and left to dry for at least 2 hours. Half the strips were left with the gelatin exposed (open feeder), half were covered with a second transparent strip of the same size preventing access (closed feeder).

Behavioural measures and data analysis:

The large shoal preference (LSP) was calculated by subtracting the time spent with the small shoal from that spent with the large shoal. We prefer this measure over a proportional score because it minimizes the impact of subjects that spend little time with either shoal, and thus do not strongly express a choice. That is, the LSP measure treats subjects shoaling 200 of 210 seconds with the large shoal as expressing a stronger preference for the large shoal than subjects spending 2 of 2.1 seconds (LSP is 190 vs. 1.9 while proportion is 0.95 for both). We then calculated the effect of treatment on the LSP by taking the difference in the LSP before and after training, allowing us to account for the considerable individual variation in shoaling preference that we observed (see figure S2.1). This score represents the change in preference for the large shoal after training, with positive scores indicating an increased preference, negative scores indicating a decreased preference and zero indicating no change in preference.

Throughout the experiment, subjects were housed and trained in pairs. During tests, subjects were tested individually. We ran a Pearson's correlation test on the difference in LSP of each fish pair to examine whether individual behaviour in the tanks was non-independent. As there was not a significant correlation between pairs (Pearson's $r = -0.04$, $p = 0.87$), we treated subjects as if they were independent.

Results:

The tight and loose shoaling measures gave the same qualitative results and the same effects were statistically significant, apart from the test of whether the change in LSP in small-shoal-rewarded fish over training was significant (table S2.2: tight shoaling: $p = 0.04$; loose shoaling: $p = 0.06$). Figure S2.1 illustrates the change in large shoal preference: a significant preference for the large shoal is seen in both treatments before training, and in the large-shoal-rewarded treatment after training. As expected, in the large-shoal-rewarded treatment, fish increased their large shoal preference, whereas in the small-shoal-rewarded treatment fish decreased their large shoal preference.

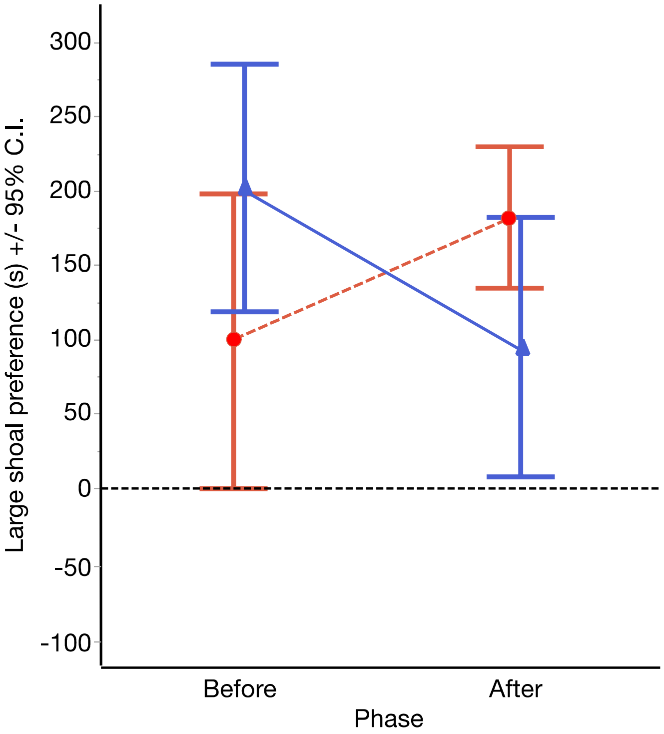

Figure S2.1: Mean large shoal preference (time with large shoal minus time with small shoal) across time within the small-shoal (blue solid line, triangles) and large-shoal (red dotted line, circles) rewarded treatments. Connected lines indicate change from before to after training. Error bars are 95% confidence intervals of the means.

Table S2.1: Training treatment shapes changes in large shoal preference. Predictor estimates of two linear models, one for tight shoaling (within two body lengths; top) and one for loose shoaling (within four body lengths; bottom). Estimate represents change in LSP over training in seconds; the reference treatment level was large-shoal-rewarded. *n* = 36. * : $p < 0.05$.

Shoaling model measure	**Predictor**	**Estimate**	**Std. Error**	**df**	**t-value**	**p-value**
Tight	Intercept	93.87	53.54	33	1.75	0.09
Tight	Treatment	-213.23	76.73	33	-2.78	0.009*
Tight	Standardized mass	-53.82	38.91	33	-1.38	0.18
Loose	Intercept	102.20	58.86	33	1.74	0.09
Loose	Treatment	-220.73	84.35	33	-2.62	0.01*
Loose	Standardized mass	-59.97	42.78	33	-1.40	0.17

Table S2.2: Effects of small and large shoal-rewarded treatments on the change in large shoal preference over training. Predictor estimates of linear models on the difference in LSP for tight shoaling (within two body lengths; top) and loose shoaling (within four body lengths; bottom), testing if the change in LSP in the large-shoal-rewarded treatment and small-shoal-rewarded treatment differs from 0. Estimates represent change in LSP over training in seconds. *n* = 18 for each treatment. * : $p < 0.05$; † : $p < 0.1$.

Model	**Shoaling measure**	**Predictor**	**Estimate**	**Std. Error**	**df**	**t-value**	**p-value**
Small-shoal-rewarded treatment	Tight	Intercept	-125.83	57.40	16	-2.19	0.044*
	Tight	Standardized mass	-82.47	57.37	16	-1.44	0.17
Large-shoal-rewarded treatment	Tight	Intercept	86.98	51.66	16	1.68	0.11
	Tight	Standardized mass	-23.32	53.19	16	-0.44	0.67
Small-shoal-rewarded treatment	Loose	Intercept	-126.54	63.37	16	-1.20	$0.06^{\dagger}$
	Loose	Standardized mass	-95.45	63.33	16	-1.51	0.15
Large-shoal-rewarded treatment	Loose	Intercept	93.68	56.02	16	1.67	0.12
	Loose	Standardized mass	-22.20	57.86	16	-0.38	0.71

Linking statement to Chapter 3:

In Chapter 2, I showed that grouping tendencies are malleable and can be changed through reinforcement training. Increased access to social information has been suggested as one of the most important benefits of group living. For fish, simply joining a group can lead to learning about their environment, with larger groups learning about their habitat and receiving rewards faster than smaller groups, in general. The experiments I performed in Chapter 2, in combination with previous research on multiple fish species, provide evidence for selective grouping, where individuals choose to join a group based on its size and/or composition. Having been able to shape one aspect of social behaviour, social grouping, I next wanted to see if I could also experientially shape social information use and learning. Using the same population of fish, and a similar training paradigm, in Chapter 3 I investigated selective learning of foraging locations from social and asocial cues to test their independence.

CHAPTER 3: EXAMINING THE INDEPENDENCE OF SOCIAL AND ASOCIAL LEARNING IN THE TRINIDADIAN GUPPY USING REINFORCEMENT TRAINING

Vassileva, I. & Reader, S.M

Unpublished manuscript

Abstract:

Social learning – learning from others – has commonly been assumed to require independent, evolutionarily specialized learning processes. Recently, however, it has been suggested that general associative learning processes can underpin much social learning, with past experience shaping social information use. We examined the independence of social and asocial learning processes by experimentally manipulating the pay-offs associated with socially and asocially acquired information. Trinidadian guppies, *Poecilia reticulata*, were trained to selectively prefer social or asocial information, with the aim of measuring the effects of this training on both social and asocial learning, thus examining any carryovers or trade-offs. In addition, we quantified personality traits including boldness and exploration. Low levels of both social and asocial learning performance prevented formal investigation of carryovers or trade-offs between social and asocial learning. Additionally, we found no correlation between the personality measures, boldness and exploration, as well as no correlation between the learning and personality measures. We discuss possible explanations for these results. If social and individual learning are not independent from one another, this will have implications for our understanding of social learning mechanisms as well as for the adaptive costs and benefits of social learning.

Introduction:

Social learning has been observed in a multitude of species from insects to primates, prompting questions about the underlying processes and mechanisms (Thorpe 1963; Galef and Laland 2005; Heyes 2012; Leadbeater 2015). Learning is seen as an adaptation to changing and variable environments; as such, social learning, or learning from others, can be particularly important as it can allow for large amounts of information to be acquired, without the costs of exploration to the individual (Laland 1996; Dunlap and Stephens 2009, 2014). The mechanisms behind social learning are currently understudied, however, as most studies to date have focused on the outcomes of social learning, rather than the underlying mechanisms (Leadbeater 2015; Reader 2016). This is slowly changing as theories are being put forward and tested (e.g. Dawson et al. 2013; Avarguès-Weber and Chittka 2014; Heinen and Stephens 2016; Leadbeater and Dawson 2017), but more concrete evidence needs to be provided to support the existing theories.

Some researchers argue that social learning involves specialized mechanisms that have evolved independently of asocial learning mechanisms, while others argue that social learning is a facet of associative learning, learning of an association between two stimuli or a stimulus and a response, sometimes in the form of conditioning (Heyes 1994, 2012; Heyes and Pearce 2015; Kendal et al. 2018). Several studies support the idea that associative learning can account for individual and species differences in social learning (Heyes and Pearce 2015), but this has only been explicitly tested in very few studies. It is possible that social learning mechanisms are not completely different from those of asocial learning, but rather an additionally evolved and specialized components of asocial learning mechanisms or even the result of differences in input mechanisms (perceptual, attentional or motivational) (Rogers 1988; Heyes 1994; Lefebvre and Giraldeau 1996; Heyes 2012; Leadbeater 2015; Reader 2016).

Our study aims to be a step in addressing the question of whether social and asocial learning are controlled by the same or different underlying mechanisms. Our experimental design has been influenced by series of previous studies (discussed in detail below) that 1) examined correlations between social and asocial learning performance, 2) compared learning of social and asocial stimuli using conditioning and 3) varied environmental reliability. We attempt to combine aspects of each by (1) comparing social learning and asocial learning performance (2) before and after a series of training sessions designed to make individuals either proficient asocial foragers or social foragers (3) by varying the reliability of either cue.

Correlational studies are a great starting point to investigate whether there are potential similarities between learning of different cues, but differences in results and design make it difficult to draw definitive conclusions (Lefebvre and Giraldeau 1996; Reader and Laland 2002; Bouchard et al. 2007; Burkart et al. 2009; Reader et al. 2011; Templeton et al. 2014). Conditioning experiments have also been instrumental in investigating whether learning from social and asocial cues occurs in the same way and in investigating whether social and asocial cues are equally salient, however their results also vary (Dawson et al. 2013; Avarguès-Weber and Chittka 2014; Dawson et al. 2016; Smolla et al. 2016; Leadbeater and Dawson 2017). Further, others have looked at varying environmental reliability and reliability of cues. Across species, there seems to be a preference for asocial information, unless social information is easier to attain and is less costly/ more reliable

(Templeton and Giraldeau, 1996; Kendal et al. 2004; van Bergen et al. 2004; Toelch et al. 2009; Leadbeater and Florent, 2014). For example, Heinen and Stephens (2016) varied the reliability of both social and asocial cues, as well as the reliability of the environment, finding that social and asocial cues were used more when they were reliable, however when the environment was unreliable, asocial cues were used more often than social cues (Heinen and Stephens 2016). Such results have been informative in identifying some trade-offs between social and asocial learning, however combined, the strengths of each approach can be used to directly address trade-offs in the use of social and asocial learning using a novel training paradigm.

Work in evolutionary developmental biology has attempted to address the issue of how traits evolve together by imposing artificial selection on pairs of traits to investigate how flexible and separable the evolution of different traits is, providing inspiration for a similar approach to examine the independence of behavioural traits within the lifetime of an individual (Reader 2006). Such an approach has been used to examine the genetic basis and developmental mechanisms of trait pairs and to help understand patterns of phenotypic variation seen in the wild (Brakefield and Roskam 2006). For example, researchers working with butterfly wing spots have modified the size of the anterior and posterior wing spots through artificial selection across generations to examine their flexibility (Brakefield and Roskam 2006). Other work has used experimental evolution to investigate the evolution of learning. For example, Dunlap and Stephens (2014) addressed how selection influences learning in fruit flies (*Drosophila* spp.), varying the reliability of colour and odour cues over multiple generations, resulting in evolved changes in cue salience (see also Dwyer 2015).

In a similar way, but within the lifetime of an individual, we propose to vary the reliance on social and asocial learning through training, and thus to investigate the independence of social and asocial learning performance. By modifying social and asocial learning reliability using conditioned training, we hope to compare effects on social and asocial learning propensities and potentially tease them apart. Learning has been shown to be able to be shaped within the lifetime of individuals (Leadbeater 2015). As previous studies have shown that guppies are capable of learning a foraging location both through asocial and asocial cues (Laland and Williams 1997; Laland and Reader 1999; Reader and Laland 2000; Dugatkin and Alferi 2003; Magurran 2005), we conducted our experiment in a foraging context. We predict that it would be possible to manipulate social and asocial learning propensities by manipulating prior experiences. By having two experimental conditions, each training for a type of learning, and a control group receiving no directed training, we hope to be able to tease apart the effect of different training conditions. The control group allows us to eliminate the possibility that time or simple repetition of the test leads to an increase in learning performance. We made the following specific predictions: 1) we can train fish to learn a foraging task socially, which will lead to an improvement on subsequent social learning tests, 2) we can train fish to learn a foraging task asocially, which will lead to an improvement on subsequent asocial learning tests, and 3) that carryover effects will be seen in both groups, as fish trained to a social task will also display an improvement on asocial learning tests, and fish trained to an asocial task will display and improvement on social learning tests (figure 3.1a). Alternative hypotheses are that a trade-off will be seen, with training in one task type leading to a deficit in another (figure 3.1b), or that no carryover or trade-off effects will be seen, with training on one task type having no effect on another (figure 3.1c). If carryovers were found, this would suggest generalization of responses to social and asocial cues, whereas if no carryovers or trade-offs are found, this would suggest there is no such generalization. If trade-offs between social and asocial learning performance were found, this would suggest that 1) experience cannot shape individual and social learning independently, restricting the flexibility of learning strategies; 2) common underlying mechanisms may be involved, and are causing some type of interference in learning of cues (e.g. subjects perceive different cue domains as the same) although identifying the type of mechanism would require further work.

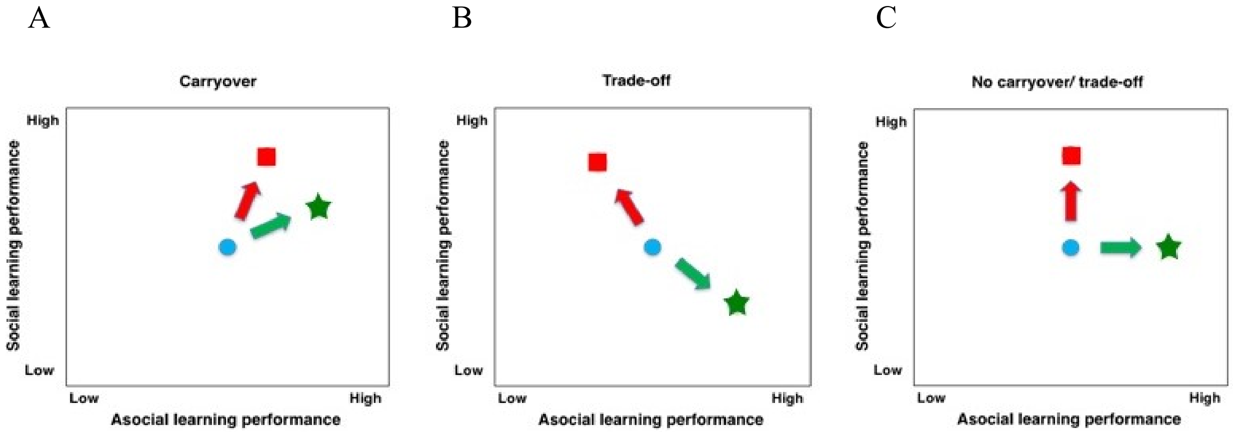

Figure 3.1: Hypothesis plots of predicted results for experiment conducted to manipulate social and asocial learning performance in guppies. Blue point indicates the average performance at baseline, which is expected to be intermediate. Red (square) indicates training for social learning and green (star) indicates training for asocial learning. A: In the case a carryover is seen, improving performance of one learning task will also lead to a subsequent increase in performance of the other. B: If a trade-off is seen, improving performance of one learning task will result in decrease in performance of the other. C: If no carryover or trade-off effects are seen, improving performance on either learning task will have no effect on learning of the other.

Personality traits of individuals, such as boldness and exploration, can also influence whether an individual will attend to and use social information (Mesoudi et al. 2016). Boldness, is a measure of the risk-taking behaviour of an individual, generally measured on a bold-shy continuum (Fraser et al. 2001). Exploration, commonly positively correlated with boldness, is a general measure of reaction to novelty (Réale et al. 2007). Results regarding the relation between boldness, exploration and social learning performance are mixed (Mesoudi et al. 2016). In fish, boldness has been positively correlated with increased learning speed and learning accuracy in both social and asocial contexts (Dugatkin and Alfieri 2003; Trompf and Brown 2014). Exploration has also been positively correlated with use of social demonstration in fish, with more exploratory individuals being more willing to follow other social demonstrators (Nomakuchi et al. 2009). In birds, trends are less clear, as fast exploring male great tits (*Parus major*) rely more on social information from a conspecific, whereas the opposite is seen in zebra finches (*Taeniopygia guttata*), with highly exploratory individuals being less likely to use social information in a foraging context (Marchetti and Drent 2000; Rosa et al. 2012). As can be seen, social information use does seem to correlate with personality type, and an individual's tendency to rely on social information may be consistent over time, and as such is an important variable to be investigated (Rosa et al. 2012). We will thus quantify personality metrics for each individual and compare these to learning performance in our different treatments (Mathot and Giraldeau 2008).

If our results were to show that we can train guppies to socially and asocially learn foraging tasks, we planned to design a 2x2 experiment, varying the reliability of social and asocial cues simultaneously, such that both are either reliable or both unreliable, or one is more reliable than the other, somewhat similar conceptually to the Dunlap and Stephens (2014) study of learning by experimental evolution. Knowing the mechanisms and specializations of social learning will be beneficial for studying the fitness consequences of the possible mechanisms, establishing the costs of benefits of any specializations as well as determining the distribution and impact of social learning through the evolution of these mechanisms (Heyes 1994; Reader 2003; Heyes 2012; Leadbeater 2015). Additionally, the processes of social and asocial learning underlie other important and highly studied areas of behaviour including foraging choices and innovation (Heyes and Galef 1996; Reader 2003). If social learning really is part of associative learning, this will be very exciting as it potentially means that any animal who can form associations can learn socially.

Methods:

Overview

We planned a repeated measures design, where the social and asocial learning propensities of the subjects were to be measured, followed by a training period to either favour social or asocial information use, after which the same social and asocial learning tests were to be repeated (see figure 3.2, discussed further below, for an overview of planned and completed tests). Before the initial learning tests, we pre-trained subjects to familiarize them with the social cue (a shoal of fish) and the asocial cue (a set of green Lego® blocks). This design allowed us to attempt to determine the independence of social and asocial learning, as well as identify any crossovers or trade-offs, by experimentally manipulating the pay-offs associated with socially and asocially acquired information.

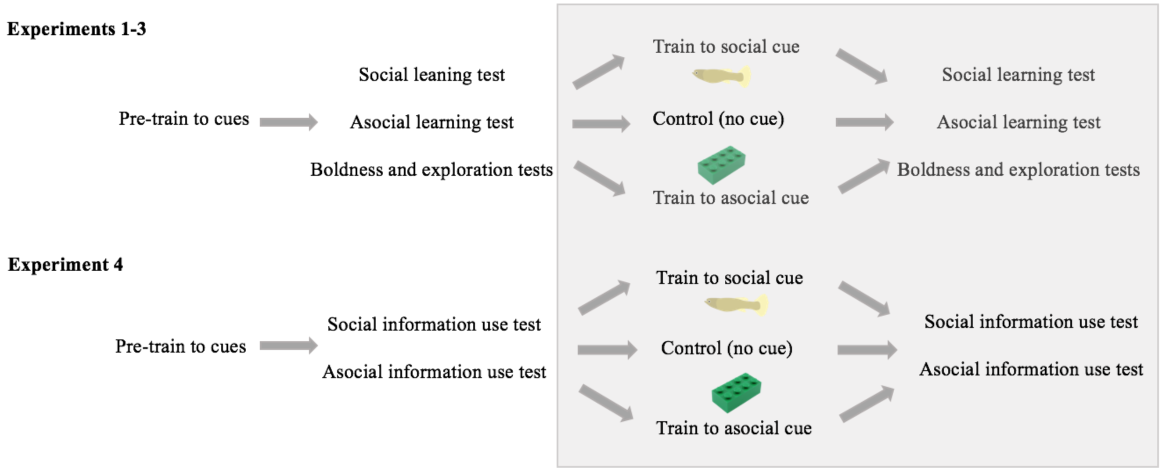

Figure 3.2: Visual representation of the experiments as planned and as actually conducted. The stages shaded in grey were planned but not carried out.

Subjects and housing

Subjects and shoal fish were taken from a domestic population of guppies, the gift of the Rodd laboratory (University of Toronto). These fish were the descendants of domestic guppies originally obtained from a mix of commercial suppliers and bred in the Rodd laboratory and subsequently our laboratory. Fish were housed in two 30-gallon (91 cm x 46 cm x 30 cm) tanks, in mixed-sex and mixed-age conditions. A total of 20 females were taken to be used as test subjects and placed in pairs (to avoid any isolation stress of individual housing) in 5-gallon (40 cm x 20 cm x 25 cm) experimental 'home tanks'. Each home tank was divided in two with a lengthwise mesh divider, such that the fish could see and smell each other, but not physically interact or enter the other half of the tank (figure 3.3). Subjects remained in their home tanks throughout the duration of the experiment, with both training and testing conducted within these tanks. This was done to minimize the potential stress of moving the fish between tanks (Sneddon et al. 2016). One subject died during the experiment (final N=19). An additional 14 'demonstrator' females, to be used as the social shoal, were taken from a separate tank to avoid any prior familiarization between subjects and shoal. Shoal fish were placed into a separate 5-gallon (40 cm x 20 cm x 25 cm) tank. All tanks were equipped with an air-driven sponge filter, thermostat-controlled heaters and were enriched with gravel and artificial plants. Water temperature was maintained at 26.0 ± 1.0 °C. 10%

of water was replaced with warm, conditioned water every 7 days. Levels of nitrate, nitrite, ammonia, hardness and pH were tested every 3-4 days, and if levels were high a 30% water change was conducted. Lights came on in 12-hour light/dark cycles, with lights on at 7:00h, and a 30-minute dusk/dawn period.

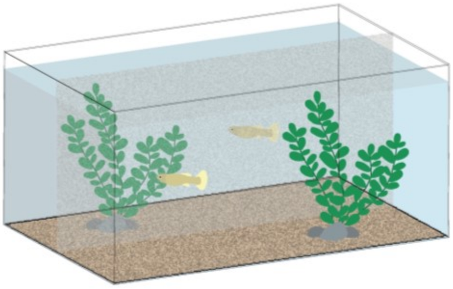

Figure 3.3: Home tank of subjects with 2 fish per tank separated by a see-through mesh divider.

Procedures:

Subjects were placed into their home tanks and then for 7 days they were trained to feed from unfamiliar petri dish feeders (5 cm diameter), with this being the only food available during this time. Unflavoured gelatin (Knox, E.D. Smith Foods Ltd., Canada) was prepared and mixed with crushed flake food (Tetramin, Tetra, Germany) and poured into the petri dishes and left to dry for at least 2 hours. Half the petri dishes were left uncovered, while half were covered with petri dish lids, such that the food looked identical but in only the uncovered dishes was the food accessible. Once all subjects were reliably feeding from the petri dishes, (i.e. approached and fed within 2 minutes of the feeder being added) pre-training began.

Pre-training:

To familiarize the fish with the different cues prior to their first learning tests, a pre-training period was conducted, during which the fish were exposed to both the social and asocial cues (shoal of 4 conspecifics and 4 green plastic Lego® blocks, respectively), and given food at the cued locations. Before the beginning of each training session, an opaque divider was placed alongside the mesh divider in the middle of the tank, such that the paired fish could not see each other and each could be trained individually. Two cylindrical glass containers (8.5 cm diameter) were suspended approximately 5 cm above the bottom of the tank, using clamps, at each end of the tank (lengthwise). One container held the cue and one was empty. Each day, the four conspecifics for the social cue were chosen semi-randomly from the group of 14 demonstrators, ensuring that the demonstrators were of different body sizes. The four green Lego® blocks for the asocial cue were also chosen randomly, from a set of ten. Ten seconds after the cue containers were placed, two petri dishes were placed underneath the cue containers: a covered petri dish under the empty container and an open petri dish under the cued container (figure 3.4a: training to fish, figure 3.4b: training to blocks). Fish were given 2 minutes to explore and feed. This was done to train the subjects to associate food location with the cues (both social and asocial) and an empty container with inability to access food. Subjects could not distinguish between the closed and open feeders until they attempted to peck at them. Cues were shown two times a day in four bouts of 5 days each. After each bout, subjects had seen each cue 10 times, and after the fourth bout, they had seen each cue a total of 40 times. Previous experiments on fish from the same origin showed learning of a binary choice task in only 20 trials (Chapter 2). The location and order in which the cues were shown was randomized.

General training:

Based on performance on the learning tests, the subjects were to be pseudo-randomized into either the social, asocial or control conditions. Pseudo-randomization was planned to ensure an even distribution of learning performance across conditions. Training was to be conducted in the same way as pre-training, except that depending on the condition, fish saw either only the group of conspecifics (social condition), only green Lego® blocks (asocial condition) or no cues at all (control condition). Training was to be done for 10 days, once a day with four trials per day. This would result in 40 trials with the training cue.

Social and asocial learning tests:

As with the training, the social and asocial learning tests were conducted in the home tanks of the subjects. An opaque divider was placed to prevent the paired subjects from seeing each other. A clear holding cylinder was placed in the center of the tank, and the subject fish was ushered inside using a small net. The subject was given 30 seconds to acclimate to the holding cylinder, after which the two containers were suspended 5 cm above the bottom of the tank, in the same way as in the training. One container was cued and the other container was empty, just as with the training. Depending on the test, either a group of 4 conspecifics were the cue, or a group of 4 green Lego® blocks, for the social and asocial tests respectively. As with the training, the four conspecifics for the social cue and four green Lego® blocks for the asocial cue were chosen semi-randomly. After the cue containers were suspended, a 2-minute observation period began, during which time the subject could observe the containers and cues, from inside the holding cylinder. No feeders were present during this period. After 2 minutes, the containers were removed, two covered petri dish feeders were placed on either end and the subject was released from the holding cylinder (figure 3.4c). The subject was given 2 minutes to explore and make feeding attempts on the two covered feeders. The time spent in the two 10-cm end zones of the cued side and empty side, the time spent interacting with the covered feeders and the time in the 20-cm neutral zone were recorded.

Social and asocial information use:

The social and asocial information use tests were identical to the social and asocial learning tests, with the only difference being that the cued containers (i.e. shoal or blocks) were not removed during the test. This allowed for the fish to interact with the cues during the 2 minutes of exploration and attempted feeding.

These tests were conducted four times (social and asocial learning three times, henceforth called experiments 1-3, and social and asocial information use once, henceforth called experiment 4), once after each pre-training bout, to test for the baseline social and asocial learning levels of the subjects. The proposed experimental design was to continue to the general training, and then once more perform the social and asocial learning tests to compare learning propensities after directed training (figure 3.2). However, after these bouts we found no evidence for learning (see Results), meaning that it seemed unlikely that we would be able to detect changes in learning. The experiment was thus stopped early. We present data from the initial social and asocial learning tests only.

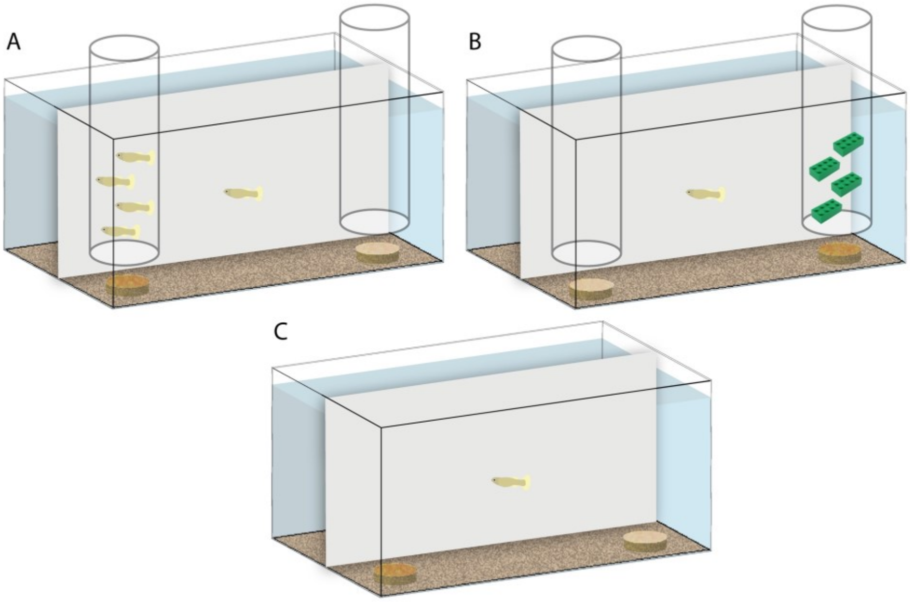

Figure 3.4: Training and testing tank set ups. All experiments were conducted in the subjects' home tanks, with an opaque divider added alongside the central mesh divider so the subjects could not see each other during experiments and training. A) Social training to shoal of 4 fish. Open feeder was placed underneath the cued cylinder and closed feeder under empty cylinder. B) Asocial training to 4 Lego® blocks. Open feeder was placed underneath the cued cylinder and closed feeder under empty cylinder. C) Learning test. Cues removed and two closed feeders placed. Closed feeders here were made a different colour for exposition, the open and closed feeders looked identical in experiments.

Boldness and exploration:

Boldness and exploration tests were conducted in a 10-gallon tank (50 cm x 25 cm x 30 cm) with a clear bottom divided into 32 squares, filled with 10 cm of water to limit vertical movement within the tank. A square plant refuge (9 cm x 9 cm) was placed in the middle, and inside it a clear plastic cylinder. The subject was placed into the plastic cylinder and acclimated for 1 minute (figure 3.5a). The cylinder was then slowly lifted, and the time until the subject emerged from the refuge was recorded, with a maximum of 120 seconds (figure 3.5b). After the subject left the refuge, the refuge was slowly and remotely removed and the exploration test began (figure 3.5c). The subject's movements were recorded for 5 minutes. Specifically, the number of squares entered and the amount of time in the periphery (outside 20 squares) and the amount of time in the inside (12 squares) were recorded (Burns 2008; Leris 2016). Boldness was recorded as the amount of time it took to leave the refuge as well as the time spent in the inside 12 squares of the open field test. Exploration was recorded as the number of squares entered during the open field test.

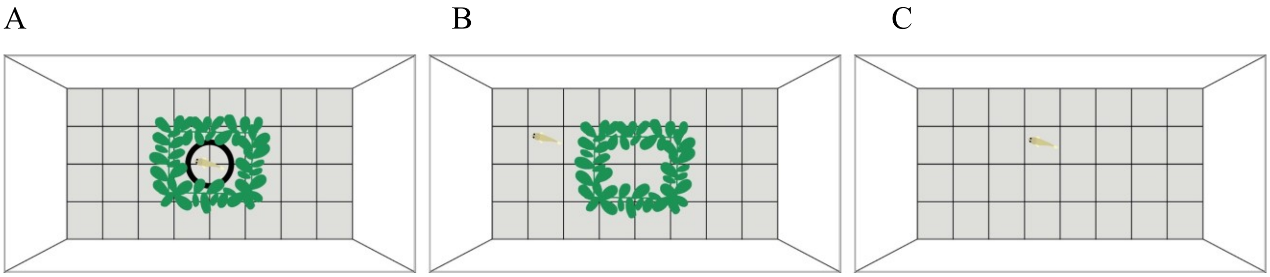

Figure 3.5: Top down view of boldness and exploration tank set ups. A) Acclimation: Subject acclimating in clear plastic cylinder inside the square plant refuge (tank center). B) Boldness (time to leave refuge): Subject released from plastic cylinder and allowed to exit plant refuge. C) Boldness (time in periphery) and exploration (number of squares entered): subject free to explore tank.

Behavioural measures and data analysis:

Subject movement was scored during the trials by hand. A high-resolution webcam (C920 HD Pro Webcam, Logitech, USA) was mounted on a tripod approximately 1-meter in front of the tank, so that the scoring could be done from behind a blind. During the learning tests, the time spent in the two 10 cm end zones of the cued and empty side, the time spent interacting with the covered feeders and the time in the 20-cm neutral zone were recorded. As each test comprised of two trials, the average of the two was taken, and from this, the difference score was calculated by taking the (time spent at the cued location and feeder) – (time spent at the empty location and feeder). This difference score was used to visualize learning, with a difference score of 120 means the subject spent all the time with the cue, a difference score of -120 means the fish spent all the time with the empty container, and a score of 0 means they spent equal amounts of time with both or that it spent no time at all with either feeder. We predicted that low but detectable levels of learning would be seen on both tests, and thus a positive difference would be expected. Alternatively, we predicted that subjects may avoid the cues, in which case a negative difference would be expected. We used the Benjamin-Hochberg procedure to correct for multiple comparisons (Benjamini and Hochberg 1995). To assess whether there were any consistencies between individuals we analyzed the repeatability of the data across attempts using a linear mixed effects model and a linear mixed effects model with weighted errors by experiment to correct for heteroscedasticity in the data

(Nakagawa and Schielzeth 2010; Mauze et al. 2015). We further ran Pearson's correlations to examine correlations between the social and asocial tests. Lastly, we ran Pearsons's correlations on the boldness measures to examine individual differences in personality traits.

Results:

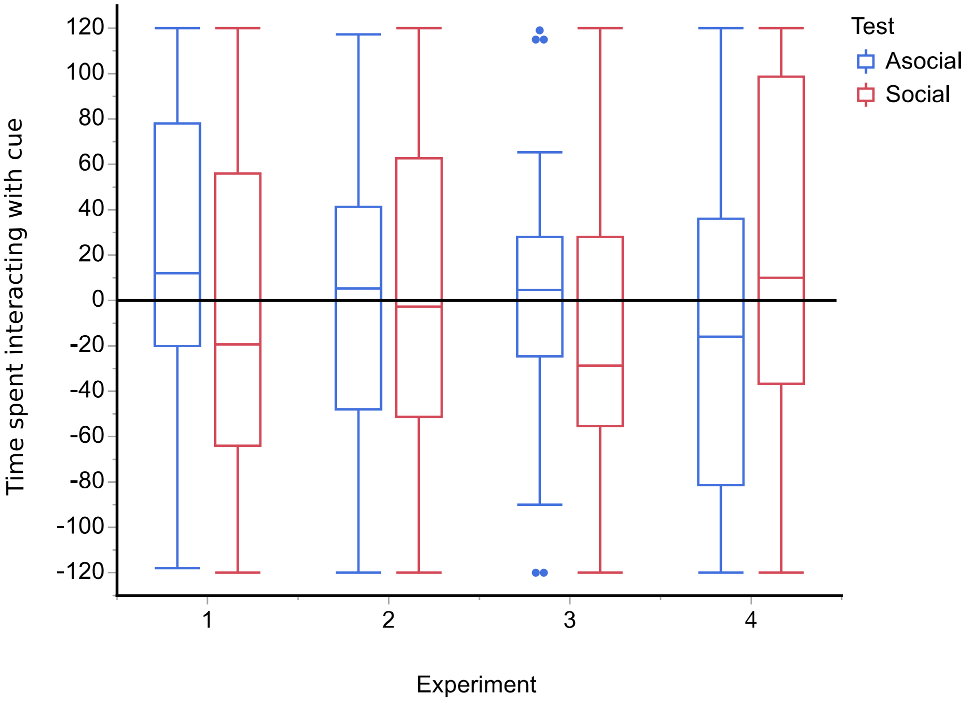

Figure 3.6: Difference in time spent (in seconds) with the cued versus empty location across the 4 experiments for the social and asocial learning tests. Experiments 1-3 tested social and asocial learning, while experiment 4 tested social and asocial information use. A difference score of 120 means that the fish spent all the time with the cued location, of -120 that the fish spent all the time at the empty location and a score of 0 means they spent equal amounts of time with both. The graph represents an outlier box plot, defined by the quartiles as hollow rectangles, with a horizontal line at the median.

Social and asocial learning and information use:

There was no evidence of learning or information use, either social or asocial, in any of the four experiments (figure 3.6). Across tests and experiments, means did not significantly differ from 0, the expected value if no learning was seen (Experiment 1 asocial $t_{37}= 1.67, p= 0.10$; Experiment 1 social $t_{37}= -0.53, p= 0.60$; Experiment 2 asocial $t_{37}= 0.18, p= 0.86$; Experiment 2 social $t_{37}=$

0.27, p= 0.79; Experiment 3 asocial t_{37}= *0.32, p= 0.75*; Experiment 3 social t_{37}= *-1.49, p= 0.14*; Experiment 4 asocial t_{37}= *-1.2, p= 0.22*; Experiment 4 social t_{37}= *1.32, p= 0.20*; p values are without Benjamini-Hochberg correction: all were non-significant prior to and thus also after correction). Only 5 instances were recorded where subjects did not approach any feeder during the trial, with only one instance where a subject did not approach a feeder in either of two trials within the experiment. Removal of the trials with no feeder approaches had no effect on the results.

Social learning, asocial learning and boldness and exploration:

After correction for multiple comparisons, there were no significant correlations in performance within each experiment between the social and asocial tests, or across the different experiments (table 3.1). To examine further any evidence for consistency across individuals, each individual's performance was compared across experiments within both the social and asocial tests using linear mixed effect models and repeatabilities were calculated (figure 3.7). There were no significant individual differences across experiments in both the social and asocial tests (Social: *R < 0.01, p= 1.00*; Asocial: *R= 0.24, p= 0.50*). Thus, there was no evidence for consistent individual differences in learning performance across or within the four experiments.

Table 3.1: Pearson's correlation comparing the social and asocial tests across the 4 experiments, including raw p-values. Correlation coefficients that remained significant after correction with Benjamini-Hochberg procedure are identified with an asterisk: no significant correlations are seen after correction for multiple comparisons. Colour scheme represents values of the correlation coefficient from -1 (red) to 1 (blue).

		1a	2s	2a	3s	3a	4s	4a
1s: Experiment 1 social learning	Correlation coefficient	0.2	0.14	0.08	-0.17	-0.33	-0.21	0.06
	p-value	0.23	0.39	0.63	0.3	0.04	0.21	0.7
1a: Experiment 1 asocial learning	Correlation coefficient		-0.44	-0.13	-0.17	-0.05	0.19	0.06
	p-value		0.006	0.42	0.32	0.74	0.26	0.74
2s: Experiment 2 social learning	Correlation coefficient			0.22	0.08	-0.03	-0.12	0.09
	p-value			0.17	0.62	0.86	0.48	0.58
2a: Experiment 2 asocial learning	Correlation coefficient				-0.17	0.29	0.15	0.37
	p-value				0.33	0.08	0.36	0.02
3s: Experiment 3 social learning	Correlation coefficient					-0.37	-0.15	-0.43
	p-value					0.02	0.38	0.007
3a: Experiment 3 asocial learning	Correlation coefficient						0.18	0.32
	p-value						0.29	0.051
4s: Experiment 4 social information use	Correlation coefficient							0.39
	p-value							0.02

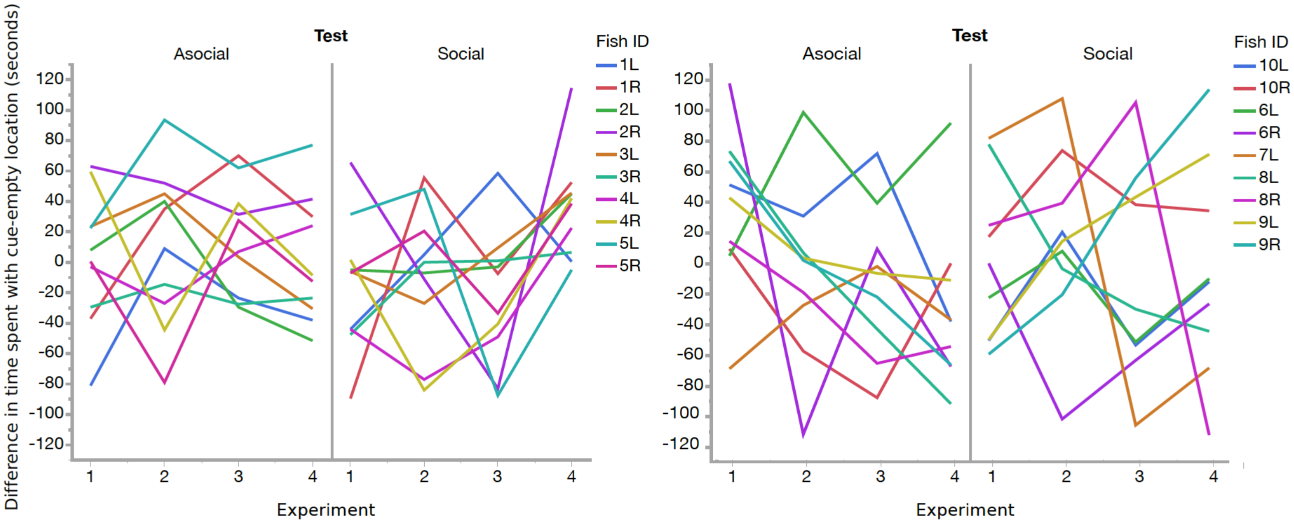

Figure 3.7: Difference in time spent (in seconds) with the cued - empty location across the 4 experiments for the social and asocial learning tests, for all 19 individuals. For exposition 10 individuals are plotted on the left and 9 individuals on the right. Each individual is represented by a different colour within each figure panel.

Boldness and exploration:

The two boldness measures (amount of time it took to leave the refuge and the time spent in the periphery of the open field test) were not significantly correlated (Spearman's rank correlation; *r = -0.08, p = 0.62*, figure 3.8). Due to insufficient variation in the data, the exploration variable (number of squares entered) was omitted. Only 2 individuals entered less than 30 squares, and the remaining 17 individuals entered 31 or 32 squares. There were no significant correlations between learning performance and either boldness measure (Pearson's correlations: *r range= -0.03 to 0.23, p range= 0.14 to 0.89*).

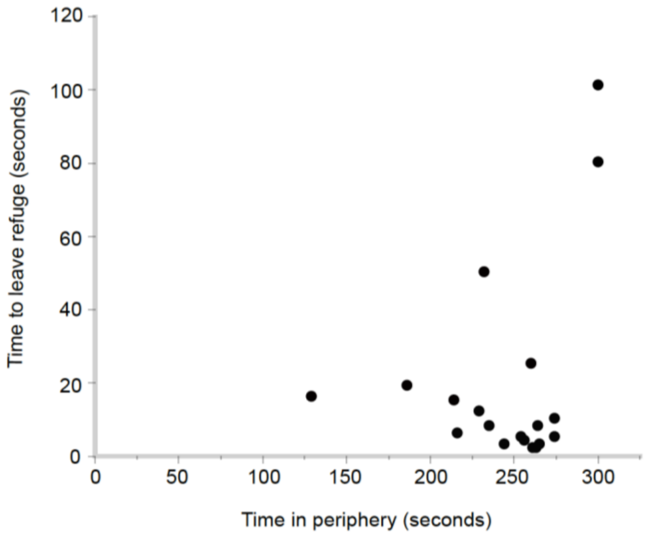

Figure 3.8: Comparison of the two boldness measures, time to leave refuge (in seconds) and time in periphery (in seconds). Relationship was not statistically significant.

Discussion:

Previous studies have shown that early, recent and current experiences can predict reliance on social and individual information use (Kendal et al. 2009). We thus expected training to result in differences in learning performance. However, no learning was seen with both social and asocial cues over the course of the experiment, with fish spending equal amounts of time at the trained-for cued location and at the empty location. No clear trends were seen over time, with no suggestion that fish were actively avoiding or approaching one of the two cues. Furthermore, no significant correlations were seen between any of the social and asocial learning tests, and there was no evidence for consistent individual differences in learning performance. As there is no evidence for learning at the group level, and no evidence that a subset of individuals learned the tasks, the planned experiment of training to cue type was not conducted. We were unable to provide support for hypotheses 1 and 2, and were unable to test hypothesis 3 and its alternatives. Our results were surprising, as social and individual learning of foraging locations are well established in fish, and particularly in guppies (Laland and Williams 1997; Laland and Reader 1999; Reader and Laland 2000; Swaney et al. 2001; Reader et al. 2003). Possible explanations for our observed results, with no evidence of learning, are the developmental experience of the fish, the fish strain used, an unknown environmental variable, or the precise methodology used.

Age, developmental experience with social information, predation and rearing density have all been shown to influence reliance on social information use and social learning, in our laboratory (Leris and Reader 2016; Leris 2016; Chouinard-Thuly 2018) and others (Chapman et al. 2008). It is possible our fish did not have the appropriate developmental experiences to demonstrate social learning, possibly because they were reared in density housing conditions that were too low or too high, or with insufficient exposure to social information. Previous results from our laboratory found evidence for social information use, but not social learning in the laboratory, and only under normal housing density rearing in a wildtype population (Chouinard-Thuly 2018), suggesting that perhaps subjects could not remember cue locations after they had been removed. To address this issue, we ran experiment 4, allowing the cues to remain in the subject's tank during testing, making the test an information use test rather than learning test. We found no evidence that the cues were used to choose a feeder in this test either.

Another possible reason for our lack of results could be the use of domesticated fish, although social learning has been seen in domesticated guppies in our laboratory and other laboratories, although in different domestic strains (Laland and Williams 1997, 1998; Lachlan et al. 1998; Brown and Laland 2002; Leris and Reader 2016). Our fish were domesticated and reared in our laboratory for several generations before being used as subjects. Domestication can lead to decreases in available space, remove the need to forage for extended periods of time, reduce predation rates and create more uniform social structures, which are all likely to influence an individual's characteristics and behaviour (Wright et al. 2006). Particularly in fish, differences and similarities between wildtype and domesticated fish have been seen across contexts and behaviours (Ruzzante 1994; Price 2000). For example, feral guppy populations shoal more than domesticated populations across contexts (Swaney et al. 2015), domesticated and wildtype sea bass (*Lateolabrax japonicas*) differ in swimming behaviours (Benheim et al. 2013), domesticated zebrafish (*Danio rerio*) have higher growth rates and a diminished fear response compared to wildtype (Robison and Rowland 2005), and a large reduction in absolute brain size was noted between wildtype and first generation laboratory reared guppies (Burns et al. 2009). However, no differences have been found between wildtype and domesticated fish in exploration and boldness and in spatial learning behaviours (Burns et al. 2009; Benheim et al. 2013; Swaney et al. 2015). Recently, as a result of the present study, comparisons of social learning have been made between a wildtype and a domestic guppy population, finding stronger social learning performance in the wildtype guppies, particularly under more stressful conditions (Foster, Guigueno and Reader, unpublished data). We suggest that the domesticated population we studied may have lost their motivation to use social information or learned feeding cues due to the lack of predation and the abundance of food and mates. However, this does not explain why other studies have found social learning in domesticated guppies. Studies in domesticated dogs (*Canis lupus familliaris*) and wolves (*Canis lupus*) have found differences and similarities in how they respond to and learn from human social cues, depending on study specifics (Hare et al. 2002; Miklosi et al. 2003; Udell et al. 2008). Researchers hypothesize that both domesticated and undomesticated canids have the genetic prerequisites to respond to humans, but there is a necessary sensitization period during development, where socialization to humans is needed in order for high levels of response to and learning from humans to occur (Udell et al. 2010). It is possible, that our fish also require a necessary sensitization period, where they are exposed to social information that they must attend to, in order to be able to attend to social information later in life: such early-life experiences does affect social learning in guppies (Leris and Reader 2016).

Other possible contributing factors are any unexpected environmental variables as well as the possibility of an experimental design that did not allow for learning to be demonstrated. Unexpected and unknown environmental or experimental effects may be present. As an example of an unexpected environmental effect, experimenter sex has been shown to influence mouse behaviour, with the odour of male experimenters resulting in higher levels of stress in mice (Sorge et al. 2014). In our case, the new experimental room utilized, or change in seasons may have influenced our subjects' behaviour. As we were able to train the present subjects to reliably feed from petri dish feeders they were unfamiliar with, filled with a novel mix of food, within only 7 trials (7 days) and results from Chapter 2 suggest that domesticated guppies from the same population can learn to shoal with different size groups, we believe that learning of the cues through the same reinforcement training with food should be possible. Similar results from reinforcement-based training have also been shown in other fish species (Ingraham et al. 2016). The subjects may have lacked sufficient motivation for the fish to display a preference. Perhaps our food motivation or the cost of not feeding during the trial was not strong enough. It is possible the cued and empty containers were not sufficiently separated, with a minimal cost to exploring both feeders. However, results from Chapter 2 show learning in a very similar set up, with feeders at the same distance (approx. 30 cm apart) in the same size tank. Further work from our laboratory found that social learning was often more strongly expressed when fish were exposed to stress (Colinet, Guigueno and Reader, unpublished data; Foster, Guigueno and Reader, unpublished data), supporting the idea that there may have been a lack of motivation to learn under the lower-stress context employed in the present study.

We had piloted various methodologies, including conducting tests in a separate, large testing tank to add a greater cost to exploring feeders, testing with companions, varying the times between feeding, adding food odour to incentivize the fish to feed, and adding cues externally to the home tanks, however none were successful in getting subjects to approach the feeders sufficiently to be able to train them. Use of the petri dish feeders with gelatin was successful in increasing time spent feeding and ensuring fish had to commit to a single feeder for an extended period of time, as the gelatin required long, repeated pecking to consume a comparable amount to floating flake food. Our employed methodology was the only one we found that ensured very reliable feeding during training and approach to feeders during tests, and ensured that subjects could see the cues as the subjects interacted with demonstrator fish consistently. Due to this we continued with the experiment as described, but were unable to detect learning. For future work, a possible alternative is fear learning, instead of reinforcement learning, as the response may be stronger and elicit learning at a faster rate (Hall and Suboski 1995; Olsson and Phelps 2007; Kenny et al. 2017). It is possible that multiple factors, namely the methodology and testing context, the subject population used, and their developmental experience together resulted in the findings we observed.

Personality traits, such as boldness and exploration are thought to be stable traits across time and conditions, which are often positively correlated with each other, especially in fish (Fraser et al. 2001; Wilson and Godin 2009; Mauze et al. 2015). They are important as they affect many behaviours, including foraging, predator avoidance, information use and learning. We expected that boldness and exploration would be correlated, however due to insufficient variation in the data we were unable to test for this correlation. In order to be able to accurately test for correlations in personality, we require a larger sample to increase the likelihood of observing a range of personality types or a test that teases apart personality differences more. Surprisingly, the two boldness measures were not correlated: it was expected that a fish that left the refuge faster would also spend less time in the periphery. The periphery, close to the tank edges, is considered a safer place than the middle area of the tank which is more exposed, so the more time a fish spends in the more exposed area, the bolder it can be considered (Burns 2008). The plant refuge is considered a safer spot to hide than in the unsheltered open tank, so a shyer fish would likely remain in the refuge for longer before going out to explore, and is commonly used to assess boldness in fish (Burns 2008; Jones and Godin 2010; Mauze et al. 2015). It is possible that some of our fish did not treat the plant refuge as a shelter, and so left quickly, which did not necessarily mean they are bolder. This may be one of the reasons for the lack of correlation between the measures. Similar results across similar boldness measures were seen in damselfishes (*Pomacentride* spp.), with the time to enter a refuge and area explored not being correlated (White et al. 2013).

The extent to which individuals rely on social and asocial information can be affected by different personality traits. It has been predicted that fast explorers/ more exploratory individuals would be more successful in learning a task through operant conditioning, compared to slow exploring individuals (Sih and Del Giudice 2012), and positive correlations between exploration and social information use and boldness and social information use have been observed (Nomakuchi et al. 2009; Trompf and Brown 2014). However, we found no significant correlations between the boldness tests and the learning tests, probably due to the low learning performance we observed. It is also possible that our boldness and exploration tests were not able to capture the personality traits in our fish, however previous research suggests the open field test and emergence test method are good tests of boldness and exploration, displaying moderate levels of reliability and good discriminate validity (Burns 2008). In sticklebacks (*Gasterosteidae* spp.) boldness was found to not affect the response of the fish to information from their social environments (Harcourt et al. 2010). Both negative and positive relationships between exploration and social information use have been proposed as possible, with a positive relationship indicating a common activity level (defined by exploration and boldness) underlying individual learning and/or social information use and a negative relationship indicating a frequency dependent equilibrium between demonstrators and observers (Mesoudi et al. 2016).

Our study aimed to address underlying cognitive mechanisms of social and asocial learning, by experimentally manipulating social and asocial information and testing to see how these manipulations affected learning. However, we were unsuccessful at establishing a protocol that allowed for learning to be observed in the guppies. Our results suggest that learning, social and asocial, is not a fully robust measure and requires a certain salience of cues, specific prior experiences and/or a particular context or motivation/cost to lead to the acquisition and use of information. This further provides support to the idea that learning is not always beneficial, and that individuals will adjust the weight they put on social and asocial information based on the costs (Kendal et al. 2004; van Bergen et al. 2004). In our study, it seems that random sampling of the environment might have been the most efficient strategy for our fish (Rendell et al. 2011). Once an experimental design is established that provides a robust learning measure, we propose follow up experiments to simultaneously manipulate the payoffs of social and asocial information use, to further examine the independence of social and asocial learning processes.

Ethics: Methods were approved by the Animal Care Committee of McGill University (Protocol 2015-7708) and were conducted in accordance with the ethical guidelines of the Canadian Council on Animal Care and ABS/ASAB.

Acknowledgements: Thank you to the Reader laboratory members and Rachel Page for their support and helpful comments in the design and analysis of the study, our work-study students for taking care of the laboratory fish, and Helen Rodd for donating fish used in this experiment.

Funding: This research was funded by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC; grants #418342-2012, #429385-2012) and the Canadian Foundation for Innovation (grant #29433), awarded to SMR, and NSERC-CREATE Biodiversity, Ecosystem Services and Sustainability award and NEO-STRI-McGill fellowships to IV.

References:

Avarguès-Weber, A., & Chittka, L. 2014. Local enhancement or stimulus enhancement? Bumblebee social learning results in a specific pattern of flower preference. *Animal Behaviour*, 97, 185-191.

Benhaïm, D., Bégout, M.-L., Lucas, G., & Chatain, B. 2013. First insight into exploration and cognition in wild caught and domesticated sea bass (*Dicentrarchus labrax*) in a Maze. *PLOS One*, 8, e65872.

Benjamini, Y., & Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Royal Statistical Society Series B*, 57, 289.

Bouchard, J., Goodyer, W., & Lefebvre, L. 2007. Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Animal Cognition*, 10, 259-266.

Brakefield, P.M., & Roskam, J.C. 2006. Exploring evolutionary constraints is a task for an integrative evolutionary biology. *The American Naturalist*, 168, S4.

Brown, C. & Laland, K. N. 2002. Social learning of a novel avoidance task in the guppy: conformity and social release. *Animal Behaviour*, 64, 41–47.

Burkart, J. M., Strasser, A., & Foglia, M. 2009. Trade-offs between social learning and individual innovativeness in common marmosets, *Callithrix jacchus*. *Animal Behaviour*, 77, 1291-1301.

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

Burns, J. G., Saravanan, A., & Rodd, H.F. 2009. Rearing environment affects the brain size of guppies: Lab-reared guppies have smaller brains than wild-caught guppies. *Ethology*, 115, 122-133.

Chapman, B. B., Ward, A. J. W., & Krause, J. 2008. Schooling and learning: early social environment predicts social learning ability in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 76, 923-929.

Chouinard-Thuly, L. 2018. Phenotypic Plasticity in Social Information Use and Stress Response in Trinidadian Guppies. PhD Thesis, McGill University, Montreal, Canada.

Dawson, E. H., Avarguès-Weber, A., Chittka, L., & Leadbeater, E. 2013. Learning by observation emerges from simple associations in an insect model. *Current Biology*, 23, 727-730.

Dawson, E. H., Chittka, L., & Leadbeater, E. 2016. Alarm substances induce associative social learning in honeybees, *Apis mellifera*. *Animal Behaviour*, 122, 17-22.

Dugatkin, L. A., & Alfieri, M. S. 2003. Boldness, behavioral inhibition and learning. *Ethology Ecology & Evolution*, 15, 43-49.

Dunlap, A. S., & Stephens, D. W. 2009. Components of change in the evolution of learning and unlearned preference. *Proceedings of the Royal Society B: Biological Sciences*, 276, 3201-3208.

Dunlap, A. S., & Stephens, D. W. 2014. Experimental evolution of prepared learning. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 11750-11755.

Dwyer, M. D. 2015. Multiple outcome domains and prepared learning. *Proceedings of the National Academy of Sciences*, 112, e345.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist*, 158, 124-135.

Galef, B. G., & Laland, K. N. 2005. Social learning in animals: Empirical studies and theoretical models. *BioScience*, 55, 489-499.

Hall, D., & Suboski, M. D. 1995. Visual and olfactory stimuli in learned release of alarm reactions by zebra danio fish (*Brachydanio rerio*). *Neurobiology of Learning and Memory*, 63, 229-240.

Harcourt, J. L., Biau, S., Johnstone, R., & Manica, A. 2010. Boldness and Information Use in Three-Spined Sticklebacks. *Ethology*, 116, 440-447.

Hare, B., Brown, M., Williamson, C., & Tomasello, M. 2002. The domestication of social cognition in dogs. *Science*, 298, 1634-1636.

Heinen, V. K., & Stephens, D. W. 2016. Blue jays, *Cyanocitta cristata*, devalue social information in uncertain environments. *Animal Behaviour*, 112, 53-62.

Heyes, C. 1994. Social learning in animals: categories and mechanisms. *Biological Reviews*, 69, 207-231.

Heyes, C. 2012. What's social about social learning? *Journal of Comparative Psychology*, 126, 193-202.

Heyes, C., & Galef, B. 1996. Social Learning in Animals: The Roots of Culture. San Diego: Academic Press.

Heyes, C., & Pearce, J. M. 2015. Not-so-social learning strategies. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20141709.

Ingraham, E., Anderson, N. D., Hurd, P. L., & Hamilton, T. J. 2016. Twelve-day reinforcement-based memory retention in African cichlids (*Labidochromis caeruleus*). *Frontiers in Behavioral Neuroscience*, 10, 7.

Jones, K. A., & Godin, J. G. J. 2010. Are fast explorers slow reactors? Linking personal type and anti-predator behavior. *Proceedings of the Royal Society B: Biological Sciences*, 277, 625-632.

Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M., & Jones, P. L. 2018. Social learning strategies: Bridge-building between fields. *Trends in Cognitive Sciences*, 22, 651-665.

Kendal, R. L., Coolen, I., & Laland, K. N. 2004. The role of conformity in foraging when personal and social information conflict. *Behavioral Ecology*, 15, 269-277.

Kendal, R. L., Coolen, I., & Laland , K. N. 2009. Adaptive Trade-Offs in the Use of Social and Personal Information. In R. Dukas & J. Ratcliffe (Eds.), Cognitive ecology II. (pp. 249-271). Chicago: University of Chicago Press.

Kenney, J. W., Scott, I. C., Josselyn, S. A., & Frankland, P. W. 2017. Contextual fear conditioning in zebrafish. *Learning & Memory*, 24, 516-523.

Lachlan, R. F., Crooks, L., & Laland, K. N. 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, 56, 181-190.

Laland, K. N. 1996. Is social learning always locally adaptive? *Animal Behaviour*, 52, 637-640.

Laland, K. N., & Reader, S. M. 1999. Foraging innovation in the guppy. *Animal Behaviour*, 57, 331-340.

Laland, K. N., & Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, 53, 1161-1169.

Laland, K. N., & Williams, K. 1998. Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, 9, 493-499.

Leadbeater, E. 2015. What evolves in the evolution of social learning? *Journal of Zoology*, 295, 4-11.

Leadbeater, E., & Dawson, E. H. 2017. A social insect perspective on the evolution of social learning mechanisms. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 7838-7845.

Leadbeater, E., & Florent, C. 2014. Foraging bumblebees do not rate social information above personal experience. *Behavioral Ecology and Sociobiology*, 68, 1145-1150.

Lefebvre, L., & Giraldeau, L.-A. 1996. Is Social Learning an Adaptive Specialization? In B. G. Galef (Ed.), Social Learning in Animals (pp. 107-128). San Diego: Academic Press.

Leris, I. 2016. Early Environment and the Development of Social Behaviours in the Trinidadian Guppy*, Poecilia reticulata*. PhD Thesis, Utrecht University, Utrecht, Netherlands.

Leris, I., & Reader, S. M. 2016. Age and early social environment influence guppy social learning propensities. *Animal Behaviour*, 120, 11-19.

Magurran, A. E. 2005. Evolutionary Ecology: the Trinidadian Guppy. Oxford University Press, Oxford

Marchetti, C., & Drent, P. 2000. Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, 60, 131-140.

Mathot, K. J., & Giraldeau, L.-A. 2008. Increasing vulnerability to predation increases preference for the scrounger foraging tactic. *Behavioral Ecology*, 19, 131-138.

Mazue, G. P. F., Dechaume-Moncharmont, F. X., & Godin, J. G. J. 2015. Boldness-exploration behavioral syndrome: interfamily variability and repeatability of personality traits in the young of the convict cichlid (*Amatitlania siquia*). *Behavioral Ecology*, 26, 900-908.

Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. 2016. The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*, 31, 215-225.

Miklósi, A., Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. 2003. A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology*, 13, 763-766.

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

Nomakuchi, S., Park, P. J., & Bell, M. A. 2009. Correlation between exploration activity and use of social information in three-spined sticklebacks. *Behavioral Ecology*, 20, 340-345.

Olsson, A., & Phelps, E. A. 2007. Social learning of fear. *Nature Neuroscience*, 10, 1095-1102.

Price, E. O. 2000. Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science*, 65, 245.

Réale, D., Reader, S. M., Sol, D., McDougall, P., & Dingemanse, N. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*, 291-318.

Reader, S. M. 2006. Evo-devo, modularity, and evolvability: Insights for cultural evolution. *Behavioral and Brain Sciences*, 29, 361-362.

Reader, S. M. 2003. Innovation and social learning: individual variation and brain evolution. *Animal Biology*, 53, 147-158.

Reader, S. M. 2016. Animal social learning: associations and adaptations. *F1000research*, 5.

Reader, S. M., Hager, Y., & Laland, K. N. 2011. The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 1017-1027.

Reader, S. M., Kendal, J. R., & Laland, K. N. 2003. Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Animal Behaviour*, 66, 729-739.

Reader, S. M., & Laland, K. N. 2000. Diffusion of foraging innovations in the guppy. *Animal Behaviour*, 60, 175-180.

Reader, S. M., & Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 4436-4441.

Rendell, L., Fogarty, L., Hoppitt, W. J., Morgan, T. J., Webster, M. M., & Laland, K. N. 2011. Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15, 68-76.

Robison, B. D., & Rowland, W. 2005. A potential model system for studying the genetics of domestication: behavioral variation among wild and domesticated strains of zebra danio (*Danio rerio*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 2046-2054.

Rogers, A. R. 1988. Does biology constrain culture. *American Anthropologist*, 90, 819-831.

Rosa, P., Nguyen, V., & Dubois, F. 2012. Individual differences in sampling behaviour predict social information use in zebra finches. *Behavioral Ecology and Sociobiology*, 66, 1259-1265.

Ruzzante, D. E. 1994. Domestication effects on aggressive and schooling behaviour in fish. *Aquaculture*, 120, 1-24.

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

Sorge, R. E., Martin, L. J., Isbester, K. A., Sotocinal, S. G., Rosen, S., Tuttle, A. H., Wieskopf, J. S., Acland, E. L., Dokova, A., Kadoura, B., Leger, P., Mapplebeck, J. C., McPhail, M.,

Delaney, A., Wigerblad, G., Schumann, A. P., Quinn, T., Frasnelli, J., Svensson, C. I., Sternberg, W. F., & Mogil, J. S. 2014. Olfactory exposure to males, including men, causes stress and related analgesia in rodents. *Nature Methods*, 11, 629-632.

Smolla, M., Alem, S., Chittka, L., & Shultz, S. 2016. Copy-when-uncertain: bumblebees rely on social information when rewards are highly variable. *Biology Letters*, 12.

Sneddon, L. U., Wolfenden, D. C. C., & Thomson, J. S. 2016. Stress Management and Welfare. In C. B. Schreck, L. Tort, A. P. Farrell, & C. J. Brauner (Eds.), Fish Physiology (Vol. 35, pp. 463-539): Academic Press.

Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, 62, 591-598.

Swaney, W. T., Cabrera-Álvarez, M. J., & Reader, S. M. 2015. Behavioural responses of feral and domestic guppies (*Poecilia reticulata*) to predators and their cues. *Behavioural Processes*, 118, 42-46.

Templeton, C. N., Laland, K. N., & Boogert, N. J. 2014. Does song complexity correlate with problem-solving performance in flocks of zebra finches? *Animal Behaviour*, 92, 63-71.

Templeton, J. J., & Giraldeau, L.-A. 1996. Vicarious Sampling: The Use of Personal and Public Information by Starlings Foraging in a Simple Patchy Environment. *Behavioral Ecology and Sociobiology*, 38, 105-114.

Thorpe, W. H. 1963. Learning and Instinct in Animals (2nd ed. ed.). London: Methuen.

Toelch, U., van Delft, M. J., Bruce, M. J., Donders, R., Meeus, M. T. H., & Reader, S. M. 2009. Decreased environmental variability induces a bias for social information use in humans. *Evolution and Human Behavior*, 30, 32-40.

Trompf, L., & Brown, C. 2014. Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. *Animal Behaviour*, 88, 99-106.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. 2008. Wolves outperform dogs in following human social cues. *Animal Behaviour*, 76, 1767-1773.

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. 2010. What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*, 85, 327-345.

van Bergen, Y., Coolen, I., & Laland, K. N. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B: Biological Sciences*, 271, 957-962.

White, J. R., Meekan, M. G., McCormick, M. I., & Ferrari, M. C. 2013. A comparison of measures of boldness and their relationships to survival in young fish. *PLOS One*, 8, e68900.

Wilson, A. D. M., & Godin, J.-G. J. 2009. Boldness and behavioral syndromes in the bluegill sunfish, Lepomis macrochirus. *Behavioral Ecology*, 20, 231-237.

Wright, D., Ward, A. J. W., Croft, D. P., & Krause, J. 2006. Social organization, grouping, and domestication in fish. *Zebrafish*, 3, 141-155.

CHAPTER 4: GENERAL DISCUSSION

My thesis investigated selective grouping and selective information use in the Trinidadian guppy, *Poecilia reticulata*, by using reinforcement-based training as a tool to shape behaviour. In Chapter 2 I investigated whether fish can learn whom to group with, and in Chapter 3 I investigated whether fish can learn where to forage from social and asocial cues. My results suggest that the population of domesticated guppies I studied are capable of learning the value of some social cues, with fish learning selective social grouping behaviours through training, but not social learning of a foraging location. This work is consistent with the idea that many factors affect whether information is acquired and subsequently used, as discussed further below.

Group living and selective grouping:

Group living is common across the animal kingdom, and confers a wide range of benefits to group members (Krause and Ruxton 2002). In guppies, grouping has been shown to aid in predator protection, increase foraging efficiency and allow for social transmission of information (Hoare and Krause 2003). My thesis focused on these social interactions within groups, thus contributing to understanding the complexity and dynamics of social behaviours. In Chapter 2, I investigated whether female guppies can be trained, using food reinforcement, to group with either a large six-fish shoal (large-shoal rewarded treatment) or a small two-fish shoal (small-shoal rewarded treatment). As fish have previously been shown to choose whom to group with and when, I wanted to investigate whether this preference could be shaped experimentally (Krause and Godin 1994; Lachlan et al. 1998). I found that female guppies were flexible in their grouping behaviours, selectively grouping with shoals of different sizes based on past foraging success. As expected and previously demonstrated, subjects exhibited a strong initial preference for the larger of two shoals (Lachlan et al. 1998; Cabrera-Alvarez et al. 2017), with this preference maintained in the large-shoal rewarded treatment. In the small-shoal rewarded treatment, there was a significant decrease in the preference for the large shoal, and a concomitant increase in preference for the small shoal. Our work supports the idea that shoaling is a flexible strategy, employed depending on various factors such as food availability, allowing for fast adjustments to changing environmental conditions (Hoare et al. 2004). Understanding the full extent of the flexibility of grouping behaviours can provide insight into the evolution of group living. Results such as mine have potential implications in understanding the driving forces of differences in shoaling tendencies across populations of guppies, potentially suggesting that successful foraging is equally as strong of a driving force as predation.

Social and asocial learning of cues:

Group living has also been implicated in facilitating social information transfer, and subsequently social learning (van der Post and Hogeweg 2008). The tendency to shoal allows for a simple form of "guided social learning," wherein individuals will learn something about their environment from their group members simply because they follow and group with them (Laland and Williams 1997). Such simple social mechanisms can maintain a behaviour within a population. For example, social learning mediated stable transmission of foraging route preferences in a small population of fish through their tendency to shoal (Laland and Williams 1997, 1998). Thus, in Chapter 3 I attempted to train guppies to learn about a foraging location using a social cue, a group of conspecifics shoaling. To compare learning performance, I attempted to simultaneously train guppies to also use an asocial cue to learn about a foraging location. It has been shown that learning such a task socially does not prevent individuals from learning a similar task asocially. Specifically, guppies will learn to take longer, more energetically costly routes to a food source when with a shoal, but when alone they learn shorter, less costly routes (Bates and Chappell 2002). This suggests guppies are capable of learning very similar tasks both socially and asocially and chose to use information selectively based on whether they are alone or not. In order to give all subjects similar prior knowledge and positive experience with both social and asocial cues (as both prior knowledge and experience have been shown to affect learning), I conducted a pre-training where food availability was indicated by cue location. Following pre-training, I tested their social and asocial learning performance.

Social learning in the Trinidadian guppy has been widely observed in a wide range of contexts, including foraging, antipredator behaviours, escape routes and mate choice copying (Brown and Laland 2003; Magurran 2005). Such instances of social learning have been observed both in the wild (Reader et al. 2003) and in the laboratory, with domesticated (Swaney et al. 2001; Leris and Reader 2016) and wildtype fish (Chapman et al. 2008). In situations where social and asocial information conflict, guppies are likely to adjust the weight they place on using social information according to the cost (Kendal et al. 2004). Fish do not just rely on the most recent information they have received in foraging contexts, instead there is evidence that decisions in nine-spined sticklebacks (*Pungitius pungitius*) seem to be shaped according to how reliable environmental cues are, and how long has passed between the time they acquired their asocial information and the conflicting social information (van Bergen et al. 2004). Considering the wealth of research on social learning, and all the factors we know that influence it (population differences, experiences and personality), I attempted to account for these factors as much as possible (Carlier and Lefebvre 1997; Kendal et al. 2009; Rosa et al. 2012; Dawson et al. 2013; Leadbeater and Florent 2014; Mesoudi et al. 2016). I used a single population within the study, gave subjects similar recent experiences with the cues through pre-training, maintained the same environmental conditions for all subjects and tested for differences in personality traits. Even with these measures in place, and extended pre-training, I was unable to detect any levels of learning. I was thus unable to address one of my main questions, whether learning about social or asocial cues results in any detectable trade-offs or carryovers between social and asocial learning performance. It is likely that social and asocial learning are not alternatives, but rather differ in the type of information gathered (possibly due to differences in 'input' systems), making some individuals better at using both social and asocial information (Reader and Leris 2014; Reader 2016). Heyes and Pearce suggest that most examples of social learning strategies, and thus individual differences in social learning, can be explained by domain general explanations of attention and associative learning (Heyes and Pearce 2015).

When considering social information use, individuals' tendencies to rely on social information is also affected by personality (Rosa et al. 2012). It is argued that social information use is not entirely flexible or context dependent, as female zebra finches (*Taeniopygia guttata*) that were less active in sampling their environment for food relied more on social information in both a foraging and mating context, compared to birds that actively sampled (Rosa et al. 2012). In Chapter 3, I measured boldness and exploration in an attempt to correlate personality type with learning propensity. Both positive and negative correlations could be expected, each with distinct explanations (Mesoudi et al. 2016). I found no correlations within personality measures or between personality measures and learning, likely due to the small sample size and the inability to pick up learning, so no definitive conclusions can be drawn. As individuals vary in their sociability due to consistent differences in personality and other factors such as age, sex and life history, it is important for them to be considered and investigated as they can provide insight into the interactions necessary for social behaviours to be exhibited in different ways.

Learning of group size but not social and asocial cues:

In Chapter 2, I successfully used reinforcement training to train fish to join social groups of certain sizes, but in Chapter 3 was unable to use reinforcement training to train fish to learn foraging locations using social and asocial cues. This is surprising, due to the similarities between the Chapter 2 and 3 studies. I suspect that this can be attributed to several factors including the population and specifics in the design, including stress and familiarity. A failure to replicate results of previous studies has previously been observed with guppy social learning. Research in female guppy mate choice copying has been quite divided with some groups finding strong support for mate choice copying (Dugatkin 1992; White et al. 2017) and mate choice copying reversal (Dugatkin and Godin 1992; 1993), while others were unable to find evidence for mate choice copying or reversal (Brooks 1996; Lafleur et al. 1997; Brooks 1999), and even found avoidance of mate choice (Scarponi et al. 2015). Most notably, all of these experiments followed the experimental design by Dugatkin (1992) closely, and yet results were still varied. In experiments where mate choice copying is found, age and sociality were found as important factors influencing decisions, which might explain why others have not found the same results (Dugatkin and Godin 1993; White et al. 2017). Similarly, in research investigating learning of foraging behaviours, many have been able to find support for social and asocial learning of foraging locations and behaviours in fish, insects and mammals (Reader et al. 2003; Page and Ryan 2006; Leadbeater and Chittka 2007), whereas some of my colleagues and I have been unable to consistently detect social learning in guppies (Chouinard-Thuly 2018; Colinet, Guigueno and Reader unpublished data). Specifically, Chouinard-Thuly (2018) reared fish in standard and high social density conditions, and subsequently tested their social information use and social learning abilities, finding evidence for social information use, but not social learning in the laboratory, and only in females under standard housing density. Using a very similar task in the wild, Chouinard-Thuly (2018) found evidence for social information use and social learning, but with differences across guppy populations. Colinet et al. (unpublished data) found that a population of wildtype guppies only exhibited evidence for social learning under stress induced by alarm cue.

Use of a domesticated population, as discussed in Chapter 3, may be one of the reasons we do not see social learning. Differences in various social behaviours, including shoaling, swimming, fear response, and social learning have been seen across wildtype and domesticated populations (Robison and Rowland 2005; Benheim et al. 2013; Swaney et al. 2015; Foster, Guigueno and Reader unpublished data). Although there is evidence for social learning in some domesticated guppies in our laboratory (Leris and Reader 2016), results from our laboratory using the same population of domestic guppies as used in the present thesis found lower social learning performance compared to a wildtype population (Foster et al. unpublished data). Social learning may be less important in domesticated populations, as they have no predators and no need to learn about food locations as they are fed ad lib on food spread throughout their tank. When considering their shoaling behaviours however, it is likely that conspecifics are a reliable predictor of food availability or not (for example, other fish may indicate that food has been added to the tank, or may defend food patches), and thus the fish are capable of adjusting their group size preference based on reward. This may explain why, I can manipulate group size preferences, but not social learning, in the domesticated guppies studies here. Wright et al. (2006) argue that domesticated laboratory populations can be used in animal behaviour research, but that it is important to bear in mind the ecological background and special characteristics of the individuals being used (Wright et al. 2006). Exploring differences between wild and domesticated populations are also a useful route to test adaptive and evolutionary hypotheses (Wright et al. 2006), thus I encourage further investigations of social grouping and learning in the wild, across different habitats in Trinidad, and in comparison with domesticated laboratory reared fish. An important question will be the extent to which domestic populations differ in their behaviour.

It is also possible that my experimental design did not allow for learning to occur in Chapter 3. Although designs in Chapter 2 and 3 were similar, they were not identical. Most notably, in Chapter 2 the fish were trained in their home tanks, but tested in another tank, whereas in Chapter 3, the fish were trained and tested in their home tanks. The reason for this was that after extensive piloting, I found that in order to get consistent and reliable feeding, fish needed to remain in their home tanks in Chapter 3. However, this difference in the level of manipulation prior to testing may be one of the causes in the differences in learning observed. Based on visible reactions to being caught and transferred (dashing and freezing behaviours exhibited), I assume that being caught and transferred to a new tank is stressful for individuals (Brown and Godin 1999). Previous work has shown that social learning is only exhibited under more stressful conditions in wildtype (but not domestic) guppies (Colinet, Guigueno and Reader unpublished data; Foster, Guigueno and Reader unpublished data) and increased use of social learning under higher stress in minnows (*Phoxinus phoxinus*) (Webster and Laland 2008). Thus, it is possible that a certain amount of stress, due to transfers or simulated predation, is necessary for learning to occur. The stress of transfers in Chapter 2 was perhaps enough to elicit learning, while the fish in Chapter 3 did not experience any substantial stressors, perhaps diminishing learning performance.

Previous research shows that familiarity between group members leads to a preference for grouping with familiar over unfamiliar conspecifics, more cohesive grouping and influences social network structure (Chivers et al. 1995; Lachlan et al. 1998; Hasenjager and Dugatkin 2017). Familiarity between individuals has also been shown to affect social information transmission due to selective grouping (Swaney et al. 2001). To reliably account for the level of familiarity between subjects and demonstrators in both Chapters 2 and 3 I used shoal demonstrators who were unfamiliar to the subjects. Familiarity has been shown to develop in 12 days in guppies (Griffiths and Magurran 1998), however due to the daily randomization of demonstrators from a stock group, I find it unlikely that familiarization developed throughout the course of the experiments and is unlikely to affect the results I see. Alternatively, it is possible, that the lack of familiarity is leading to diminished social learning, and this may be more important when considering who to learn from, rather than who to group with. There is evidence from several species that animals will choose who to learn from, with possible rules such as copy-the-majority, copy-successful-individuals and others (Laland 2004). Further modifications of the learning experiment could consider familiarizing individuals prior to testing (Morrell et al. 2008).

The fact that I can train our fish to feed from novel feeders and to group selectively in Chapter 2, and specifically that I can get them to feed from novel feeders in Chapter 3 (gelatin petri dish feeders) suggests that they are capable of learning, just not from my social and asocial cues within the experimental set up. Studies have shown that guppies (domestic and wildtype descendants) can learn a multitude of tasks through reinforcement training, including discrimination of shapes (Petrazzini et al. 2012) and numerical discriminations including fixed values and relative ratios (Petrazzini et al. 2014; Bisazza et al. 2014; Agrillo et al. 2014; Petrazzini et al. 2015). Other animals, such as bees (*Bombus* spp.), are also capable of learning flower preference, flower size and colour preferences (Gumbart 2000; Essenberg et al. 2015; Russell et al. 2015). As such, I believe some specifics in the difference in design between Chapter 2 and 3 must have led to the difference in results I see, either in the cues themselves, the motivation or the stress experienced by the subjects. Positive, negative results and non-significant results all contribute to establishing the extent to which conclusions can be generalized, while offering new perspectives and allow for alternative explanations to be investigated. Being able to train for group size, but not social and asocial cue use, provides us with some insights into the relative importance of certain social cues and behaviours to domesticated guppies.

Implications and further questions:

Investigating the fitness consequences of social interactions and grouping can help us understand the selective forces that allow for the evolution of various social behaviours (Kutsukake 2009). The Chapter 2 results seem to suggest that with all else equal between groups, successful foraging with a certain size group is a sufficient advantage for individuals to once again join that size group. I suggest further experiments attempting to manipulate group size by reinforcing for different group sizes, including subjects being alone (e.g. 2, 4, or 6 fish vs. no fish). This can allow for a better understanding of the flexibility and costs and benefits of grouping. If individuals of a social species, such as the guppy, can be trained to avoid grouping all together simply through food reinforcement, there can be something said about the strength of foraging success in driving grouping behaviour. These methods can also be used to train fish to selectively shoal with groups of different sizes, and then use these modified phenotypes to test adaptive hypotheses and to address ecological questions on the evolution of grouping and sociality (Ward and Webster 2016). Knowing the differences in shoaling tendencies of guppies in the wild, between high-predation and low-predation populations (Magurran 2005), another interesting question to explore would be whether the flexibility of shoaling tendencies under both predation regimes is the same. Can we experimentally train individuals from both populations to shoal with a large or small shoal to the same degree, or is there a restriction (genetic or otherwise) limiting the flexibility of shoaling with different size groups? Further integration of studies looking at grouping behaviours at the individual and the population level could be useful in helping address fundamental questions about group formation and how and why groups differ in sizes across contexts and environments (Ward and Webster 2016).

One limitation of my Chapter 2 study is that I did not measure personality traits, which could have added to our understanding of the influence personality may have on grouping behaviours. In order to be able to fully understand the evolution of social behaviours and the factors influencing these behaviours, it is important to consider individual differences in the tendency to associate with others (Ward and Webster 2016). Personality types have been thought to be adaptive, as they have direct fitness consequences, for example, more active, bold and exploratory guppies surviving for a longer time when exposed to a predator (Smith and Blumstein 2012). In grouping, shoals comprising of a mix of bold and shy individuals have been shown to have higher foraging success than pure shoals of either personality type (Dyer et al. 2009). Using my design, it would be interesting to see if boldness or sociality influence whether individuals more readily switch their shoal preference through food reinforcement training. Laboratory and field work in fish have found conflicting results, with laboratory work on three-spined sticklebacks showing bolder fish associating with more individuals, whereas in the wild this same tendency was found in shyer guppies, and wild caught laboratory reared guppies showing no correlation between boldness and shoaling (Pike et al. 2008; Croft et al. 2009; Jacquin et al. 2016).

Social learning has manifold ecological and evolutionary consequences, distinct from asocial learning (Reader 2016). It is important to try and investigate the underlying mechanisms of social learning, as it is possible that the different mechanisms have different transmission pathways and fitness consequences (Reader 2016). If social learning does have adaptive specializations in neurocognitive processes, this might help us in investigating the function of these specializations and for further investigations of their costs and benefits, in a similar way to social learning strategies (Lefebvre and Giraldeau 1996; Chouinard-Thuly and Reader 2015; Kendal et al. 2018). Understanding the trade-offs in the adaptive use of social and asocial learning can contribute to our understanding of the observed patterns of social learning seen in the wild, especially how social information can lead to cultural evolution, as in humans, the use and reliance on social learning and social information use has been attributed to our success and formation of cultures (Boyd and Richerson 1985; Herrmann et al. 2007; Kendal et al. 2009; Rendell et al. 2011). The mechanisms of social learning will inform study of the evolution of behaviour, cognition and culture: knowing the mechanisms will further allow us to investigate what evolved for social learning to occur (Heyes and Pearce 2015; Leadbeater 2015: Reader 2016).

In Chapter 3 I was unable to make any conclusions about the possible carryovers or trade-offs between social and asocial learning. Binary choice tests, as used in Chapter 2 and Chapter 3, are useful in quantifying many behaviours, and have widely been used for investigations of both grouping and learning (Lachlan et al. 1998; Chapman et al. 2008). However, they have also been criticized for lacking other potentially biologically relevant variables that might influence choice (Ward and Webster 2016). In grouping investigations, the motivation and grouping preference of the individuals in the stimulus/demonstrator group are often overlooked or not accounted for, negating the possibility of a two-way choice (Ward and Webster 2016). One way to overcome some of these issues is to investigate free ranging groups, and include social network analyses, with records of most or all individual's grouping behaviours (Croft et al. 2009), which I suggest for further work. Once learning is achieved through appropriate experimental design and controls, further considerations are important in terms of how social learning is assessed. Considering multiple measurements including speed of learning, accuracy, generalization, resistance to extinction and various others, and their correlation to one another is also important to be able to distinguish if social learning is a multidimensional trait itself (Reader 2016). Addressing this issue is a complicated task, requiring multiple well controlled and designed experiments that can tease apart variation in different traits, and provide more clues into the mechanisms responsible for social learning.

General conclusions and summary:

The aim of my thesis was to investigate flexibility and selectivity of social grouping and learning through reinforcement-based training. I was able to provide support for the hypothesis that grouping tendencies in the Trinidadian guppy are flexible and can be trained for through food-based reinforcement. However, I was not able to test hypotheses on learning from social or asocial cues. Due to a lack of learning, I was unable to test hypotheses regarding trade-offs and carryover effects. As suggested by Leadbeater (2015), attending to social stimuli is likely a consequence of grouping, and not a behaviour that has evolved to specifically facilitate social learning. However, it is important to repeat that grouping is not necessary for social learning, but rather can facilitate social interactions and influence the number of interactions that can lead to social learning. Studies such as mine, investigating flexibility of social grouping and learning tendencies, can shed light on questions of evolution and ecology, such as the evolution of sociality and how species can adapt to changing environmental conditions, both natural and human-induced (Ward and Webster 2016). Patterns of social grouping and social learning may further have impacts on animal management and conservation (Suboski and Templeton 1989; Brown and Laland 2001; Griffin 2004). For example, social learning of novel foods, predators and habitats within social groups can help train animals reared or rehabilitated in captivity, with important survival skills for the wild, decreasing post-release mortality rates (Suboski and Templeton 1989; Brown and Laland 2001; Griffin 2004). In order to establish proper conservation programs including social learning of skills, we need to understand if, and under what conditions, animals can socially learn. The guppy remains an ideal system to test questions on both grouping and learning, as it allows for within species differences to be tested within natural guppy systems of varying predation pressures and shoaling tendencies (Ward and Webster 2016). Further research investigating whether more instances of social learning or more effective social learning is seen in lineages with a longer history of group living could shed fresh light on questions about the flexibility of grouping and social learning.

References:

Agrillo, C., Miletto Petrazzini, M. E., & Bisazza, A. 2014. Numerical acuity of fish is improved in the presence of moving targets, but only in the subitizing range. *Animal Cognition*, 17, 307-316.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. 2014. Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518, 538.

Aplin, L. M., Sheldon, B. C., & Morand-Ferron, J. 2013. Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Animal Behaviour*, 85, 1225-1232.

Avarguès-Weber, A., & Chittka, L. 2014. Local enhancement or stimulus enhancement? Bumblebee social learning results in a specific pattern of flower preference. *Animal Behaviour*, 97, 185-191.

Baracchi, D., Vasas, V., Jamshed Iqbal, S., Alem, S., & Papaj, D. 2018. Foraging bumblebees use social cues more when the task is difficult. *Behavioral Ecology*, 29, 186-192.

Bates, L., & Chappell, J. 2002. Inhibition of optimal behavior by social transmission in the guppy depends on shoaling. *Behavioral Ecology*, 13, 827-831.

Behrens, T. E., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. 2007. Learning the value of information in an uncertain world. *Nature Neuroscience*, 10, 1214-1221.

Benhaïm, D., Bégout, M.-L., Lucas, G., & Chatain, B. 2013. First insight into exploration and cognition in wild caught and domesticated sea bass (*Dicentrarchus labrax*) in a maze. *PLOS One*, 8.

Bisazza, A., Agrillo, C., & Lucon-Xiccato, T. 2014. Extensive training extends numerical abilities of guppies. *Animal Cognition*, 17, 1413-1419.

Boogert, N. J., Giraldeau, L. A., & Lefebvre, L. 2008. Song complexity correlates with learning ability in zebra finch males. *Animal Behaviour*, 76, 1735-1741.

Boogert, N. J., Reader, S. M., & Laland, K. N. 2006. The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, 72, 1229-1239.

Bouchard, J., Goodyer, W., & Lefebvre, L. 2007. Social learning and innovation are positively correlated in pigeons (*Columba livia*). *Animal Cognition*, 10, 259-266.

Boyd, R., & Richerson, P. J. 1985. Culture and the Evolutionary Process. Chicago: University of Chicago Press.

Brakefield, P. M., & Roskam, J. C. 2006. Exploring evolutionary constraints is a task for an integrative evolutionary biology. *American Naturalist*, 168, 4-13.

Brooks, R. 1996. Copying and the repeatability of mate choice. *Behavioral Ecology and Sociobiology,* 39, 323-329.

Brooks, R. 1999. Mate choice copying in guppies: females avoid the place where they saw courtship. *Behaviour*, 136, 411-421.

Brown, C., & Laland, K. 2001. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, 59, 471-493.

Brown, C., & Laland, K. N. 2002. Social learning of a novel avoidance task in the guppy: conformity and social release. *Animal Behaviour*, 64, 41–47.

Brown, C., & Laland, K. N. 2003. Social learning in fishes: a review. *Fish and Fisheries*, 4, 280-288.

Brown, G. E., & Godin, J.-G. J. 1999. Chemical alarm signals in wild Trinidadian guppies (*Poecilia reticulata*). *Canadian Journal of Zoology*, 77, 562-570.

Bshary, R., Gingins, S., & Vail, A. L. 2014. Social cognition in fishes. *Trends in Cognitive Sciences*, 18, 465-471.

Burkart, J. M., Strasser, A., & Foglia, M. 2009. Trade-offs between social learning and individual innovativeness in common marmosets, *Callithrix jacchus*. *Animal Behaviour*, 77, 1291-1301.

Cabrera-Álvarez, M., Swaney, W. T., & Reader, S. M. 2017. Forebrain activation during social exposure in wild-type guppies. *Physiology & Behavior*, 182, 107-113.

Cantor, M. C., Shoemaker, L. G., Cabral, R. B., Flores, C. O., Varga, M., & Whitehead, H. 2015. Multilevel animal societies can emerge from cultural transmission. *Nature Communications*, 6, 8091.

Carlier, P., & Lefebvre, L. 1997. Ecological differences in social learning between adjacent, mixing, populations of Zenaida doves. *Ethology*, 103, 772-784.

Chapman, B. B., Ward, A. J. W., & Krause, J. 2008. Schooling and learning: early social environment predicts social learning ability in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 76, 923-929.

Chittka, L., & Leadbeater, E. 2005. Social learning: public information in insects. *Current Biology*, 15, R869-R871.

Chivers, D. P., Brown, G. E., & Smith, R. J. F. 1995. Familiarity and shoal cohesion in fathead minnows (*Pimephales promelas*): implications for antipredator behaviour. *Canadian Journal of Zoology*, 73, 955.

Chouinard-Thuly, L. 2018. Phenotypic Plasticity in Social Information Use and Stress Response in Trinidadian Guppies. PhD Thesis, McGill University, Montreal, Canada.

Chouinard-Thuly, L., & Reader, S. M. 2015. Does all teaching rest on evolved traits? *Behavioral and Brain Sciences*, 38.

Coolen, I., van Bergen, Y., Day, R. L., & Laland, K. N. 2003. Species difference in adaptive use of public information in sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*, 270, 2413-2419.

Coussi-Korbel, S. & Fragaszy, D. M. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, 50, 1441-1453.

Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. 2009. Behavioural trait assortment in a social network: Patterns and implications. *Behavioral Ecology and Sociobiology*, 63, 1495-1503.

Curley, E. A., Rowley, H. E., & Speed, M. P. 2015. A field demonstration of the costs and benefits of group living to edible and defended prey. *Biology Letters*, 11, 20150152.

Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20, 187-193.

Dawson, Erika H., Avarguès-Weber, A., Chittka, L., & Leadbeater, E. 2013. Learning by observation emerges from simple associations in an insect model. *Current Biology*, 23, 727-730.

Dawson, E. H., Chittka, L., & Leadbeater, E. 2016. Alarm substances induce associative social learning in honeybees, *Apis mellifera*. *Animal Behaviour*, 122, 17-22.

Day, R. L., Coe, R. L., Kendal, J. R., & Laland, K. N. 2003. Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, 65, 559-571.

Day, R. L., MacDonald, T., Brown, C., Laland, K. N., & Reader, S. M. 2001. Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour*, 62, 917-925.

Duffy, G. A., Pike, T. W., & Laland, K. N. 2009. Size-dependent directed social learning in nine-spined sticklebacks. *Animal Behaviour*, 78, 371-375.

Dugatkin, L. A. 1992. Sexual selection and imitation- Females copy the choice of others. *American Naturalist*, 139, 1384-1389.

Dugatkin, L. A., & Godin, J. G. J. 1992. Reversal of female mate choice copying in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society B: Biological Sciences*, 249, 179-184.

Dugatkin, L. A., & Godin, J.-G. J. 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behavioral Ecology*, 4, 289-292.

Dunlap, A. S., & Stephens, D. W. 2014. Experimental evolution of prepared learning. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 11750-11755.

Dyer, J. R. G., Croft, D. P., Morrell, L. J., & Krause, J. 2009. Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20, 165-171.

Essenberg, C. J., Easter, R. A., Simmons, R. A., & Papaj, D. R. 2015. The value of information in floral cues: bumblebee learning of floral size cues. *Behavioral Ecology*, 26, 1335-1344.

Fiorito, G., & Scotto, P. 1992. Observational learning in *Octopus vulgaris*. *Science*, 256, 545-547.

Galef, B. G., & Wigmore, S. W. 1983. Transfer of information concerning distant foods: A laboratory investigation of the 'information-centre' hypothesis. *Animal Behaviour*, 31, 748-758.

Godin, J.-G. J., & Morgan, M. J. 1985. Predator avoidance and school size in a Cyprinodontid fish, the banded killifish (*Fundulus diaphanus Lesueur*). *Behavioral Ecology and Sociobiology*, 16, 105-110.

Griffin, A. S. 2004. Social learning about predators: a review and prospectus. *Animal Learning & Behavior*, 32, 131-140.

Griffiths, S., & Magurran, A. 1998. Sex and schooling behaviour in the Trinidadian guppy. *Animal Behaviour*, 56, 689-693.

Grüter, C., & Leadbeater, E. 2014. Insights from insects about adaptive social information use. *Trends in Ecology & Evolution*, 29, 177-184.

Gumbert, A. 2000. Color choices by bumble bees (*Bombus terrestris*): Innate preferences and generalization after learning. *Behavioral Ecology and Sociobiology*, 48, 36-43.

Hasenjager, M.J., & Dugatkin, L.A. 2016. Familiarity affects network structure and information flow in guppy (*Poecilia reticulata*) shoals. *Behavioral Ecology*, 28, 233-242.

Hasenjager, M. J., & Dugatkin, L. A. 2017. Fear of predation shapes social network structure and the acquisition of foraging information in guppy shoals. *Proceedings of the Royal Society B: Biological Sciences*, 284.

Heathcote, R. J. P., Darden, S. K., Franks, D. W., Ramnarine, I. W., & Croft, D. P. 2017. Fear of predation drives stable and differentiated social relationships in guppies. *Scientific Reports*, 7, 41679.

Herbert-Read, J. E., Rosén, E., Szorkovszky, A., Ioannou, C. C., Rogell, B., Perna, A., Ramnarine, I.W., Kotrschal, A., Kolm, N., Krause, J., Sumpter, D. J. T. 2017. How predation shapes the social interaction rules of shoaling fish. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20171126.

Herrmann, E., Call, J., Hernández-Lloreda, M. V., Hare, B., & Tomasello, M. 2007. Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science*, 317, 1360-1366.

Heyes, C. 2012. What's social about social learning? *Journal of Comparative Psychology*, 126, 193-202.

Heyes, C. 2016a. Who knows? Metacognitive social learning strategies. *Trends in Cognitive Sciences*, 20, 204-213.

Heyes, C. 2016b. Blackboxing: social learning strategies and cultural evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371.

Heyes, C., & Pearce, J. M. 2015. Not-so-social learning strategies. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20141709.

Heyes, C. M. 1994. Social learning in animals: categories and mechanisms. *Biological Reviews*, 69, 207-231.

Hoare, D. J., Couzin, I. D., Godin, J. G. J., & Krause, J. 2004. Context-dependent group size choice in fish. *Animal Behaviour*, 67, 155-164.

Hoare, D. J., & Krause, J. 2003. Social organization, shoal structure and information transfer. *Fish and Fisheries*, 4, 269-279.

Hoppitt, W., & Laland, K. N. 2013. Social Learning: An Introduction to Mechanisms, Methods, and Models. Princeton University Press

Jacquin, L., Reader, S. M., Boniface, A., Mateluna, J., Patalas, I., Pérez-Jvostov, F., & Hendry, A. P. 2016. Parallel and nonparallel behavioural evolution in response to parasitism and predation in Trinidadian guppies. *Journal of Evolutionary Biology*, 29, 1406-1422.

Jones, K. A., Croft, D. P., Ramnarine, I. W., & Godin, J.-G. J. 2010. Size-assortative shoaling in the guppy (*Poecilia reticulata*): The role of active choice. *Ethology*, 116, 147-154.

Kappeler, P. M., Barrett, L., Blumstein, D. T., & Clutton-Brock, T. H. 2013. Constraints and flexibility in mammalian social behaviour: introduction and synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368.

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. 2008. Early experience affects producer-scrounger foraging tendencies in the house sparrow. *Animal Behaviour*, 75, 1465-1472.

Katsnelson, E., Motro, U., Feldman, M. W., & Lotem, A. 2011. Individual-learning ability predicts social-foraging strategy in house sparrows. *Proceedings of the Royal Society B: Biological Sciences*, 278, 582-589.

Kelley, J. L., Evans, J. P., Ramnarine, I. W., & Magurran, A. E. 2003. Back to school: can antipredator behaviour in guppies be enhanced through social learning? *Animal Behaviour*, 65, 655-662.

Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M., & Jones, P. L. 2018. Social learning strategies: Bridge-building between fields. *Trends in Cognitive Sciences*, 22, 651-665.

Kendal, R. L., Coolen, I., & Laland, K. N. 2004. The role of conformity in foraging when personal and social information conflict. *Behavioral Ecology*, 15, 269-277.

Kendal, R. L., Coolen, I., & Laland , K. N. 2009. Adaptive Trade-Offs in the Use of Social and Personal Information. In R. Dukas & J. Ratcliffe (Eds.), Cognitive Ecology II. (pp. 249-271). Chicago: University of Chicago Press.

Kendal, R. L., Coolen, I., Van Bergen, Y., & Laland, K. N. 2005. Trade-Offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*. 35, 333-380.

Krause, J., & Godin, J.-G. J. 1994. Shoal choice in the banded killifish (*Fundulus diaphanus, Teleostei, Cyprinodontidae*): Effects of predation risk, fish size, species composition and size of shoals. *Ethology*, 98, 128-136.

Krause, J. D., & Ruxton, G. D. 2002. Living in Groups. Oxford University Press.

Kutsukake, N. 2009. Complexity, dynamics and diversity of sociality in group-living mammals. *Ecological Research*, 24, 521-531.

Lachlan, R. F., Crooks, L., & Laland, K. N. 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, 56, 181-190.

Lachlan, R. F., & Servedio, M. R. 2004. Song learning accelerates allopatric speciation. *Evolution*, 58, 2049-2063.

Lafleur, D. L., Lozano, G. A., & Sclafani, M. 1997. Female mate-choice copying in guppies, *Poecilia reticulata*: a re-evaluation. *Animal Behaviour*, 54, 579-586.

Laland, K. N. 2004. Social learning strategies. *Learning & Behavior*, 32, 4-14.

Laland, K. N., & Hoppitt, W. 2003. Do animals have culture? *Evolutionary Anthropology: Issues, News, and Reviews*, 12, 150-159.

Laland, K. N., & Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, 53, 1161-1169.

Laland, K. N., & Williams, K. 1998. Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, 9, 493-499.

Leadbeater, E. 2015. What evolves in the evolution of social learning? *Journal of Zoology*, 295, 4-11.

Leadbeater, E., & Chittka, L. 2007a. The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behavioral Ecology and Sociobiology*, 61, 1789-1796.

Leadbeater, E., & Chittka, L. 2007b. Social learning in insects--from miniature brains to consensus building. *Current Biology*, 17, 703-713.

Leadbeater, E., & Chittka, L. 2009. Bumble-bees learn the value of social cues through experience. *Biology Letters*, 5, 310-312.

Leadbeater, E., & Dawson, E. H. 2017. A social insect perspective on the evolution of social learning mechanisms. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 7838-7845.

Leadbeater, E., & Florent, C. 2014. Foraging bumblebees do not rate social information above personal experience. *Behavioral Ecology and Sociobiology*, 68, 1145-1150.

Lefebvre, L., & Giraldeau, L.-A. 1996. Is Social Learning an Adaptive Specialization? In B. G. Galef (Ed.), Social Learning in Animals (pp. 107-128). San Diego: Academic Press.

Leris, I., & Reader, S. M. 2016. Age and early social environment influence guppy social learning propensities. *Animal Behaviour*, 120, 11-19.

Lindeyer, C. M. & Reader, S. M. 2010. Social learning of escape routes in zebrafish and the stability of behavioural traditions. *Animal Behaviour*, 79, 827-834.

Lindeyer, C. M., Meaney, M. J., & Reader, S. M. 2013. Early maternal care predicts reliance on social learning about food in adult rats. *Developmental Psychobiology*, 55, 168-175.

Lindstrom, K., & Ranta, E. 1993. Social preferences by male guppies, *poecilia reticulata*, based on shoal size and sex. *Animal Behaviour*, 46, 1029-1031.

Lucon-Xiccato, T., Dadda, M., & Bisazza, A. 2016. Sex differences in discrimination of shoal size in the guppy (*Poecilia reticulata*). *Ethology*, 122, 481-491.

Magurran, A. E. 2005. Evolutionary Ecology: the Trinidadian Guppy. Oxford University Press

Magurran, A. E., & Seghers, B. H. 1991. Variation in schooling and aggression amongst guppy (*Poecilia reticulata*) populations in Trinidad. *Behaviour*, 118, 214-234.

Magurran, A. E., & Seghers, B. H. 1994. Predator inspection behaviour covaries with schooling tendency amongst wild guppy, *Poecilia reticulata*, populations in Trinidad. *Behaviour*, 128, 121.

Magurran, A. E., Seghers, B. H., Carvalho, G. R., & Shaw, P. W. 1992. Behavioural consequences of an artificial introduction of guppies (*Poecilia reticulata*) in N. Trinidad: evidence for the evolution of anti-predator behaviour in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 248, 117-122.

Marchetti, C., & Drent, P. 2000. Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, 60, 131-140.

Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. 2016. The evolution of individual and cultural variation in social learning. *Trends in Ecology & Evolution*., 31, 215-225.

Metcalfe, N. B., & Thomson, B. C. 1995. Fish recognize and prefer to shoal with poor competitors. *Proceedings of the Royal Society B: Biological Sciences*, 207.

Morrell, L. J., Croft, D. P., Dyer, J. R. G., Chapman, B. B., Kelley, J. L., Laland, K. N., & Krause, J. 2008. Association patterns and foraging behaviour in natural and artificial guppy shoals. *Animal Behaviour*, 76, 855-864.

Nicol, C. J. 2004. Development, direction, and damage limitation: social learning in domestic fowl. *Learning & Behavior*, 32, 72-81.

Petrazzini, M. E., Agrillo, C., Izard, V. r., & Bisazza, A. 2015. Relative versus absolute numerical representation in fish: Can guppies represent "fourness"? *Animal Cognition*, 18, 1007-1017.

Petrazzini, M. E., Agrillo, C., Piffer, L., & Bisazza, A. 2014. Ontogeny of the capacity to compare discrete quantities in fish. *Developmental Psychobiology*, 56, 529-536.

Petrazzini, M. E., Agrillo, C., Piffer, L., Dadda, M., & Bisazza, A. 2012. Development and application of a new method to investigate cognition in newborn guppies. *Behavioural Brain Research*, 233, 443-449.

Page, R. A., & Ryan, M. J. 2006. Social transmission of novel foraging behavior in bats: Frog calls and their referents. *Current Biology*, 16, 1201-1205.

Pike, T. W., Samanta, M., Lindström, J., & Royle, N. J. 2008. Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2515-2520.

Pitcher, T. J., Magurran, A. E., & Winfield, I. J. 1982. Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology*, 10, 149-151.

Reader, S. M. 2003. Innovation and social learning: individual variation and brain evolution. *Animal Biology*, 53, 147-158.

Reader, S. M. 2016. Animal social learning: associations and adaptations. *F1000research*, 5.

Reader, S. M., & Biro, D. 2010. Experimental identification of social learning in wild animals. *Learning & Behavior*, 38, 265-283.

Reader, S. M., Hager, Y., & Laland, K. N. 2011. The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 1017-1027.

Reader, S. M., Kendal, J. R., & Laland, K. N. 2003. Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Animal Behaviour*, 66, 729-739.

Reader, S. M., & Laland, K. N. 2000. Diffusion of foraging innovations in the guppy. *Animal Behaviour*, 60, 175-180.

Reader, S. M., & Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 4436-4441.

Reader, S. M., & Lefebvre, L. 2001. Social learning and sociality. *Behavioral and Brain Sciences*, 24, 353-355.

Reader, S. M., & Leris, I. 2014. What shapes social decision making? *Behavioral and Brain Sciences*, 37, 96-97.

Rendell, L., Fogarty, L., Hoppitt, W. J., Morgan, T. J., Webster, M. M., & Laland, K. N. 2011. Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15, 68-76.

Reznick, D., Butler IV, M. J., Rodd, H., & Dolph, S. 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *The American Naturalist*, 157, 126-140.

Robison, B. D., & Rowland, W. 2005. A potential model system for studying the genetics of domestication: behavioral variation among wild and domesticated strains of zebra danio (*Danio rerio*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 2046-2054.

Rodd, F. H., & Reznick, D. N. 1991. Life history evolution in guppies: III. The impact of prawn predation on guppy life histories. *Oikos*, 62, 13-19.

Rosa, P., Nguyen, V., & Dubois, F. 2012. Individual differences in sampling behaviour predict social information use in zebra finches. *Behavioral Ecology and Sociobiology*, 66, 1259-1265.

Russell, A. L., Golden, R. E., Leonard, A. S., & Papaj, D. R. 2015. Bees learn preferences for plant species that offer only pollen as a reward. *Behavioral Ecology*, 27, 731-740.

Ruxton, G. D., & Sherratt, T. N. 2006. Aggregation, defence and warning signals: The evolutionary relationship. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2417-2424.

Sasvàri, L. 1979. Observational learning in great, blue and marsh tits. *Animal Behaviour*, 27, 767-771.

Sasvàri, L. 1985a. Different observational learning capacity in juvenile and adult individuals of cogeneric bird species. *Zeitschrift für Tierpsychologie*, 69, 293-304.

Sasvàri, L. 1985b. Keypeck conditioning with reinforcements in two different locations in thrush, tit and sparrow species. *Behavioural Processes*, 11, 245-252.

Scarponi, V., Chowdhury, D., & Godin, J.-G. J. 2015. Male mating history influences female mate choice in the Trinidadian guppy (*Poecilia reticulata*). *Ethology*, 121, 1091-1103.

Seghers, B. H. 1974. Schooling behavior in the guppy (*Poecilia reticulata*): An evolutionary response to predation. *Evolution*, 28, 486.

Shettleworth, S. J. 2010. Cognition, Evolution, and Behavior (2nd ed.). Oxford University Press.

Smith, B. R., & Blumstein, D. T. 2012. Structural consistency of behavioural syndromes: does predator training lead to multi-contextual behavioural change? *Behaviour*, 149, 187-213.

Smolla, M., Alem, S., Chittka, L., & Shultz, S. 2016. Copy-when-uncertain: bumblebees rely on social information when rewards are highly variable. *Biology Letters*. 12

Song, Z., Boenke, M. C., & Rodd, F. H. 2011. Interpopulation differences in shoaling behaviour in guppies (*Poecilia reticulata*): Roles of social environment and population origin. *Ethology*, 117.

Suboski, M. D., & Templeton, J. J. 1989. Life skills training for hatchery fish: Social learning and survival. *Fisheries Research*, 7, 343-352.

Swaney, W. T., Cabrera-Álvarez, M. J., & Reader, S. M. 2015. Behavioural responses of feral and domestic guppies (*Poecilia reticulata*) to predators and their cues. *Behavioural Processes*, 118, 42-46.

Swaney, W. T., Kendal, J., Capon, H., Brown, C., & Laland, K. N. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. *Animal Behaviour*, 62, 591-598.

Templeton, C. N., Laland, K. N., & Boogert, N. J. 2014. Does song complexity correlate with problem-solving performance in flocks of zebra finches? *Animal Behaviour*, 92, 63-71.

Templeton, J. J., & Giraldeau, L.-A. 1996. Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. *Behavioral Ecology and Sociobiology*, 38, 105-114.

Templeton, J. J., Kamil, A. C., & Balda, R. P. 1999. Sociality and social learning in two species of corvids: the pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*). *Journal of Comparative Psychology*, 113, 450-455.

Trompf, L., & Brown, C. 2014. Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. *Animal Behaviour*, 88, 99-106.

Udino, E., Perez, M., Carere, C., & d'Ettorre, P. 2017. Active explorers show low learning performance in a social insect. *Current Zoology*, 63, 555-560.

van Bergen, Y., Coolen, I., & Laland, K. N. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B: Biological Sciences*, 271, 957-962.

van der Post, D. J., & Hogeweg, P. 2008. Diet traditions and cumulative cultural processes as side-effects of grouping. *Animal Behaviour*, 75, 133-144.

Ward, A., & Webster, M. 2016. Sociality: The Behaviour of Group-Living Animals. Switzerland: Springer

Ward, A. J. W., Herbert-Read, J. E., Sumpter, D. J. T., & Krause, J. 2011. Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America*, 108.

Webster, M. M., & Laland, K. N. 2008. Social learning strategies and predation risk: minnows copy only when using private information would be costly. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2869-2876.

Webster, M. M., & Laland, K. N. 2011. Reproductive state affects reliance on public information in sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*, 278, 619-627.

Webster, M. M., & Laland, K. N. 2018. Experience shapes social information use in foraging fish. *Animal Behaviour*, 146, 63-70.

White, D. J., Watts, E., Pitchforth, K., Agyapong, S., & Miller, N. 2017. 'Sociability' affects the intensity of mate-choice copying in female guppies, Poecilia reticulata. *Behavioural Processes*, 141, 251-257.

Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. 2010. Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, 6, 614-616.

Wright, D., Ward, A. J. W., Croft, D. P., & Krause, J. 2006. Social organization, grouping, and domestication in fish. *Zebrafish*, 3, 141-155.