Behavioural innovation: Sources and predictors of intraspecific variation in Trinidadian guppies (*Poecilia reticulata*)

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Abstract

Animals often experience both predictable and unpredictable environmental change throughout their lifetimes. In many animals, behaviour is thought to be an important response to such changes as it can allow individuals to respond rapidly. Considerable individual variation has been noted in behaviour, yet it is unclear why individuals vary. In this thesis, I examined the geographic sources and behavioural and physical predictors associated with individual variation in the propensity to innovate (i.e. the production of novel behaviours) in the Trinidadian guppy (*Poecilia reticulata*). In Chapter 2, I characterised and compared two populations of female guppies in Trinidad in their propensity to innovate and its predictors. I found that populations varied, but that activity-exploration only correlated with innovation in one population. These results suggest population differences may be an important source of intraspecific variation, both in the expression of innovation and the characteristics associated with it. I then, in Chapter 3, tested the propensity to innovate in the laboratory, using male and female guppies from a single population, and examined a battery of behaviours and learning speed to understand the role of a broader range of predictors and a cognitive factor on innovation. I found that males and females differed in both in the propensity to innovate and learn, but there were no influences of any of the behavioural predictors, including learning, on innovation. This sex difference might suggest males and females exhibit speed versus accuracy trade-offs in innovation and learning propensities. The lack of consistency with the Chapter 2 predictor results raises questions about what factors moderate these differences as the field and laboratory studies differed in the type of innovation task. Thus, in Chapter 4, I examined whether the propensity to innovate and its predictors were generalizable across tasks by comparing individual performance across four novel tasks and two task types using male and female guppies. Similar to Chapter 3, I found that sex is an important source of variation as males and females varied in their repeatability, with some evidence of task general repeatability in males (though strongly influenced by two tasks) and limited evidence of task type specific repeatability in females. My results also suggest that the behavioural predictors were repeatable, but their influence was task specific, potentially explaining the diverse findings of previous work. Overall, my thesis shows that intraspecific behavioural variation might arise from a variety of sources and raises important questions about how different measures of a particular behavioural propensity may be related to each other.

Résumé

Au cours de leurs vies, la plupart des animaux vivront des changements environnementaux prévisibles et non-prévisibles. Pour plusieurs espèces, les adaptations comportementales sont importantes pour répondre rapidement aux ces changements. Nous observons de la variation notable en comportement chez les individus, mais les raisons pour cette variation ne sont pas claires. Dans ce travail de thèse, j'ai examiné les origines géographiques, ainsi que les indicateurs physiques et comportementales associés avec la variation individuelle dans la tendance d'innover (c'est-à-dire, la production des comportements novateurs) dans les guppy Trinidadiens (*Poecilia retuculata*). En chapitre 2, j'ai caractérisé et comparé les tendances d'innover et leurs indicateurs en deux populations femelles de guppy à Trinidad. J'ai démontré qu'il existe de la variation entre les populations, mais que les comportements actifs et exploratoires sont liés avec l'innovation dans une seule population examinée. Ces résultats suggèrent qu'il se peut que les différences entres des populations constituent une source importante de la variation intraspécifique, à la fois dans l'expression de l'innovation et leurs caractéristiques associées. Ensuite, en chapitre 3, j'ai analysé les tendances d'innover dans un contexte de laboratoire chez des guppy mâles et femelles. Pour mieux comprendre les indicateurs et les facteurs cognitives qui influencent l'innovation, j'ai examiné plusieurs comportements divers tel que la vitesse d'apprentissage. J'ai trouvé des différences en tendances d'innover ainsi que des différences en apprentissage entres les sexes, mais aucune influence des indicateurs comportementales, incluant apprentissage, sur l'innovation. Ceci peut suggérer que les tendances d'innover et d'apprendre sont soumises à des compromis entre la vitesse et la précision qui diffèrent pour les mâles et femelles. Cette incohérence avec les résultats vus en chapitre 2 soulève des questions à propos de quels facteurs soutiennent ces différences, puisque les expériences laboratoires et sur places utilisaient des tâches d'innovation différentes. Alors, j'ai examiné en chapitre 4 si les tendances d'innover et ses indicateurs étaient spécifiques à la tâche présentée ou pas, en faisant une comparaison de la performance individuelle des guppy mâles et femelles à travers quatre tâches nouvelles, comprenant deux styles de tâches. Semblable à chapitre 3, j'ai établi que le sexe d'un individu est une source importante de variation car les mâles et les femelles varient en répétabilité; quelques indices suggèrent une capacité générale pour les tâches présentées chez les mâles (cependant fortement influencé par deux tâches en particulier), contrairement aux femelles qui démontrent peu de répétabilité pour des tâches

spécifiques. De plus, mes résultats suggèrent que les indicateurs comportementaux sont reproductibles, mais leurs influences dépendent de la tâche spécifique. Ceci explique peut-être les conclusions diverses des chapitres précédents. Dans l'ensemble, ma thèse démontre que la variation comportementale intraspécifique peut se produire d'une variété des sources, et soulève des questions importantes au sujet de comment les mesures différentes d'un comportement particulier sont reliées les uns aux autres.

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Contribution to original knowledge

This thesis provides original scholarship to the study of the propensity to innovate and expands upon our knowledge of this behaviour in fish using Trinidadian guppies, *Poecilia reticulata*. In Chapter 2, I provide novel evidence that populations of fish can also vary in their propensities to innovate, as found in birds and mammals. I also found that population origin can influence the nature of the characteristics associated with innovation, shedding light on the environmental conditions, suggesting novel factors like predation risk that might promote such characteristics to be correlated with innovation. This chapter is also one the first studies to experimentally examine innovation in fish in the wild. In Chapter 3, I examined a battery of cognitive, behavioural, and physical characteristics of individual variation in innovation in male and female guppies. I found that male and female guppies varied in their innovation and learning propensities but that these behaviours were not related – a finding previously undocumented in fish and rarely found in other taxa. Furthermore, none of the behavioural and physical characteristics explained individual differences, thus contrasting with Chapter 2 but matching the presence of contradictory findings in the avian and mammalian literature. In Chapter 4, I examined whether innovation was generalizable across task types and tasks in male and female guppies. I found evidence for general repeatability across three tasks in males but only limited evidence for repeatability within a task type in females, whereas the predictors of individual differences varied by task, showing that individuals may exhibit repeatability in behaviour but raising questions as to common predictors. This study provides novel insight into one of the first experimental manipulations of how task type influences repeatability estimates for innovation as well as its predictors. While much of the innovation literature focuses on foraging tasks, throughout my thesis I show that I show that non-foraging tasks with a social reward can also be implemented when ecologically relevant. Furthermore, I also add to the relatively scant literature on non-problem-solving exploratory innovation tasks. Overall, my thesis shows that sex and task type can have significant contributions to the study of individual variation in innovation. The consistent and strong influence of sex potentially highlights the usefulness of examining such questions in species with a relatively large degree of sexual dimorphism. Furthermore, my findings in fish show some similarities with those in other taxa, indicating that fish may provide useful insights into innovation in other taxa as well.

Contribution of authors

Chapter 1: General introduction. Paul Q. Sims wrote the introduction with input from Simon M. Reader.

Chapter 2: An investigation of population variation in maze exploration and its predictors in wild Trinidadian guppies (*Poecilia reticulata*). Paul Q. Sims conceived and set up the experiment and collected the data. P. Q. S. analysed the results and wrote the manuscript with input from Simon M. Reader in all stages of the process. Data and code are permanently archived at Zenodo: https://zenodo.org/record/4628215. In revision at *Behavioural Processes*.

Chapter 3: Predictors of the propensity to innovate in Trinidadian guppies (*Poecilia reticulata*). Paul Q. Sims conceived the experiment. Ariel Grenier collected the data with help from P.Q.S. P.Q.S analysed the data and wrote the manuscript with input from Simon M. Reader in all stages of the process. Ariel Grenier provided comments on the manuscript and approves its inclusion in this thesis. To be submitted to *Animal Behaviour*.

Chapter 4: Is the propensity to innovate repeatable across tasks and sexes in Trinidadian guppies, *Poecilia reticulata*? Paul Q. Sims conceived and set up the experiment and collected the data. P. Q. S. analysed the data and wrote the manuscript with input from Simon M. Reader in all stages of the process. To be submitted to *Animal Behaviour*.

Chapter 5: General discussion. Paul Q. Sims wrote the discussion with input from Simon M. Reader.

All data and code for Chapters 2-4 will be publicly available and permanently archived at Zenodo.

Chapter 1: General introduction

Animals can experience variable environments, both across and within generations. These environmental changes are not always predictable (e.g. timing of oak, genus *Quercus*, masting) or familiar (e.g. anthropogenic changes: habitat loss, invasive species, climate change, etc.) and can change the adaptive values of different phenotypes. While natural selection provides one mechanism in which populations might adapt to changes (Endler, 1986; Hendry, 2016), behaviour can allow immediate or rapid individual responses (West-Eberhard, 2003). For instance, Duvaucel's geckos (*Hoplodactylus duvaucelii*) demonstrated reduced activity and minimal overlapping habitat preferences in the presence of predatory Pacific rats (*Ratus exulans*), but these behaviours increased when the rats were eradicated (Hoare, Pledger, Nelson, & Daugherty, 2007), suggesting the change in behaviour was in response to the rat presence, likely to avoid predation risk. Thus, behaviour can provide rapid means by which individuals can respond to environmental variability.

Behaviour is thought to play a significant role in understanding and managing animal responses to increasing anthropogenic changes (Bro-Jørgensen, Franks, & Meise, 2019; Candolin & Wong, 2012). For instance, noise pollution from anthropogenic sources can disrupt or mask important biological sounds such as birdsong (Templeton, Zollinger, & Brumm, 2016; Slabbekoorn, Dooling, Popper, & Fay, 2018). However, correlational evidence suggests that bird species inhabiting noisy urban environments sing at higher minimum frequencies than those in quieter rural areas (Slabbekoorn & Ripmeester, 2008), possibly allowing them to overcome masking effects, with some evidence suggesting that these differences may have a plastic basis (Slabbekoorn, 2013). Thus, variation in behaviour may explain and even predict differences in how animals deal with the consequences of anthropogenic disturbances as well as environmental change.

Consistent among-individual variation in traits, including behaviour (e.g. animal personality), has long been observed but more recently has been thought to play an important role in species' ecology (Bolnick et al., 2011, 2003; Dall, Bell, Bolnick, & Ratnieks, 2012; Dall, Houston, & McNamara, 2004; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, & Johnson, 2004; D. S. Wilson, 1998; Wolf & Weissing, 2012). These consistent individual differences are proposed to influence population dynamics, life history, community structure and interactions, and evolution, among many other phenomena (Bolnick et al., 2011; Wolf & Weissing, 2012). For instance, studies have found that such individual differences in behaviour (often termed 'animal personality') can have fitness consequences (Smith & Blumstein, 2007), which can contribute to their maintenance and importance in populations (Bergeron et al., 2013; Dall et al., 2004; Wolf, Doorn, Leimar, & Weissing, 2007; Wolf & McNamara, 2012; Wolf & Weissing, 2010). Thus, understanding both how and why individuals vary consistently will provide important insights into the presence of intraspecific variation.

Behavioural innovation in non-human animals, henceforth 'behavioural innovation', is the production of novel behaviours (Reader & Laland, 2003), and is thought to be an important component of how animals can respond to environmental variability by allowing individuals to produce new behavioural responses (Griffin & Guez, 2016; Reader & Laland, 2003; Roth, LaDage, & Pravosudov, 2010; Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005; Sol, Lefebvre, & Rodriguez-Teijeiro, 2005; Sol, Sayol, Ducatez, & Lefebvre, 2016; Wong & Candolin, 2015). Reader and Laland (2003) operationally define behavioural innovation at the population level as both a product, i.e. "a new or modified learned behaviour not previously found in the population" (Reader & Laland, 2003, p. 14), such as a new foraging technique, and as a process that "results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire" (Reader & Laland, 2003, p. 14), though alternative viewpoints on defining innovation exist (e.g. see Ramsey, Bastian, & van Schaik, 2007 and discussion within; Reader, Morand-Ferron, & Flynn, 2016). These innovations (products) can be either a familiar behaviour in a new context or a novel behaviour itself, though distinguishing an entirely novel behaviour may be difficult (Kummer & Goodall, 1985; Reader & Laland, 2003). Reader and Laland's definition concerns identification of innovative behaviours found in populations, rather than at an individual level. Instead, innovation is often operationally measured at the individual level in intraspecific studies as the propensity to innovate when exposed to a new situation, for example, via problem-solving performance on novel tasks (Griffin & Guez, 2014; Reader et al., 2016). Here, I use the definition of innovation put forth by Reader and Laland (2003) and widely used by other researchers examining intraspecific variation (see Griffin & Guez, 2014, 2016 for reviews) as my thesis focuses on experimentally induced innovation, though operationalized to an individual level whereby a behaviour is considered an innovation based on its novelty relative to that individual, rather than a population. Innovation is well known to vary widely, with counts of innovation reports differing between species (Lefebvre, Reader, & Sol, 2004; Overington, Griffin, Sol, & Lefebvre, 2011; Reader & Laland, 2001), and populations (Bastian, van Noordwijk, & van Schaik, 2012; Preiszner et al., 2017; Roth et al., 2010) and individuals reported to differ in the propensity to innovate (Cole, Cram, & Quinn, 2011; Laland & Reader, 1999a; Thornton & Samson, 2012). This variation might also have significant ecological consequences, from allowing individuals to use novel resources or food processing techniques (e.g. Fisher & Hinde, 1949; Kawai, 1965), to providing greater provisioning rates to offspring (Cauchard et al., 2017), furthering successful invasion of new habitats (Sol, Duncan, et al., 2005; Sol & Lefebvre, 2000; Sol, Timmermans, & Lefebvre, 2002), and even providing the building blocks for population differences in behavioural traditions (Allen, Weinrich, Hoppitt, & Rendell, 2013; Aplin et al., 2014; van Schaik et al., 2003). Variation in the propensity to innovate has also been linked with indirect and direct measures of fitness in some studies (Cauchard et al., 2017; Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole, Morand-Ferron, Hinks, & Quinn, 2012; Cole & Quinn, 2011; Huebner, Fichtel, & Kappeler, 2018; Laland & Reader, 1999b; Mateos-Gonzalez, Quesada, & Senar, 2011), indicating a potential for natural selection to act on this behaviour. Innovation might also result in evolutionary changes as a consequence of adaptive (or perhaps even adaptively neutral) behavioural changes exposing animals to new evolutionary regimes. For instance, the behavioural drive hypothesis posits that behavioural innovations and novel ways of exploiting the environment lead to increased exposure to a variety of selection pressures and therefore higher rates of evolution in larger brained, more flexible species (Tebbich, Griffin, Peschl, & Sterelny, 2016; A. C. Wilson, 1985; Wyles, Kunkel, & Wilson, 1983). This hypothesis is supported in comparative studies of birds (Lapiedra, Sol, Carranza, & Beaulieu, 2013; Lefebvre, Ducatez, & Audet, 2016; Nicolakakis, Sol, & Lefebvre, 2003; Sol, Stirling, & Lefebvre, 2005) and one in mammals (Cantalapiedra et al., 2014), though debate also exists as to the nature of the role behaviour plays (Huey, Hertz, & Sinervo, 2003). While the propensity to innovate itself might be linked to some measures of fitness (e.g. Cauchard et al., 2013) and theoretically undergo selection, more recently however, it has been proposed to be an adaptive generalist emergent property in response to variable environments (Griffin, 2016; Griffin & Guez, 2016; Sol et al., 2016) and composed of multiple processes having undergone correlational selection or selection on shared mechanisms (Griffin, 2016; Quinn, Cole, Reed, & Morand-Ferron, 2016; Tebbich et al., 2016). While this viewpoint generally fits within previous ideas about the evolution and nature of innovation (Reader & Laland, 2003) and has initial support within the comparative avian and primate literature (Navarrete, Reader, Street, Whalen, & Laland, 2016; Sol et al., 2016), it is unknown if such conclusions can also be made on an intraspecific level due to a lack of studies examining this hypothesis (but see Quinn et al., 2016). Furthermore, general conclusions about the mechanisms underlying the innovation process remain elusive or limited in scope (Amici, Widdig, Lehmann, & Majolo, 2019; Griffin, 2016; Griffin & Guez, 2014, 2016; Tebbich et al., 2016), thus restricting the ability to test such hypotheses.

Despite the prevalence of inter- and intraspecific variation in innovation, our knowledge is limited as to the sources of this variation, its underlying processes, and the characteristics associated with it. For instance, several authors have proposed that environmental harshness or variable environments can select for innovation (Lee, 2003; Reader, 2007; Sol, 2009), but it is unclear what kinds of environmental conditions might select for innovation and the generality of these predictions. Individual characteristics like exploratory propensity, cognitive factors such as learning performance, and state dependent influences such as satiation and motivation levels (Reader & Laland, 2003; Rowe & Healy, 2014; Tebbich et al., 2016) have also been proposed to influence the innovation process (Reader & Laland, 2003). However, studies often identify different predictors as important (reviewed in: Griffin & Guez, 2014), though a few common factors have emerged such as persistence and motor diversity in some of the extractive foraging literature (see Griffin & Guez, 2016 for a review of the avian literature). In addition, explanations are needed for the varied findings involving the same predictors of the propensity to innovate, to better understand the role these predictors play in the innovation process. Comparisons among studies can also be difficult as a wide range of taxa have been studied, from insects, fish, birds, and mammals (though most commonly birds and mammals), and studies often employ taxa or species specific tasks, though usually in an extractive foraging context with a visible food reward (Griffin & Guez, 2014; Reader et al., 2016). Indeed, the extent to which results can be generalized from different taxa and tasks is poorly understood (Tebbich et al., 2016) and may contribute to the variation among studies in which factors promote innovation. Thus, examining factors that might influence variation in predictor relationships within a single species may provide insight into the diverse findings in the literature.

Broadly, my thesis seeks to understand why individuals vary in their propensity to innovate. I address this question in three ways: 1) by characterizing population differences in the propensity to innovate (Chapter 2), 2) by observing the behavioural predictors and characteristics of among-individual variation in the propensity to innovate (Chapters 2, 3, 4) and how these relationships are influenced by population (Chapter 2) and task (Chapter 4), and 3), by examining the generality of the propensity to innovate across a variety of tasks (Chapter 4). This work further expands the innovation literature on these topics from birds and mammals to fish and provides some degree of within species replication of the individual characteristics associated with the propensity to innovate, and offers novel insights into innovation in non-extractive foraging contexts with social rewards.

Measuring and comparing innovation in non-human animals

Measuring innovation

In the wild, innovation has primarily been studied via counts of reports in journals of novel behaviours, particularly foraging on novel resources or novel foraging techniques and most notably in birds (Lefebvre, 2010; Lefebvre et al., 2004; Lefebvre, Whittle, Lascaris, & Finkelstein, 1997) and primates (Reader & Laland, 2001, 2002). These counts, after being corrected for potential confounds such as research effort and observer bias, are then used to compare innovation rates across taxa, providing insights into the adaptive role innovation might play such as facilitating invasion success (Ducatez, Audet, Rodriguez, Kayello, & Lefebvre, 2016; Sol, Duncan, et al., 2005; Sol et al., 2002) as well as its relationship to various putative measures of cognition, e.g. counts of social learning and tool use (Navarrete et al., 2016; Reader, Hager, & Laland, 2011), brain volume (Navarrete et al., 2016; Overington, Morand-Ferron, Boogert, & Lefebvre, 2009; Reader et al., 2011; Reader & Laland, 2002), ecological generalism (Ducatez, Clavel, & Lefebvre, 2014; Overington, Griffin, et al., 2011), species richness

(Nicolakakis et al., 2003), and life history (Sol et al., 2016). The use of innovation counts to represent species differences in innovation rate is also supported by among-species comparisons on performance in novel problem-solving tasks (Audet et al., 2018; Diquelou, Griffin, & Sol, 2016; S. J. Webster & Lefebvre, 2001), thus this measure has provided a useful metric for understanding the evolution and correlates of innovation rates among species.

Experimentally, behavioural innovation is measured in different ways, though most commonly via 'problem-solving' tasks partially inspired by Thorndike's (1911) classic studies of cats, in which individuals are presented with a novel 'problem' restricting access to a known reward, thereby motivating task engagement and providing a 'goal' (Beck, Walkup, & Shumaker, 2012). Performance is then measured either quantitatively by the speed at which individuals obtain the reward (e.g. latency to solve, number of trials till first solve) or qualitatively by whether they obtained the reward or not (e.g. solver versus non-solver). To ensure ecological relevance, tasks are often designed to require behavioural patterns, processes and motivations/rewards to solve relevant to the ecology of the species. For example, using male satin bowerbirds', *Ptilonorhynchus violaceus,* aversion to red objects, Keagy et al. (2009) examined problem-solving performance as removing or covering red objects on the bower. Alternatively, many studies use food rewards constrained within transparent 'puzzle boxes' or tasks, which can be solved by manipulating the task, such as removing a lever or lifting a lid, potentially involving operant conditioning processes (i.e. associative learning processes where the response is moderated through reinforcement of an outcome) presumed to be present in some natural foraging scenarios (Cole et al., 2011; S. J. Webster & Lefebvre, 2001). This approach has resulted in a large variety of problem-solving tasks, though there is a general congruence of task types within particular taxa (e.g. extractive foraging via lid piercing or pushing tasks in birds) and phylogenetic grouping (e.g. object removal tasks in bowerbirds), and in a rare and noteworthy case, a large scale comparative study modified extractive foraging puzzle box tasks to be species specific while still maintaining the underlying solving features (Benson-Amram, Dantzer, Stricker, Swanson, & Holekamp, 2016). Thus in many cases problem-solving tasks are within an extractive foraging context, particularly within the avian and mammalian literature, involving motor manipulation of an apparatus to obtain a visible food reward, similar to technical innovation reports in the comparative avian literature. Indeed, the problem-solving paradigm is thought to be a useful measure of innovation as it is hypothesized (with some support) to share similar processes with innovation broadly (Griffin & Guez, 2014; Reader et al., 2016).

In contrast, some studies in fish have examined innovation via the propensity to explore novel structures containing a hidden food reward (e.g. Laland & Reader, 1999a), although subjects were thought to have detected the presence of the reward through odour cues and been motivated to 'solve' the maze. This measure slightly differs from traditional problem-solving tasks in that the knowledge and motivation of the specific reward is less clearly known to subjects beginning the test. It is also difficult to distinguish whether behaviour in this context is driven purely by exploratory behaviour or if such propensities are driven via a specific motivation, such as seeking food or conspecifics. Following comparative work in birds on reports of foraging innovations, researchers have also measured innovation by the propensity to consume novel food items (e.g. Sol, Griffin, Bartomeus, & Boyce, 2011). Last, some authors use a more conservative descriptive comparative approach (i.e. the "geographic technique": Bastian et al., 2012; Krützen, Willems, & van Schaik, 2011; Ramsey et al., 2007), which attempts to identify unique behavioural variants or innovations between populations that cannot be explained by genetic or ecological factors, though more recent viewpoints acknowledge the importance of ecological factors in shaping such population differences (Koops, Visalberghi, & van Schaik, 2014).

These diverse measures have allowed researchers to examine a wide range of taxa and questions regarding the nature of innovators and the innovation process itself. For instance, some extractive foraging problem-solving tasks have been designed to examine whether individuals rely on perceptual motor feedback processes, such as operant conditioning, when solving these tasks via the time spent on functional versus non-functional areas of the apparatus (Cole et al., 2012; Thornton & Samson, 2012). Indeed, several authors have suggested that tasks be designed in this manner to allow explicit testing of specific psychological processes hypothesized to be involved in the innovation process, though these are rarely examined (Boogert, Madden, Morand-Ferron, & Thornton, 2018; see Rowe & Healy, 2014 and replies for a discussion of these issues; Thornton, Isden, & Madden, 2014). Using different tasks also allows examination of a wider range of animals (Kolm, 2014) and helps to mitigate or avoid potential task related biases to performance, such as motivational, perceptual, or motor capabilities (Rowe & Healy, 2014). Some caution, however, is needed for interpreting performance on different tasks as it is questionable whether the consumption of a food item (Sol, Griffin, & Bartomeus, 2012), exploration of a maze (Laland & Reader, 1999a), and manipulation of a puzzle box (Benson-Amram & Holekamp, 2012) can be generalized to the same behaviour (Reader, 2003). Indeed, while many studies use extractive foraging goal directed problem-solving it is not well known how performance on these tasks relates to non-goal directed exploration of the environment and the appearance of spontaneous behaviours (Reader, 2003; Tebbich et al., 2016; van Schaik et al., 2016).

Is the propensity to innovate general or context/task specific?

The variety of tasks used raises important methodological and theoretical questions about the relationships between performance on different tasks and their utility as a measure of the propensity to innovate (Reader, 2003). For instance, individual performance on a particular task is often assumed to be a stable measure of the propensity to innovate yet such consistency is not always assessed (Biondi, Bó, & Vassallo, 2010; Overington, Cauchard, Côté, & Lefebvre, 2011), and some studies find that this assumption is not valid (e.g. Keagy et al., 2009; Keagy, Savard, & Borgia, 2011; Prasher, Evans, Thompson, & Morand-Ferron, 2019; Preiszner et al., 2017). Moreover, in some cases consistency can be conditional on particular factors, such as housing/testing conditions (captive versus wild testing: Morand-Ferron, Cole, Rawles, & Quinn, 2011) or the specific tasks being compared (e.g. Bókony et al., 2014). Therefore, it is crucial to understand how performance on different tasks is related for designing, interpreting, and comparing studies on innovation, as I address in Chapter 4 of this thesis.

While some authors suggest that the propensity to innovate is a general propensity, independent of context, and moderated by common factors such as motor flexibility (Griffin & Guez, 2016), several studies indicate the contrary. For instance, comparative studies in birds have found that foraging versus technical innovation counts differ in their relationship with measures of brain size (Overington et al., 2009), ecological generalism (Ducatez, Clavel, et al., 2014), and life history (Sol et al., 2016), perhaps indicating that there are different types of innovation.

Similarly, Lefebvre and Nicolakakis (2000) found that foraging and nesting innovations in birds displayed different relationships with forebrain size. On an intraspecific level, performance on problem-solving tasks in a foraging context did not correlate with performance in a mating context (Isden, Panayi, Dingle, & Madden, 2013). In addition, observational reports of innovation in the wild have noted innovations occurring in multiple contexts, such as foraging, technical/ecological, and social contexts in primates (Kummer & Goodall, 1985). Some authors have gone even further in delineating primate innovations, such as separate categories for aggression and communication, though notably nearly half of the reported innovations fell into a foraging category (Reader & Laland, 2001). Furthermore, differences in task types within a context may not be similar. A study examining among-individual differences in performance across three tasks in an extractive foraging context found that performance was consistent across task types of a similar nature, i.e. flipping a top off a cup, but not with that of a dissimilar task, i.e. petri-dish lid removal by pulling or pushing (van Horik & Madden, 2016). Together, this work suggests that innovation rates may vary depending on the context in which they occur and the type of task used, though this topic has received relatively less attention in the literature and its significance is not well understood. Thus, in Chapter 4, I examine the generality of the propensity to innovate by comparing task performance across four novel tests and two task types. In the General Discussion, I consider how task performance can be compared and interpreted across Chapters 2-4 in light of task design differences between Chapters 2-4 and Chapter 4's findings. Throughout my thesis, I also examine the propensity to innovate in social, non-foraging contexts and compare my results to the literature on innovation in extractive foraging contexts.

If individual differences in the propensity to innovate are due to context or task type specific processes or individual specialization within a context or task type, it may provide important insights into the nature of intraspecific variation, such as through differences between local environments or populations (Roth et al., 2010), trade-offs between contexts or task types (Réale et al., 2010; Sih & Giudice, 2012), or individual specialization within a context or task type (Bolnick et al., 2003; Tebbich & Teschke, 2014; Teschke, Cartmill, Stankewitz, & Tebbich, 2011). Indeed, some authors have suggested that we might expect species to show enhancements in specialized cognitive abilities matched to their environments, rather than enhancement in their cognitive abilities in general, as well as advocating an increased consideration of whether such differences have an adaptive value and if so, the benefit of these differences (Sherry, 2006; Sherry & Schacter, 1987). Such ideas might also be applied at an intraspecific level to understand the nature of among-individual differences, for instance, in the case of population variation (e.g. Roth et al., 2010). Thus, examining the context and task type specificity of innovation has implications for understanding the consistency of among-individual variation (Réale et al., 2007) and may further inform hypotheses and predictions about how such variation may be distributed.

Sources, processes, and characteristics associated with intraspecific variation in the propensity to innovate

Sources of intraspecific variation

While innovation can provide benefits, such as increased foraging diversity, it might also incur significant costs, such as the development and maintenance of the neural substrates (e.g. brain component size: Snell-Rood, 2013) associated with greater innovation rates across bird and primate species (Navarrete et al., 2016; Overington et al., 2009). The innovation process itself may be risky or costly (Lee, 2003) by increasing exposure to a wider range of environments, and therefore greater variety and quantity of parasites (Garamszegi, Erritzøe, & Møller, 2007; McCabe, Reader, & Nunn, 2015; Soler et al., 2012; Vas, Lefebvre, Johnson, Reiczigel, & Rózsa, 2011). Some authors also suggest that the propensity to innovate may be part of a cognitive syndrome representing speed versus accuracy behavioural types (Sih & Giudice, 2012), where greater propensities to innovate (e.g. solving speed) might be negatively correlated with other behaviours, such as the speed to learn colour discrimination (Ducatez, Audet, & Lefebvre, 2014) and reversal learning tasks (Griffin, Guez, Lermite, & Patience, 2013). The propensity to innovate might also experience trade-offs if it is driven by state-dependency and body condition, with less competitive individuals being more willing to seek out novel foraging opportunities (Cole & Quinn, 2011; Laland & Reader, 1999b). Alternatively, benefits associated with the propensity to innovate such as increased fitness (clutch size, offspring fledged) and foraging efficiency may be traded-off with other measures of reproductive success, such as increased nest desertion rates (Cole et al., 2012). Local environmental conditions likely moderate the costs and benefits of the propensity to innovate (Quinn et al., 2016), but empirical evidence for which environmental factors are important and how they moderate these factors is generally lacking.

The environment might influence the propensity to innovate in different ways, either through selection acting on the innovation processes directly, through developmental plasticity (e.g. influences during specific life history stages, experience, or learning), or via impacts of current state (e.g. body condition). Environmental predictability, resource availability, and novel conditions are often, but not always (Fox, Sitompul, & van Schaik, 1999; Kummer & Goodall, 1985; van Schaik et al., 2016), important factors, as are the relative costs and benefits of innovating (Reader & Laland, 2003). For instance, harsh environments or years with greater scarcity of resources might induce greater rates of innovation, potentially due to evolved (Kozlovsky, Branch, & Pravosudov, 2015; Roth et al., 2010) or plastic responses (Quinn et al., 2016). Here, increased propensities to innovate might allow individuals to better cope with decreased resource availability. In line with this reasoning, the ‘necessity’ hypothesis suggests that individuals are more likely to innovate out of need, predicting that individuals in poorer body condition (Laland & Reader, 1999a) or those with greater energetic requirements (such as pregnant females: Lee, 2003) or who are less competitive may be more likely to innovate in foraging contexts (Cole & Quinn, 2011; Laland & Reader, 1999b). Alternatively, other authors have hypothesized that some innovation might be driven by environmental opportunities, i.e. the ‘opportunity’ hypothesis (Fox et al., 1999), perhaps explaining higher rates of innovation propensity in some urban bird populations (Audet, Ducatez, & Lefebvre, 2016; Preiszner et al., 2017). From another perspective, the ‘free time and energy’ hypothesis (Kummer & Goodall, 1985) suggests that innovation is a by-product of excess time and energy, an idea supported by the high numbers of innovations reported in captive primates (Kummer & Goodall, 1985; van Schaik et al., 2016). This hypothesis has also been supported by greater propensities to innovate in a captive population of spotted hyenas, *Crocuta crocuta* (Benson-Amram, Weldele, & Holekamp, 2013), though see Brubaker et al. (2017) for higher propensities to innovate in wild wolves, *Canis lupus*, as compared to domestic dogs, *Canis lupus familiaris*, as well as positive relationships between some measures of body condition/physiology and propensities to innovate in house sparrows, *Passer domesticus* (Bókony et al., 2014).

Population comparisons provide a useful method for examining how environmental conditions influence such differences. Furthermore, such comparisons provide a natural setting to examine how such variation might evolve in the wild. A few studies have examined population differences in the propensity to innovate via housing settings (captive versus wild: Benson-Amram et al., 2013), urbanization (Audet et al., 2016; Liker & Bókony, 2009; Papp, Vincze, Preiszner, Liker, & Bókony, 2015; Prasher et al., 2019; Preiszner et al., 2017), and environmental harshness/elevation (Kozlovsky et al., 2015; Roth et al., 2010; Tebbich & Teschke, 2014), and in some cases, provided tentative observational support for both the necessity (Kozlovsky et al., 2015; Roth et al., 2010) and free time hypotheses (Benson-Amram et al., 2013; Lehner, Burkart, & van Schaik, 2010). Yet, the generality of these findings to other species and environmental conditions is unclear. Understanding the environmental characteristics associated with intraspecific variation in innovation is a necessary step for deducing the factors that might select for individual differences. Thus, in Chapter 2, I extend prior work in birds and mammals to fish by examining population variation in the propensity to innovate and its underlying processes in a study system, the Trinidadian guppy, *Poecilia reticulata*, well known to exhibit population differences in ecology, morphology and behaviour (Endler, 1995; Magurran, 2005).

Processes and characteristics associated with among-individual differences

Innovation is thought to be a product of many different processes (Reader & Laland, 2003), ranging from state-dependent characteristics such as motivation or sex differences in energetic requirements, to behavioural propensities such as exploration and neophilia, as well as cognitive processes such as operant conditioning for motor based extractive foraging innovations (reviewed in: Brosnan & Hopper, 2014; Griffin & Guez, 2014; Reader & Laland, 2003; Reader et al., 2016 and papers therein). However, general conclusions for the role these predictors play in the innovation process has been unclear since many studies find conflicting or null results when assessing these relationships (Griffin & Guez, 2014).

While evidence that many of the proposed predictors of the propensity to innovate are consistently important is mixed, persistence (time spent interacting with a task) and motor diversity (the number of different behaviours expressed when attempting the task) often appear to be shared components of the solving process in several extractive foraging tasks in mammals and birds (reviewed in: Griffin & Guez, 2014, 2016). More recently, however, a meta-analysis examined the general effect of these predictors on the propensity to innovate, separating predictors associated with the necessity and free time and energy hypotheses and those associated with behavioural propensities and social facilitation hypotheses (Amici et al., 2019). In contrast to Griffin and Guez's literature reviews (2014, 2016), this meta-analysis found that persistence did not influence the propensity to innovate in a consistent manner across studies, though the effect of motor diversity was unable to be evaluated due to a paucity of studies. Furthermore, both exploration and neophilia were positively associated with relatively more innovation, though the strength of this relationship varied by setting (Amici et al., 2019), in line with earlier views of the role of these predictors (Reader & Laland, 2003). While this meta-analysis is a noteworthy and significant contribution to the field, these findings should be interpreted with some caution. The study of innovation in animals is still in its infancy, with a limited number of studies available for meta-analyses. For instance, only seven studies were available for exploration, eight for neophilia, and nine for persistence, though importantly, some studies had large sample sizes and one had a range of species examined, both of which were accounted for in the analysis (Amici et al., 2019). Differences between captive and wild settings was also extremely limited as there was only one study examining such variation for exploration and neophilia, and two for persistence. Both study and species accounted for significant proportions of the total variance (Amici et al., 2019), indicating significant among-study and among-species variance. Furthermore, only a single search term was used and without wildcard variations, likely limiting in search results. Thus, while Amici et al. (2019) show some general trends across the literature, understanding how and why species and studies vary in the nature of predictor relationships with innovation remains an important area of investigation.

Generally, studies describing the characteristics and processes associated with animal innovation have focused on how these predictors influence the speed at which individuals solve a given task after making initial contact. However, more recently it has been proposed that predictors of innovation might vary depending on the phase of the innovation process (Tebbich et al., 2016). For instance, exploration and neophilia might be expected to play a relatively large role in the discovery of an environmental opportunity, e.g. a novel food item, as well as in subsequent favourable interactions with the opportunity, e.g. an initial attempt to obtain the item and discovering what interactions yield positive feedback, whereas learning may be more important during repetition and testing phases, e.g. learning how to get the item and generalizing to other opportunities (Tebbich et al., 2016). Tebbich et al.'s (2016) proposal may shed some light on why studies vary in the influence of these predictors if different tasks vary in the phases of the innovation process tested. Furthermore, different tasks may involve different psychological processes. For instance, inhibitory control (i.e. a process that allows an individual to inhibit a response to a stimulus) may have a significant role in mediating solving success in tasks involving transparency and detour reaching as opposed to a task involving the consumption of a readily available but novel food item. These relationships may also be mediated by the environment (Dingemanse et al., 2007), thus examining their presence in different environments may provide further insight into among-study variation in results. In Chapter 2, 3, and 4, I examine the influence and nature of phenotypic characteristics, behavioural propensities, and cognitive processes thought to be associated with innovation, expanding previous work to fish and social maze exploration tasks. I also ask whether these relationships are dependent on population (Chapter 2) and if they are general or specific to task type, or even the task itself (Chapter 4) and whether there are general predictors of the propensity to innovate (Chapters 2-4).

Is innovation a measure of cognition?

Behavioural innovation is often referred to as a cognitive measure and associated with advanced cognition due to the processes thought to be involved in successfully innovating and correlations with other purported cognitive measures as well as with brain or brain component volumes, often assumed to be associated with advanced cognitive abilities (see discussions in: Cole et al., 2012; Isden et al., 2013; Keagy et al., 2011; Lefebvre et al., 2004; Reader & Laland, 2003; Sol, Duncan, et al., 2005). Yet it is not always clear what, if any, cognitive processes underpin the propensity to innovate (Boogert et al., 2018; Griffin, 2016; Lefebvre et al., 2004; Morand-Ferron, Cole, & Quinn, 2015; Reader & Laland, 2003; Rowe & Healy, 2014; Thornton et al., 2014).

Broadly, cognition is defined as “the mechanisms by which animals acquire, process, store, and act on information from the environment. These include perception, learning, memory, and decision-making” (Shettleworth, 2010b, p. 4). Measures of aspects of cognition can vary widely, from the speed or accuracy of performance with various types of learning (e.g. asocial/individual, social, reversal, discrimination, spatial) or the ability to manufacture and use tools (Shettleworth, 2010b). This broad definition and range of measures has highlighted the need to confirm what is meant by labelling a behaviour as ‘cognitive’ (Boogert et al., 2018; Griffin, 2016; Rowe & Healy, 2014). Several studies have found evidence for a general intelligence ‘*g*’ factor across various domains of cognitive measures (see Burkart, Schubiger, & van Schaik, 2017 for a recent review), across primate species or genera (Deaner, van Schaik, & Johnson, 2006; Johnson, Deaner, & van Schaik, 2002; Reader et al., 2011; Shultz & Dunbar, 2010), and to varying degrees within mammalian (Banerjee et al., 2009; Herrmann, Hernandez-Lloreda, Call, Hare, & Tomasello, 2010; Matzel et al., 2003) and avian species (Isden et al., 2013; Shaw, Boogert, Clayton, & Burns, 2015; van Horik, Langley, Whiteside, Laker, & Madden, 2018), however, such data is lacking or contradictory in other within-species studies (Ducatez, Audet, et al., 2014; Griffin et al., 2013; Tebbich & Teschke, 2014; Teschke et al., 2011; Thornton & Lukas, 2012; van Horik et al., 2018). Thus, one might parsimoniously assume measures of different cognition types are limited to the type of cognition measured, rather than a general cognitive ability. Understanding whether and how different cognitive measures correlate with the propensity to innovate and whether these relationships are present across different types of innovation remains an important area of study, as investigated in Chapters 3 and 4.

Studies have found support for a positive relationship between the propensity to innovate and measures of cognition when comparing taxa, but more mixed findings within species. When examining the evolution of innovation, several studies have examined indirect links with cognition via correlations with different measures of brain size, assuming that taxonomic variation in relative brain size measures provides a proxy for cognitive measures (reviewed in: Griffin & Guez, 2016; Lefebvre et al., 2004). These studies have found a positive link between the number of reported innovations and different measures of brain size across avian (Lefebvre et al., 1997; Overington et al., 2009; Timmermans, Lefebvre, Boire, & Basu, 2000), primate (Navarrete et al., 2016; Reader et al., 2011), and non-primate mammalian taxa (via experimentally measured solving success: Benson-Amram et al., 2016). In a few cases, innovation counts have been split into categories, such as technical (e.g. production of novel motor behaviours) versus foraging innovations (e.g. consuming novel food items), finding that technical, but not foraging, innovations largely explain the relationship with brain size in birds (Overington et al., 2009). However, more detailed causal path analyses in primates comparing technical innovations (narrowly defined as tool use only, and broadly defined as tool use and extractive foraging innovations) suggest that the direct brain size and innovation relationship is specific to technical innovation (tool use only), and that technical (tool use and extractive foraging) and non-technical innovations are indirectly related to brain size (Navarrete et al., 2016). Generally, these results have been interpreted to indicate evidence for the technical intelligence hypothesis (Whiten & Byrne, 1997), which postulates that the cognitive requirements of technical skills have led to the evolution of larger brains. Research in primates also supports the assumption that brain size co-varies with cognitive measures, finding that counts of behaviours such as tool use, tactical deception, innovation, and social learning are positively correlated and load onto a single factor, which is significantly correlated with some metrics of brain component size (Reader et al., 2011). Laboratory performance on batteries of cognitive tests is also correlated with this single factor, further supporting this link (Reader et al., 2011). However, the use of brain size measures as an indirect proxy for cognitive performance has been criticized in the literature (discussed in: Healy & Rowe, 2007; Herculano-Houzel, 2017; Logan et al., 2018) and as Griffin and Guez (2016) note, experiments are needed to infer causality.

Studies on an intraspecific level have also suggested a positive relationship between the propensity to innovate and cognitive measures, such as learning speed or accuracy (Boogert, Reader, Hoppitt, & Laland, 2008; Reader & Laland, 2003), though some authors have noted that such relationships might differ between taxonomic levels (Griffin & Guez, 2016; Reader, 2003). Extractive foraging problem-solving paradigms are often considered as measures of motor cognition (Boogert, Anderson, Peters, Searcy, & Nowicki, 2011; Shaw et al., 2015; Thorndike, 1911), and some studies support this viewpoint, showing that performance on these tasks is mediated by operant conditioning via perceptual motor feedback with functional and non-functional parts of a foraging apparatus (Cole et al., 2012; Overington, Cauchard, et al., 2011;

Thornton & Samson, 2012). In relation to '*g*', a few studies have also examined whether problem-solving performance positively correlates with different measures of cognition, though results are mixed (Griffin & Guez, 2014, 2016). For instance, problem-solving performance was positively correlated with social learning in pigeons, *Columba livia* (Bouchard, Goodyer, & Lefebvre, 2007), but negatively correlated in common marmosets, *Callithrix jacchus*, and only in one innovation task (Burkart, Strasser, & Foglia, 2009). Further, the propensity to innovate was not consistently positively correlated with various measures of cognition in satin bowerbirds, *Ptilonorhynchus violaceus* (Keagy et al., 2011), spotted bowerbirds, *Ptilonorhynchus maculates* (Isden et al., 2013), pheasants, *Phasianus colchicus* (van Horik et al., 2018), or New Zealand robins, *Petroica longipes* (Shaw et al., 2015). In an attempt to resolve the contrast of the inconsistent relationship between the propensity to innovate and cognitive measures within species and the relatively consistent findings across species, Griffin and Guez (2016) suggest that the positive correlations between cognitive measures and innovation rates among avian species are a result of common selective factors, i.e. environmental variability, for similar traits but that these traits remain mechanistically distinct, as explained below. Furthermore, they suggest that motor diversity, not learning, is the main predictor of the innovation process, as supported by the relatively consistent role of motor diversity in extractive foraging studies in comparison to learning (reviewed in Griffin & Guez, 2016). These ideas are conceptualized in a theoretical model where environmental variability moderates the evolution of cognition and diet generalism independently, with variability in diet generalism influencing motor diversity and in turn the propensity to innovate (Griffin & Guez, 2016). Thus, depending on environmental variability, populations within a species might display different relationships between measures of cognition and the propensity to innovate, whereas measures of motor diversity are expected to consistently correlate with the propensity to innovate. However, it is unknown whether such predictions are supported in a range of other taxa and non-extractive foraging tasks, as predicted by Griffin and Guez (2016). Furthermore, studying if the propensity to innovate and learn co-varies within species may shed important light into the selective factors that promote such correlations and the presence of potential trade-offs (Sih & Giudice, 2012). While there is a need to establish causality in such relationships (Griffin, 2016; Reader & Laland, 2003; Rowe & Healy, 2014; Tebbich et al., 2016), observational studies are first required to determine whether these relationships exist, the factors, if any, associated with the presence of these relationships (e.g.

Dingemanse et al., 2007), and their reliability within a species (Garamszegi, Markó, & Herczeg, 2012; Quinn et al., 2016). Thus, in Chapter 2, I characterise whether populations differ in their propensities to innovate and learn and in Chapter 3 examine the correlation between innovation propensity and learning speed, and finally in Chapter 4 I examine the influence of inhibitory control on propensities to innovate, in all chapters, using fish exposed to non-extractive foraging tasks.

In some cases of innovative behaviour, so called 'higher order' or 'intelligent' cognitive processes such as 'insight' have been proposed to play an important role (Bird & Emery, 2009; Foerder, Galloway, Barthel, Moore, & Reiss, 2011; Heinrich, 1995; Köhler, 1925; Taylor, Elliffe, Hunt, & Gray, 2010; von Bayern, Heathcote, Rutz, & Kacelnik, 2009). However, factors such as previous experience, motivation, and perceptual motor feedback have been shown to provide alternative explanations to 'insight' (Birch, 1945a, 1945b; Epstein, Kirshnit, Lanza, & Rubin, 1984; Köhler, 1925; Lind, Ghirlanda, & Enquist, 2009; Shettleworth, 2009; Taylor, Knaebe, & Gray, 2012). While proposals of higher cognitive function provide an appealing anthropomorphic explanation for how individuals solve a task as well as links to human cognition, simpler so-called 'killjoy' explanations can be difficult to exclude (Shettleworth, 2010a). As noted by many authors (Griffin, 2016; Reader & Laland, 2003; Tebbich et al., 2016; S. J. Webster & Lefebvre, 2001; see Morand-Ferron et al., 2015; Rowe & Healy, 2014 for detailed reviews), the innovation process is likely multifaceted and influenced by a variety of sources, including biases from prior experience, motivation, or task engagement, as well as other 'killjoy' explanations. Indeed, understanding of the importance of such factors, alongside specific measures of cognition, is needed for a holistic perspective. Thus, I examine both non-cognitive and cognitive predictors of the innovation process throughout this thesis.

Studying innovation in fish and in Trinidadian guppies

Innovation has been relatively poorly studied outside of birds and mammals, and much of the mammalian literature focuses on primates, though research into non-primate species has increased (Benson-Amram et al., 2016; Chow, Lurz, & Lea, 2018; Huebner & Fichtel, 2015; Marshall-Pescini, Frazzi, & Valsecchi, 2016; Waroff, Fanucchi, Robbins, & Nelson, 2017).

Large scale comparative studies on innovation have been restricted to birds and mammals (particularly primates), though whether such information is available to the same degree outside of birds and primates is a potential limitation. Similarly, at an intraspecific level, a review of innovative problem-solving did not report any fish studies (Griffin & Guez, 2014) and a more recent meta-analysis of innovation found only one study on fish (Amici et al., 2019) and none for other taxonomic groups such as reptiles, insects, or crustaceans out of the 37 studies used, though notably the former review's criteria excluded some early fish studies and the latter meta-analysis was likely conservative. While these studies might suggest that innovation has only been studied in birds and mammals, as discussed below, they instead indicate a paucity of studies in other species and biases or restrictions due to the selection criteria used when examining the literature.

Many studies show that individuals in other taxa exhibit the capacity to innovate via problem-solving tasks (crustaceans: Duffield, Wilson, & Thornton, 2015; cephalopods: Fiorito, von Planta, & Scotto, 1990; lizards: Leal & Powell, 2011; Manrod, Hartdegen, & Burghardt, 2008; bees: Loukola, Perry, Coscos, & Chittka, 2017; Mirwan & Kevan, 2014; fish: Kuba, Byrne, & Burghardt, 2009; Lucon-Xiccato, Gatto, & Bisazza, 2019; Millot et al., 2014; ants: Cammaerts, 2017; Dussutour, Deneubourg, Beshers, & Fourcassié, 2009) as well as through the exploration and navigation of novel maze structures (Berdal, Rosenqvist, & Wright, 2018; Laland & Reader, 1999a) and obstacles (ants: Cammaerts, 2017; Dussutour et al., 2009), suggesting a taxonomically widespread capacity to innovate. However, given the small number of studies within each of these taxa, it is less well understood if innovation is predicted by similar factors as in the avian and mammalian literature.

In fish, field reports of potentially innovative behaviour such as tool use has been reported (Bernardi, 2011; Coyer, 1995; Dunn, 2015, 2015; Jones, Brown, & Gardner, 2011; Paśko, 2010), though these not been compiled, counted, and examined as in birds and primates. Furthermore, a large body of work indicates that fish share many behavioural and cognitive characteristics such as personality, social learning, cooperation, problem-solving, tool use, behavioural traditions, and spatial learning, among others found in avian and mammalian taxa (Brown, Laland, & Krause, 2006; Grosenick, Clement, & Fernald, 2007; Laland, Atton, & Webster, 2011; Laland, Brown, & Krause, 2003; Lucon-Xiccato, Gatto, & Bisazza, 2017; Magnhagen, 2008; Moretz, Martins, & Robison, 2007; Pitcher, 2012; M. M. Webster, Whalen, & Laland, 2017). Relative brain size measures also vary among fish species and several studies have examined similar hypotheses as to the evolution of brain expansion in mammalian and avian taxa (Bauchot, Bauchot, Platel, & Ridet, 1977; Carlson et al., 2011; Drake, 2007; Gonzalez-Voyer, Winberg, & Kolm, 2009; K. Kotrschal, Van Staaden, & Huber, 1998; Northcutt, 2008; Pollen et al., 2007; Rodríguez et al., 2002; Shumway, 2010). Convergent evolution of brain volume measures and innovation is possible but has not been examined. Considering these links, fish represent a useful taxon for examining questions of innovation to establish the generality of hypotheses and to illuminate alternate ways in which the propensity to innovate has evolved.

Trinidadian guppies (Figure 1.1), *Poecilia reticulata*, are a small tropical freshwater fish originating in Trinidad and nearby Northern South America, but can be found around the world via domesticated strains and introductions and are considered a highly successful invasive species (El-Sabaawi et al., 2016; Lindholm et al., 2005; Magurran, 2005). Many of the rivers in the Northern mountain range of Trinidad are divided by large waterfalls, resulting in significant ecological differences (e.g. in predation regime, primary productivity, competition) above and below the waterfalls as well as among rivers that have influenced guppy ecology (Magurran, 2005). These differences have led to a large body of work examining the presence and drivers of such variation across a range of behavioural, morphological, life history, and physiological variables (Endler, 1986, 1995; Fischer, Harris, Hofmann, & Hoke, 2014; Harris, Ramnarine, Smith, & Pettersson, 2010; Hendry, Kelly, Kinnison, & Reznick, 2006; Magurran, 2005; Reznick & Endler, 1982). Guppies are also sexually dimorphic in size, coloration, and some behaviour, with females typically larger and less colourful compared to males (Magurran, 2005; Magurran, Seghers, Shaw, & Carvalho, 1995; and Figure 1.1). Females choose mates based on coloration in some populations and their mating system is a classic example of sexual selection (Brooks, 2002; Magurran, 2005). Females spend much of their time foraging or searching for food whereas males spend the majority of their time seeking copulation opportunities (Magurran & Seghers, 1994). Guppies are a social species and while both sexes generally prefer to shoal (Griffiths & Magurran, 1998), the extent of this preference can differ between sexes (Croft et al., 2003; Croft, Krause, & James, 2004) and populations (Magurran & Seghers, 1991; Seghers, 1974; Seghers & Magurran, 1995). Thus, they provide a useful system to examine the role of ecological influences and sex differences on behaviour.

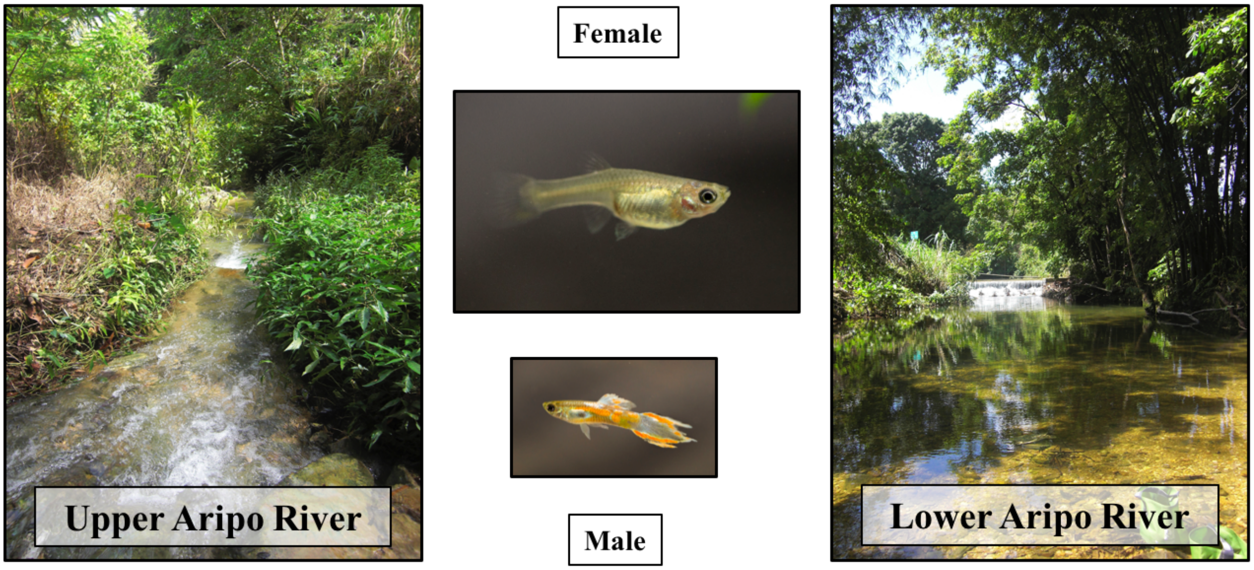

Figure 1.1. A typical wild type female (top) and more colourful male (bottom) guppy with images scaled to represent size differences between the sexes. The Upper and Lower Aripo populations illustrate the substantial ecological differences above (left) and below (right) the waterfalls. Guppy images taken by Raina Fan and used with permission.

Research on guppies has examined a broad range of behavioural phenomena, including personality (Budaev, 1997; Harris et al., 2010; Jacquin, Dybwad, Rolshausen, Hendry, & Reader, 2017; Jacquin et al., 2016; O'Steen, Cullum, & Bennett, 2002; Smith & Blumstein, 2010), innovative maze exploration and problem-solving (Berdal et al., 2018; Laland & Reader, 1999b, 1999a; Lucon-Xiccato & Bisazza, 2014; Lucon-Xiccato, Gatto, et al., 2019; Reader & Laland, 2000), spatial learning (Burns & Rodd, 2008; A. Kotrschal, Corral-Lopez, Amcoff, & Kolm, 2015; Lucon-Xiccato & Bisazza, 2017b, 2017a; Reader, Kendal, & Laland, 2003), social learning and information use (Brown & Laland, 2002; Kelley, Evans, Ramnarine, & Magurran, 2003; Lachlan, Crooks, & Laland, 1998; Laland & Williams, 1997, 1998; Reader et al., 2003; Trompf & Brown, 2014), reversal, discrimination, and numerical learning (Bisazza, Agrillo, & Lucon-Xiccato, 2014; A. Kotrschal et al., 2013; Lucon-Xiccato & Bisazza, 2014, 2016), and inhibitory control (Lucon-Xiccato et al., 2017; Lucon-Xiccato, Montalbano, & Bertolucci, 2019). Guppies breed well in laboratories and can be observed in the field, they lend well to both laboratory and field approaches, allowing ecological inference as well as experimental rigor and the sample sizes necessary for examining individual variation (Dingemanse & Dochtermann, 2013). In the wild, guppies experience frequent environmental change due to regular flooding during the rainy season and subsequent movement (Magurran, 2005) and some populations also experience anthropogenic influences due to close proximity with human habitations (Budaev, 1997; Rolshausen et al., 2015). Guppies also appear quite resilient and successful in novel conditions as illustrated by their high invasion success (El-Sabaawi et al., 2016; Lindholm et al., 2005; Magurran, 2005) and populations living in polluted areas (Jacquin et al., 2017; Rolshausen et al., 2015). Indeed, recent work suggests that behaviour, including innovation, may play an important role in survival and propagation in such conditions (Holway & Suarez, 1999; Rehage & Sih, 2004; Sol et al., 2002; Webb, Letnic, Jessop, & Dempster, 2014; Wright, Eberhard, Hobson, Avery, & Russello, 2010; Magellan, 2019 and papers within). Thus, guppies provide a useful system to examine innovation in relation to local ecology.

Thesis aims and outline

In this thesis, I examined the predictors of innovation, assessing individual characteristics, population differences, and contextual influences in both wild caught and wild descended guppies. Throughout my thesis, I measure the propensity to innovate in guppies using the latency to solve novel maze exploration and problem-solving tasks, most often with a shoal reward. While innovation is often tested in a foraging context, my pilot studies indicated that fish did not reliably feed upon solving tasks, potentially indicating differential interest in a food reward. Thus, I used a conspecific shoal reward given that guppies generally show a preference for shoaling (Croft et al., 2003, 2004; Griffiths & Magurran, 1998; Magurran, 2005; Magurran & Seghers, 1991; Seghers, 1974; Seghers & Magurran, 1995) and from pilot observations of consistent interest in a shoal reward. All tasks involved familiar motor behaviours such as swimming but in the context of navigating a novel structure. Given that both social and foraging tasks in guppies have required similar motor behaviours, I expected performance in relation to navigation would be similar regardless of the nature of the reward (e.g. social versus food), though motivational influences might differ between reward types. Analogues of the extractive foraging tasks used in birds and mammals such as lid removal (Lucon-Xiccato & Bisazza, 2014; domestic guppies: Lucon-Xiccato, Gatto, et al., 2019) or motor manipulation of a feeder

(Atlantic cod, *Gadus morhua*: Millot et al., 2014) exist for fish, but these paradigms were not ideal for two reasons. One, the lid removal task required significant shaping and showed high failure rates (Lucon-Xiccato, Gatto, et al., 2019) and smaller fish may be disadvantaged as they appeared less able to move the lid during pilot trials in our laboratory (personal observations). This bias may have been even more pronounced in the wild derived guppies used for the studies in this thesis, which are noticeably smaller than their domestic counterparts. Two, the motor manipulation task required individuals to grab and pull a tag to solve the task. However, guppies are primarily benthic consumers (Magurran, 2005) and feed either by drawing free floating food into their mouth by suction or by grasping and tearing algae (Dussault & Kramer, 1981). Thus given how guppies naturally feed, I did not expect individuals to be able to solve the feeder tag task used for testing larger fish due to motor and size constraints.

In Chapter 2, I compared two populations in the field in Trinidad in their maze exploration performance, also measuring body mass and activity-exploration behaviours, predicting that the propensity to innovate would be greater in the population experiencing higher intraspecific competition levels following the necessity hypothesis. This prediction was supported, but I also found that activity-exploratory rates only predicted innovation in one of the populations, suggesting population specific characteristics of individual differences. I found no evidence that individuals learned the task, perhaps because individuals had insufficient repetitions (two trials) to do so. Thus, in Chapter 3, I measured the latency to escape a predator stimulus over 10 trials and examined a wider range of behavioural predictors. I found that learning performance and innovation were not correlated, nor did any of the behavioural measures predict the propensity to innovate, in conflict with the field study. However, males and females varied in both their innovation and learning propensities, potentially suggesting sex specific cognitive styles such as speed versus accuracy trade-offs (Sih & Giudice, 2012). One possibility for the differences between Chapters 2 and 3 may be that task context differed: the Chapter 2 task involved exploring a novel structure whereas the Chapter 3 task involved escaping from an aversive stimulus into a novel structure. I examined the influence of task type further in Chapter 4 by comparing the repeatability and predictors of innovation across four tasks and two task types. I find some support for task general repeatability in males and limited support for task type specific repeatability in females, with significant differences between some of the male and female repeatability estimates, further supporting the idea that males and females may exhibit different cognitive styles (Sih & Giudice, 2012). However, the predictors of innovation varied by test, indicating test specific influences. Overall, these chapters show that both population origin and task choice can influence innovation, indicating some caution in generalizing findings from studies and raising questions regarding whether the propensity to innovate and its predictors are general, task type specific, or limited to the test itself.

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Chapter 2: An investigation of population variation in maze exploration and its predictors in wild Trinidadian guppies (*Poecilia reticulata*)

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In revision at *Behavioural Processes*

Abstract

Individuals often face unpredictable and harsh environments, presenting them with novel ecological problems. Behaviour can provide an adaptive response in such conditions and where these conditions vary between populations, we may predict development and evolution to shape differences in behaviour such as exploration, innovation, and learning, as well as other traits. Here, we compared in the wild the maze swimming performance of groups of female guppies from two Trinidadian populations that differ in numerous ecological characteristics, the Upper and Lower Aripo river. Compared to Upper Aripo fish, Lower Aripo fish were slower to complete the maze, our measure of propensity to innovate, and scored lower on a combined measure of activity and exploration. More active-exploratory groups were faster to complete the maze, but only in the Lower Aripo. We found no evidence for learning the maze. Our results suggest that activity-exploratory and innovative propensities can vary between populations, as can predictors of innovation. These findings are consistent with high predation risk shaping decreased activity-exploratory propensities, but further population comparisons are required to reliably determine the drivers of the observed population difference. Our results emphasize that individual and population differences in activity-exploration and innovation can be shaped by numerous factors.

Keywords: behavioural innovation; fish behaviour; fish cognition; guppy (*Poecilia reticulata*); problem-solving; population comparisons

1. Introduction

Animals often face novel challenges for which they may not be specifically adapted to. Behavioural innovation can allow appropriate responses to these challenges, either by producing a novel behaviour pattern or modifying an existing behaviour pattern to a novel context (Reader & Laland, 2003; Reader, Morand-Ferron, & Flynn, 2016). Commonly, the propensity to innovate is measured by presenting novel 'problems' to individuals, ranging from simple problems such as navigating a maze (Laland & Reader, 1999a) to more complex ones that may require increased understanding of the task affordances, e.g. removing a lever from a feeder to obtain access to a food reward (Cole, Cram, & Quinn, 2011). Behavioural innovations can facilitate exploitation of novel resources (Fisher & Hinde, 1949) and the formation of behavioural traditions within groups (Warner, 1988), and measures of innovative propensity correlate with successful invasion of new habitats (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005), meaning that innovation may have important consequences for individual and species' ecology.

Despite these potential benefits of behavioural innovations, several studies find significant intraspecific variation in the propensity to innovate (Cole et al., 2011; Laland & Reader, 1999a; Roth, LaDage, & Pravosudov, 2010; Thornton & Samson, 2012) which in some cases, has been linked to different measures of fitness, such as competitive ability (Benson-Amram & Holekamp, 2012; Cole & Quinn, 2011; Laland & Reader, 1999b; but see Prasher, Evans, Thompson, & Morand-Ferron, 2019), reproductive success (Cauchard et al., 2017; Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Morand-Ferron, Cole, Rawles, & Quinn, 2011; Preiszner et al., 2017; Wetzel, 2017), antioxidant levels (Bókony et al., 2014), and mating success (Keagy, Savard, & Borgia, 2011, 2009; but see Isden, Panayi, Dingle, & Madden, 2013) suggesting that this variation can have important consequences. However, as we discuss below, how local ecology influences both intraspecific variation in behavioural innovation and the predictors underlying this variation is relatively understudied (Griffin, 2016; Griffin & Guez, 2014; Tebbich, Griffin, Peschl, & Sterelny, 2016).

Several factors have been proposed to underlie individual variation in the processes leading to innovation, such as novelty responses, exploratory propensities, general activity, learning performance, age, experience, and state-dependent or motivational factors (reviewed in: Griffin & Guez, 2014; Reader & Laland, 2003). For instance, more active and exploratory individuals have been thought to be faster and more successful innovators, possibly because these behaviours increase the chance of discovering the solution to a problem and an increased likelihood of interacting with novelty (Griffin & Guez, 2014; Reader & Laland, 2003). Additionally, individual learning could enable individuals to learn the affordances of the task and thus faster learners may also be faster problem-solvers (Griffin & Guez, 2014; Reader & Laland, 2003). Older and more experienced individuals may also be better able to solve novel problems, though this could intersect with age related differences in neophobia where if younger individuals are less neophobic they may have a greater propensity to innovate (Griffin & Guez, 2014; Reader & Laland, 2003). Motivation is also thought to play an important role with more motivated individuals being more inclined to interact with and thus solve a novel task. However, conflicting findings in the literature illustrate that the relationship between these factors and innovation remains poorly understood (Griffin & Guez, 2014). Furthermore, studies within species are often few in number and mostly restricted to birds and mammals, thus studies encompassing other taxa and replications within taxa are needed to draw general conclusions and clarify species versus study specific findings.

There is increasing evidence for population differences in innovative problem-solving propensity (Papp, Vincze, Preiszner, Liker, & Bókony, 2015; Tebbich & Teschke, 2014; but see Berdal, Rosenqvist, & Wright, 2018), though the hypothesized causal factors investigated vary, including the effects of captivity and domestication (Benson-Amram, Weldele, & Holekamp, 2013; Brubaker, Dasgupta, Bhattacharjee, Bhadra, & Udell, 2017), urbanization (Audet, Ducatez, & Lefebvre, 2016; Papp et al., 2015; Prasher et al., 2019; Preiszner et al., 2017; Sol, Griffin, Bartomeus, & Boyce, 2011), and other environmental conditions, such as elevation and ‘harshness’ (Kozlovsky, Branch, & Pravosudov, 2015; Roth et al., 2010). Alternative hypotheses have been proposed for individual and population differences in innovation. The ‘free time and energy’ hypothesis suggests that animals are more likely to innovate during periods of excess energy and high survival probability (such as in captive conditions or for dominant individuals) as the costs of innovation may be relatively low (Kummer & Goodall, 1985). In contrast, the ‘necessity’ hypothesis predicts that animals will be more likely to innovate during times of need, such as in harsh environmental conditions with few resources available, or when they are less competitive individuals (Fox, Sitompul, & van Schaik, 1999; Laland & Reader, 1999a). The ‘opportunity’ hypothesis (Fox et al., 1999) posits that animals will be more likely to innovate in favourable conditions for innovations where there is repeated exposure to environmental opportunities, for example animals in urban habitats regularly exposed to food in trash cans. While several studies have investigated these hypotheses, evidence is mixed (Griffin & Guez, 2014; van Schaik et al., 2016) and the causes of this variation and generalizability across contexts are unclear. Some authors suggest that intraspecific variation in the propensity to innovate is the result of varied costs and benefits in the environment, but it is unclear which particular ecological factors are important, such as resource availability, predation pressure, environmental stability, etc. (Reader & Laland, 2003). Furthermore, since there are few studies on population differences it is unknown how widespread population variation is.

Here, we addressed population differences and factors favouring the propensity to innovate when navigating a novel maze in Trinidadian guppies (*Poecilia reticulata*), a tropical poeciliid fish. Wild Trinidadian guppies inhabit streams and rivers, and in Northern Trinidad waterfalls create populations within the rivers that differ in ecological conditions (Magurran, 2005). Trinidadian guppies are well studied, with population differences in behavioural, morphological, and physiological traits (Fischer, Harris, Hofmann, & Hoke, 2014; Magurran, 2005), though the ecological conditions shaping such variation can differ among rivers (Jacquin, Dybwad, Rolshausen, Hendry, & Reader, 2017; Magurran, 2005). In Northern Trinidad, populations are notably characterized by differences in ecological factors such as predation pressure, primary productivity, parasitism and fish density, and differences have been reported in behaviour patterns such as grouping, intraspecific aggression and competition, as well as exploratory propensities (Harris, Ramnarine, Smith, & Pettersson, 2010; Jacquin et al., 2016; Magurran, 2005). Guppies thus provide a useful system to explore and formulate hypotheses on the role of ecological factors on population differences in behaviour.

Guppies are known to be highly successful invaders, having been introduced throughout the world (Magurran, 2005) and show tolerance to anthropogenic habitat disturbances such as crude oil pollution (Rolshausen et al., 2015) and urbanization (Budaev, 1997). In addition, wild populations in Trinidad experience seasonal habitat changes and flooding (Magurran, 2005) that can transport individuals to new locations. Thus, the ability to successfully navigate and explore novel structures and contexts as well as learning new spatial locations may play an important role in guppy ecology and their success in colonizing new habitats and responding to anthropogenic changes. Innovation has also been successfully studied in guppies using mazes, both in domestic (Laland & Reader, 1999a) and wild-derived laboratory populations (Berdal et al., 2018). Furthermore, individual performance in such tasks is repeatable across different maze variations (Laland & Reader, 1999a). Sex, satiation, body size, previous experience, activity and exploratory propensities influence individual variation in innovative propensities (Berdal et al., 2018; Laland & Reader, 1999a), though little work exists on the role of cognitive mechanisms (Reader & Laland, 2000). However, studies in avian taxa suggests links between innovative problem-solving and social learning (Bouchard, Goodyer, & Lefebvre, 2007), individual learning (Boogert, Reader, Hoppitt, & Laland, 2008), and other forms of cognition (e.g. Ducatez, Audet, & Lefebvre, 2014; Isden et al., 2013).

Here, we tested the propensity to innovate and learn in groups of female guppies using a two-route maze floating in the river, where one route led to a stimulus shoal held within a container in the 'goal zone' and the other to a dead end. Innovation was measured as the latency of the group to reach the goal zone. Groups were sampled from the Aripo (Upper and Lower populations) river in Trinidad to assess potential population differences. In addition to learning, we also measured several predictors which might influence group variation, including body size (i.e. body length), activity, and exploratory propensities as exhibited in the maze. We measured activity and exploration together as our procedure was not designed to tease them apart. Body size might be considered as a proxy for age/experience as females have indeterminate growth and smaller fish are generally younger (Magurran, 2005). We predicted that faster innovators would be more active-exploratory and smaller bodied. Given that solving our task involves a simple motor skill (swimming) exhibited by both juvenile and adult guppies and does not require an accumulation of experience and skill to solve, following previous ideas (Reader & Laland, 2003) we predicted that smaller (and thereby younger) individuals might be more innovative as a function of reduced neophobia in juveniles. Alternatively, smaller bodied fish may be in poorer body condition and less competitive and therefore more motivated to solve the task as predicted via the necessity hypothesis. Fish from the Upper Aripo experience greater aggression from conspecifics, lower primary productivity, and higher densities compared to the Lower Aripo, consistent with higher rates of competition (Magurran, 2005). The Upper Aripo is also notably characterized by lower predator diversity and predation risk as compared to the Lower Aripo (Magurran, 2005) and activity-exploratory behaviour might carry less risks in this population (Jacquin et al., 2016). Thus based on both the necessity hypothesis and the potential risks of exploration, we predicted that fish from Upper Aripo would be more innovative than those from the Lower Aripo. Since we only compared two populations, we could not address or determine the specific ecological factors that may shape population variation. However, at this early stage of investigation we wanted to address whether population differences in the propensity to innovate exist. Our study serves as a basis to examine existing variation and to formulate future hypotheses on causal factors.

2. Materials and Methods

2.1 Subjects and field sites

In June 2013 we tested adult female guppies from two populations in northern Trinidad's Aripo river. We tested fish of the Lower Aripo and Upper Aripo populations, at locations 'Ap2' and 'Ap4' of Gotanda et al. (2013), respectively. We tested at two sites within each location, focusing on a single site each day with testing from 10:00-15:00. We chose sites separated by at least 80 meters to further reduce the chance that the same fish were re-tested on a different day. Shoals of fish were caught using butterfly nets with juveniles, males, and non-focal species released on site immediately. The remaining female guppies were placed together into a shaded holding container (34.5 x 19.5 x 13 cm) with shelter. Female subjects were haphazardly selected from this container for tests as subjects. Shoal fish were caught in the same way as subjects and were kept in a shaded and sheltered collapsible bucket (25 x 25 cm) separate from the tested fish. We used females because we used a shoal as a goal stimulus in our maze and females have been found to have higher shoaling propensities than males (Magurran, 2005). Guppies in the Aripo are generally observed in shoals (Magurran, 2005) and subjects were tested in groups of three to minimize any isolation stress.

2.2 Apparatus

We tested groups of three female guppies in a two route maze (45 x 23 x 26 cm high; Figure 1) of white opaque acrylic plastic partially submerged in the river (water depth ~ 21 cm). We used a two-route maze to increase the likelihood if maze completion was faster on re-test that this was due to learning a route through the maze rather than for example habituation to the maze apparatus and faster swimming in any direction. The maze was divided into 11 approximately equal-sized zones to track subject locations. A stimulus shoal of four female guppies was placed in the goal-zone of the maze in a sealed transparent cylinder (19 x 7 cm) to act as a rewarding stimulus. Previous studies in guppies and zebrafish have successfully used visual exposure to conspecifics as an attractive stimulus (Mühlhoff, Stevens, & Reader, 2011) or reward in learning tests (Al-Imari & Gerlai, 2008; Lucon-Xiccato & Bisazza, 2017) and our pilot trials found little response to various types of food under our testing conditions (P.Q.S., personal observation). The stimulus shoal consisted of two large and two small female guppies randomly chosen from a separate site at the same location to avoid familiarity biases (Swaney, Kendal, Capon, Brown, & Laland, 2001). We replaced the shoal after testing every fourth group of subjects. Shoal members were never tested in the maze and were allowed to habituate for 10 minutes before trials began.

2.3 Procedure

The stimulus shoal was added to the tank 10 minutes before a trial began. We then placed the subject group inside a small plastic transparent cylinder (30 x 6.5 cm) and allowed them two minutes to habituate. After habituation, we gently removed the cylinder, began timing, and video recorded Trial 1 for 10 minutes using a GoPro Hero 3 camera (Black Edition; 1080 p, wide format, 30 fps). A trial always ended after 10 minutes regardless of whether subjects had completed the task or not. The group was then returned to the start zone inside the cylinder, given two minutes to habituate, and released for the 10 minute Trial 2. After testing, we measured subjects' standard lengths (to the nearest 2 mm) by placing them in a petri dish on top of ruled paper. To avoid re-testing the same fish, subjects were placed in a container with shelter and shade and subsequently released at the end of the day. We tested 29 groups at two Upper

Aripo sites over three days but only 16 groups at two Lower Aripo sites over two days due to time constraints.

2.4 Video analyses

We extracted multiple behavioural measures (see below) from the videos using an event recorder program, JWatcher v1.0 (Blumstein & Daniel, 2007). We were unable to reliably distinguish individuals between the two trials and since fish spent the majority of their time shoaling (a mean of 480 s or 80% of their time was spent within four body lengths (Magurran, 2005) of groupmates and/or the stimulus shoal), we analysed groups rather than individuals. Our replicate was thus the group: all statistical analyses and sample sizes are based on subject groups. We used the minimum time for any group member to reach the goal zone as our measure of the latency to reach the goal zone ('goal zone latency') since the group mean could be influenced by the degree to which individuals group, follow, or learn from other group members during a trial. For all other measures, including body length, we used the median group score rather than the mean due to a small number of individuals within each group.

We used the 'goal zone latency' on the first trial as our measure of the propensity to innovate. Groups that did not reach the goal zone were the given maximum latency scores (600 s): this happened twice. Learning was assessed by including trial as a factor in the model and examining whether there were differences in the goal zone latency between Trial 1 and 2. This model also included group as a random effect, allowing us to account and test for among-group differences in behaviour. To measure activity-exploration in a novel environment, we initially counted the number of zones entered, either including zone re-entries ('total zones entered'), or not ('unique zones entered'). On Trial 1, mean total zones entered was high, 89 ± 26 (mean ± S.E.). However, most groups (84%) explored all 11 zones on Trial 1 and there was little variation in 'unique zones entered'. Thus, we did not analyse 'unique zones entered' further. Thus we analysed two behavioural measures, 'goal zone latency' and 'total zones entered', and one morphological measure, body length.

A small portion of videos could not be analysed due to poor visibility in field conditions. In some cases, trials were also discarded due to subjects swimming under the maze partitions when water movement caused the partitions to float upwards slightly. Thus some groups only had a recording of one trial (Trial 1: $n = 35$; Trial 2: $n = 38$). We used Trial 1 for 'total zones entered' in order to assess initial behavioural responses to the maze. However, we included both trials for analysis of goal zone latency, as this procedure helped reduce residual heterogeneity that would violate model assumptions and goal zone latency did not significantly differ between trials (see Results), suggesting minimal effects of maze habituation on this behaviour.

Twenty-four percent of videos, selected at random, were checked for inter-observer reliability, which was good (zone location: $r = 0.94$). All videos were coded blind to population origin.

2.5 Statistical analyses

We used R Statistical Software (R Core Team, 2020) to perform analyses. A repository containing data and code is permanently archived with Zenodo (Sims & Reader, 2021). When necessary, response variables were natural log transformed to meet model assumptions. In some cases, we detected among site heterogeneity in the residuals (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), thus we used Generalized Least Squares (GLS) in our linear models to weight the errors with site nested in population as a stratified variance (R package 'nlme') following Pinheiro and Bates (2000). All models containing trial included group as a random effect to account for repeated measures and were fit as linear-mixed effect models. Continuous predictors were standardized (mean-centered and scaled to one standard deviation). Model assumptions were examined following Zuur et al (2009). For linear-mixed effect models, we calculated marginal and conditional R^2 values using the R package 'MuMIn', representing the variance explained by the fixed effects and fixed and random effects respectively, following Nakagawa and Schielzeth (2013) and Nakagawa et al. (2017).

2.5.1 Predictors of maze completion and learning

We first examined population differences in our behavioural measures (total zones entered, goal zone latency) and body length by fitting models with the response variable of interest predicted by population. For goal zone latency, we examined the influence of the behavioural predictors and body length by fitting all terms into a global model, including interactions of each predictor with population to examine population specific effects. We then simplified the interactions using a backwards stepwise procedure via Likelihood Ratio Tests (LRT) with a $P \leq 0.1$ cut-off.

2.6 Ethical Note

All procedures were carried out in accordance with Trinidadian and Canadian law, with Animal Behaviour Society and Canadian Council for Animal Care guidelines, and were approved by the Animal Care Committee of McGill University (Protocol # 2012-7133). All fish were released at the site of capture at the end of testing.

3. Results

3.1 Did groups complete and learn the task?

Most groups completed the task on the first trial. We found no evidence for significant among-group differences in goal zone latency over the two trials ($V_{group} = 0.49 \pm 0.35$, LRT: $X_1^2 = 2.7$, $P = 0.1$), suggesting any intraspecific variation was largely due to differences at the population and site level. Groups did not improve in goal zone latency when retested (trial estimate: $P = 0.52$, Table 1), and our learning measure did not significantly differ between populations (trial measure: trial by population estimate: $X_1^2 = 0.55$, $P = 0.46$, Table 2). Thus we had no evidence that groups learned the location of the shoal and therefore did not analyse further predictors of our learning measure.

3.2 Population comparisons

Groups from the Upper Aripo, compared to those from the Lower Aripo, were faster to reach the goal zone (Figure 2; $P = 0.016$) and entered more zones ($P = 0.009$; all variables summarised in Table 2). The population difference in goal zone latency remained statistically significant when total zones entered and body length were entered into the model (Table 1).

3.3 Predictors of among-group differences in goal zone latency

Groups from the Lower Aripo that entered more zones were faster to reach the goal zone ($P < 0.001$, Figure 3, Table 1). However, this relationship was not found in the Upper Aripo (total zones entered estimate ± S.E.: 0.17 ± 0.15, $t_{39} = 1.14$, $P = 0.26$), and significantly varied from that in the Lower Aripo (population by total zones entered interaction: $P < 0.001$, Table 1). No other predictors significantly affected variation in goal zone latency, either across or within populations (all $P > 0.1$).

4. Discussion

We had two main findings. First, groups of guppies from the Upper Aripo were faster to innovate (measured as the minimum individual latency to complete the maze) than the Lower Aripo population. Second, groups that were faster innovators were more exploratory and/or active within the maze, but only in the Lower Aripo population. (Our methods did not allow exploration and activity to be separately measured). These data support our hypothesised population difference in the propensity to innovate and also suggest that predictors of individual differences in innovation may differ between populations. Furthermore, we provide evidence that variation in the propensity to innovate can be partially explained by relatively simple propensities such as activity-exploration; however, other factors also likely play an important role.

We found no evidence that groups learned to solve the maze task to reach the stimulus shoal. We discuss four potential explanations for this result. First, perhaps there were insufficient opportunities to learn the task given that groups were only tested twice. Many studies of learning examine performance over longer periods of time, e.g. multiple days and opportunities to learn the task (Arthur & Levin, 2001; Kotrschal, Corral-Lopez, Amcoff, & Kolm, 2015; Lucon-Xiccato & Bisazza, 2017; Odling-Smee & Braithwaite, 2003). Additionally, the maze dead end was asymmetrically located nearer to the starting zone and may have reduced the penalty for making an initial error. Second, floor effects could make learning difficult to detect if subjects were fast to reach the goal zone on the first trial. However, this seems unlikely given Trial 1 performance. Third, guppies may have been incapable of learning the task, though previous work shows that guppies can learn the location of a reward (Burns & Rodd, 2008; Kotrschal et al., 2015; Laland & Williams, 1997), including work conducted in the wild in northern Trinidad and with single training trials (Reader, Kendal, & Laland, 2003). Finally, subjects may simply not have been motivated to return to the stimulus shoal. Future work might examine learning over longer periods of time as well as an independent measure of shoaling preference to better distinguish between a lack of learning versus a lack of motivation. Alternatively, incorporating measures of learning accuracy (Burns & Rodd, 2008), rather than speed, may provide additional insights.

Groups from the Upper Aripo were faster to complete the maze than Lower Aripo fish, supporting our initial prediction following the necessity hypothesis. In the Upper Aripo predation risk and primary productivity is relatively low, while conspecific aggression and density is relatively high (Magurran, 2005). Together, these may simultaneously reduce the risk of exploring and exploiting novel resources as well as increasing the benefits of seeking out novel resources that are not being exploited by conspecifics. Indeed, in male domestic guppies and male great tits (*Parus major*) poorer competitors are reported to be more innovative (Cole & Quinn, 2011; Laland & Reader, 1999b). Population comparisons in another poeciliid, *Brachyraphis episcopi*, also found that fish from low predation and high competition populations were marginally faster to reach a novel foraging patch over repeated testing (C. Brown & Braithwaite, 2005). Similarly, sticklebacks from low predation populations were faster to learn the location of a novel food patch (Brydges, Heathcote, & Braithwaite, 2008), supporting the idea that predation and competition regime may influence similar exploratory behaviour (though see Burns & Rodd, 2008). However, replication across multiple populations and experimental manipulation would be needed to firmly infer the causal factors (e.g. competition) proposed to explain the differences. It would also be valuable to present fish with a battery of tests, to establish whether results generalize across tests (Bókony et al., 2014). Furthermore, since we tested guppies in the wild, evolved changes, recent experience and early-life experience could all play a role in the population difference we observed (Quinn, Cole, Reed, & Morand-Ferron, 2016; Roth et al., 2010). Indeed, captivity effects, including reduced selection pressure and a lack of wild developmental influences may explain the lack of variation in maze exploration rate between populations in Berdal et al.'s (2018) study, which used wild-derived guppies housed over 20 years in laboratory conditions. Thus, common garden and developmental studies may help shed light on the relative and interactive roles of genetics and developmental experience.

As predicted, faster innovators were more active-exploratory, supporting a role for activity and exploratory propensities in the innovation process (Reader & Laland, 2003), though we were unable to evaluate independent influences of these behaviours and this relationship was only present in the Lower Aripo. Similar interactive effects associated with ecological factors have been previously documented along different urban settings with body mass, neophobia, and dominance status differing in their relationship with the propensity to innovate between urban versus rural environments (Papp et al., 2015; Prasher et al., 2019; Sol et al., 2011; but see Audet et al., 2016). Variation in selective pressures, such as predation risk (Sol et al., 2011) and competition (Prasher et al., 2019), have been hypothesized to explain these differences. Variation in predation risk has been associated with the evolution of behavioural variation (C. Brown & Braithwaite, 2005; Brydges et al., 2008; Réale & Festa-Bianchet, 2003), though learning and plasticity might also play a notable role (Chivers & Smith, 1994; Griffin, Blumstein, & Evans, 2000). Predation risk could also influence the existence of behavioural correlations, potentially due to trade-offs in risk strategies (Bell & Sih, 2007; Dingemanse et al., 2007). The Lower Aripo is characterized by greater predation risk and in our study, groups of fish from the Lower Aripo were less active-exploratory than those from the Upper Aripo, similar to other studies showing fish with a history of high predation have reduced activity compared to fish with a low predation history (G. E. Brown, Ferrari, Elvidge, Ramnarine, & Chivers, 2013; Giles & Huntingford, 1984). Individuals in this Lower Aripo population might adopt a range of behavioural strategies to reduce predation risk, from avoiding novelty and reducing activity to actively seeking out novelty but quickly, potentially explaining the correlation between activity-exploration and the propensity to innovate. Alternatively, activity-exploratory propensities may be linked to shoaling propensities such that the most active fish are those most motivated to find shoalmates. Since shoaling is higher and serves to help mitigate predation risk in the Lower Aripo, it may explain why such a relationship was not found in the Upper Aripo. Future studies might examine the role of predation in driving such correlations by sampling multiple population contrasts from replicate rivers. Previous work in guppies also found that faster innovators were also more exploratory and had higher activity levels (Berdal et al., 2018), thus at least in guppies of the Lower Aripo, we find some consistency in results.

In contrast, the propensity to innovate did not correlate with body size. Previous work in domestic and laboratory reared guppies has shown influences of body size (Berdal et al., 2018; Laland & Reader, 1999a) on the propensity to innovate, though in our case, body size and the propensity to innovate were measured differently. Furthermore, some studies in birds and insects have shown differences between captive/domestic versus wild populations (Morand-Ferron et al., 2011; Wiggins, Bounds, & Wilder, 2018; but see Yuen, Pillay, Heinrichs, Schoepf, & Schradin, 2016) which may have influenced the comparability of our results. For instance, domestication might result in lower risk aversion and higher attraction to novelty, which might subsequently influence predictors of among-individual variation. In addition, guppies from the high and low predation wild populations have been previously reported to differ in body size (Magurran, 2005; but see Hendry, Kelly, Kinnison, & Reznick, 2006), yet our study found no significant population differences in body length, potentially suggesting our measure was underpowered.

Our innovation test was conducted in a social context (i.e. groups of fish) to reduce potential isolation stress. Several studies have investigated whether innovation differs between isolated and social contexts, with mixed results (Griffin, Lermite, Perea, & Guez, 2013; Krasheninnikova & Schneider, 2014; Overington, Cauchard, Morand-Ferron, & Lefebvre, 2009). For instance, in Carib grackles (*Quiscalus lugubris*), Overington et al. (2009) found that individuals took longer to contact a novel foraging task in a social context compared to performance in an individual control task, though there was no difference in the latency to solve, suggesting that the social context can inhibit the propensity to engage in a novel task, possibly to prevent others from scrounging the rewards, but not the propensity to solve it. Using orange-winged amazons (*Amazona amazonica*), Krasheninnikova and Schneider (2014) found that social context did not affect solving performance, however, individuals in the social context were much faster to contact the task, with the authors suggesting an effect of social facilitation mitigating the potential perceived danger of novelty. Factors such as species ecology and the nature of the task likely influence the role of social context as the cost and benefits of grouping will vary. If social context influenced our task, we might have expected a social facilitation effect and faster latency to reach the shoal in the Lower Aripo population given the higher shoaling propensities of fish in this location and the nature of our stimulus reward. However, subjects were not able to see or smell the shoal initially, thus the motivation behind swimming through the maze could be due to a number of factors, including activity-exploratory propensities, as seen in the Lower Aripo. An independent measure of shoaling preference might help elucidate the relative role of social motivation in exploring the maze.

Potential correlates of innovative propensity were measured simultaneously with our measure of innovation, within the same test. This might increase the probability that these measures correlate together. However, the fact that different patterns were observed in the two populations suggests that our results are not simply the outcome of non-independence in measures due to them being measured within the same test. Nevertheless, when logistically feasible, we suggest future work should use independent standardized tests to confirm the generality of the results.

Our study adds to the relatively limited literature uncovering population variation in innovative behaviour and suggests that such variation can also have important influences on the predictors of innovation. Our latter finding also supports the idea that propensities to innovate may be part of a suite of correlated traits and may be difficult to separate from propensities such as exploration (Berdal et al., 2018; Griffin, 2016), including non-cognitive behaviours, though it is unclear why these correlations differed between populations. The observed differences could arise from genetic and environmental differences between populations, including non-adaptive sources such as genetic drift, though we cannot presently determine their relative roles. Future work might examine multiple population comparison replicates to determine the common factors driving these differences. Additionally, independent measures of competitive ability, exploration, and risk-taking propensities would help to assess potential behavioural mechanisms driving such differences, though experimental manipulations would be needed to confirm a causal role (Griffin, 2016; Tebbich et al., 2016). The population variation in the predictors of innovation suggests that consideration and future study of population origin and the factors which shape such variation may help shed light on why predictors of the propensity to innovate vary across studies (Griffin & Guez, 2014).

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7. Figures

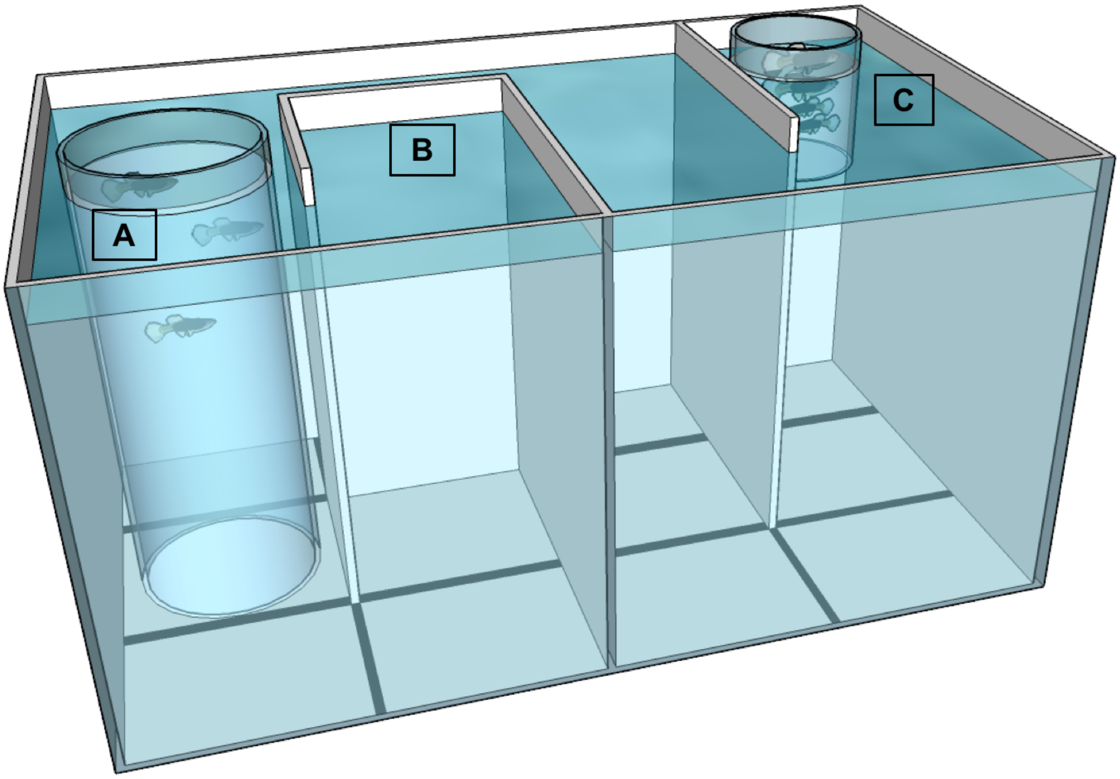

Figure 1. Maze apparatus (45 x 23 x 26 cm) placed into the river for testing groups of guppies in the field. [A]: Starting zone, [B]: dead end, and [C]: Stimulus shoal reward and goal zone. The 11 zones used for measurement were distinguished using black electrical tape on the bottom of the tank. We also placed opaque aquarium paper with images of plants and shelter (not pictured) on the inside walls of the tank and maze walls. The subject group was unable to see the stimulus shoal until the last sections of the maze, near "C". Image approximately to scale.

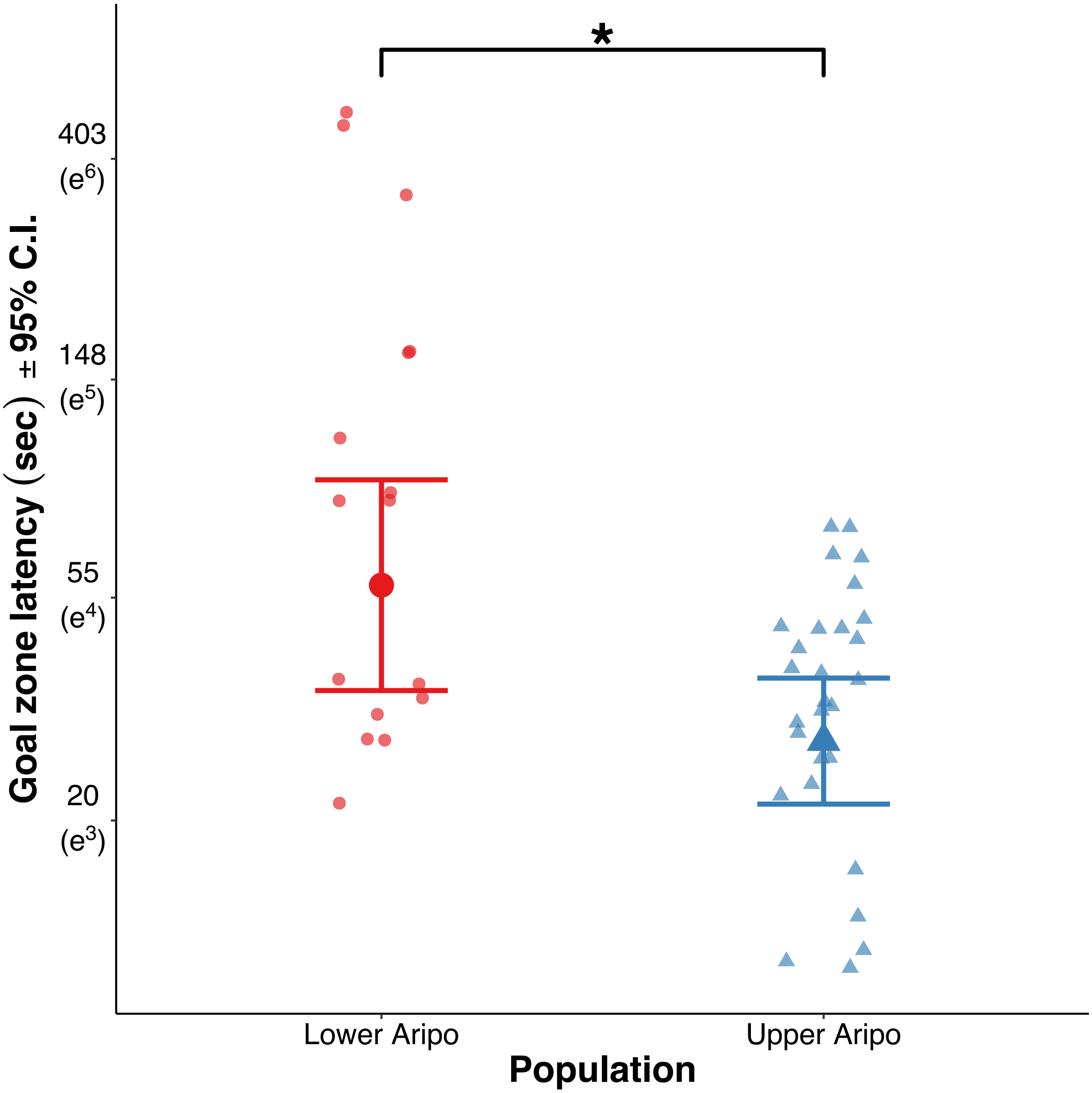

Figure 2. Population comparison between the Lower Aripo (red circles) and Upper Aripo (blue triangles) populations in their latency to reach the goal zone. Smaller points represent averaged raw data from trials 1 and 2 for each subject group. Larger points represent marginal means (± 95% Confidence Intervals) from a model accounting for the effects of body length, total zones entered, and trial. Darker points represent overlapping points. * = $P \leq 0.05$. Note the y-axis is on a natural log scale.

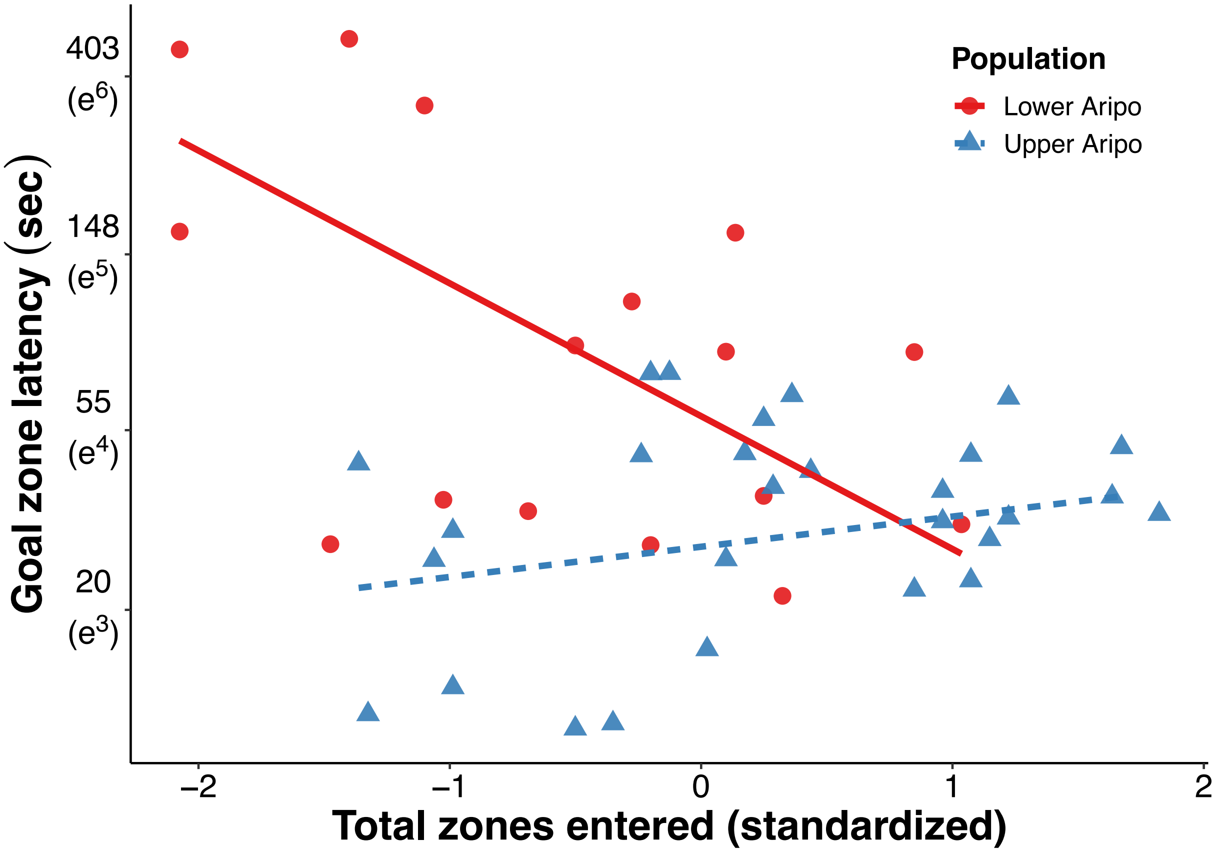

Figure 3. Lower Aripo fish (red circles and solid line) that entered more zones were faster to reach the goal zone, while this relationship was not observed in Upper Aripo fish (blue triangles and dotted line). The x-axis is standardized (mean centred and one standard deviation). Lines represent model predicted values for each population from a model accounting for the effects of body length, total zones entered, and trial. Points represent averaged raw data from trials 1 and 2 for each subject group. Note the y-axis is on a natural log scale.

8. Tables

Table 1. The reduced linear mixed effect model (after removing non-significant interactions) predicting the natural log goal zone latency with group (*n* = 44) as a random effect (V_{group} = 0.49), and controlling for among site heterogeneity using generalized least squares weighting. R_m^2 = 0.59, R_c^2 = 0.87 (Nakagawa & Schielzeth, 2013). Marginal R_m^2 represents the variance explained by the fixed effects and the conditional R_c^2 represents the variance explained by both the fixed and random effects. Continuous predictors were mean centred and scaled by one standard deviation. The reference level for trial is the first trial, for population it is the Lower Aripo; trial is coded as -1,1 to examine marginal effects.

Predictor	Estimate	S. E.	d.f.	t-value	P-value
Intercept	4.08	0.24	40	17.24	<0.001
Total zones entered	-0.75	0.19	39	-3.88	<0.001
Population: Upper Aripo	-0.73	0.28	39	-2.62	0.013
Body length	-0.08	0.12	39	-0.64	0.52
Trial: Second trial	-0.04	0.07	40	-0.65	0.52
Total zones entered x Population: Upper Aripo	0.92	0.25	39	3.74	<0.001

Table 2. Population comparisons (model estimates ± S.E.) between the Lower and Upper Aripo in behaviour and body length with Lower Aripo as the reference level. Goal zone latency was natural log transformed and modelled as a mixed model with a Gaussian distribution. This model accounted for variance among sites nested within populations using generalized least squares and fit group as a random effect. The predictors of interest were fit as fixed effects as detailed in the methods. Marginal R_m^2 represents the variance explained by the fixed effects and the conditional R_c^2 represents the variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013). Total zones entered and body length were natural log transformed and modelled with a Gaussian distribution as linear models with standard and adjusted R^2 values.

Response	Predictor	Estimate	S. E.	t-value	d.f.	P-value	R^2	Adj. R^2	R_m^2	R_c^2
Goal zone latency	Intercept	3.96	0.19	20.65	42	<0.001	-	-	0.59	0.87
	Population: Upper Aripo	-0.56	0.22	-2.52	42	0.016				
Total zones entered	Intercept	4.27	0.08	53.56	42	< 0.001	0.15	0.13	-	-
	Population: Upper Aripo	0.28	0.1	2.76	42	0.009				
Body length	Intercept	3.00	0.03	101.17	42	< 0.001	0.07	0.05	-	-
	Population: Upper Aripo	0.07	0.04	1.84	42	0.07				

Linking statement to Chapter 3

In Chapter 2, I showed that populations can differ in their propensity to innovate and that the correlation between activity-exploration behaviours and innovation can vary depending on the population. This result suggests that geographical variation can be an important contributor to intraspecific variation in innovation and its predictors. However, I was only able to examine the role of activity-exploration behaviours and other behaviours and characteristics such as sex or shoaling propensities, may also play important roles in individual variation. There was no evidence that individuals learned and improved their performance on the task, but this result could have been due to only a few learning opportunities. The role of cognitive factors, such as individual learning propensity, is often thought to be an important component of innovation, though it is not always assessed and it remains an open question of whether innovation requires high levels of cognition. Recent theoretical work has suggested that innovation may be an emergent property, composed of and correlated with multiple processes and traits, including both non-cognitive and cognitive factors; however, the relative importance of these factors has been evaluated in only a few studies and general conclusions are tentative based on a variety of findings. Furthermore, no study had yet examined the concurrent influence of both non-cognitive and cognitive factors on innovation in fish. Thus, in Chapter 3, I examined a battery of behavioural and physical predictors in the laboratory thought to influence innovation, including learning speed across ten trials. I also tested males and females to see if sexes differ in innovation and learning given the substantial sexual dimorphism in guppies.

Chapter 3: Predictors of the propensity to innovate: Escape performance in Trinidadian guppies (*Poecilia reticulata*)

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Abstract

Previous work has found significant individual variation in the propensity to innovate but the predictors and characteristics of these differences vary widely among studies. One difficulty with interpreting these varying results is the lack of replication within a species. Here we examined the role of sex, body mass, activity, exploration, risk-taking, shoaling propensities, and learning in predicting among-individual variation in innovation, building upon previous work in guppies. We tested innovation and learning propensities using a trawl escape task, repeated over ten trials. There was no evidence that activity, exploration, risk-taking, shoaling propensities, or body mass influenced the propensity to innovate (i.e., speed of initial escape), but we found sex differences in the propensities to innovate and learn. Males were initially faster to solve the task but only females showed evidence for learning and increased their solving efficiency over trials. Innovation and learning propensities were not significantly correlated. Our results suggest that sex can be a significant factor explaining variation in innovation and learning in guppies, but further work is needed to understand their precise role as well as the role of task related motivation. Furthermore, understanding how different task contexts and types influence variation in the predictors of innovation may explain inconsistencies among studies.

Keywords: *Poecilia reticulata*, guppies, innovation, innovative problem-solving, cognition, learning, sex differences

1. Introduction

Animals experience a variety of environments and situations where adaptive behavioural responses will vary. Behavioural innovation, i.e. the production of novel behaviours, either through a modification of existing behaviour patterns or producing new ones (Reader & Laland, 2003), may be a useful way in which animals can exploit an environment in new ways, potentially accessing novel resources and/or avoiding competing for known resources. In animals, behavioural innovation, often studied operationally via novel problem-solving tasks, has been linked to various fitness proxies such as reproductive success (Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole, Morand-Ferron, Hinks, & Quinn, 2012), mating success (Keagy, Savard, & Borgia, 2009; Mateos-Gonzalez, Quesada, & Senar, 2011), and competitive ability (Cole & Quinn, 2011; Laland & Reader, 1999b), suggesting that this variation can have important consequences.

However, our understanding is limited as to why individuals vary in their performance on these tasks. Previous work has hypothesized a role of various factors, including behavioural propensities, motivational and age related influences, as well as cognitive processes (Griffin, 2016; Reader & Laland, 2003; Tebbich, Griffin, Peschl, & Sterelny, 2016) to either inhibit or promote the innovation process. However, general conclusions are limited due to a paucity of research, particularly within species and in non-avian taxa, as well as inconsistent results (Amici, Widdig, Lehmann, & Majolo, 2019; Griffin & Guez, 2014; Guez & Griffin, 2016). Within-task measures of motor diversity and motivation such as persistence are a notable exception in the context of extractive foraging tasks (Griffin, Diquelou, & Perea, 2014; Griffin & Guez, 2014; Guez & Griffin, 2016), particularly in birds. While processes such as learning are often thought to be a component of the innovation process (Reader & Laland, 2003), evidence for such influences is lacking (Griffin & Guez, 2014, 2016). Furthermore, researchers have questioned the independence of measures of innovation from other behavioural and motivational traits, such as exploratory propensities and task-directed motivation (Griffin, 2016; see Healy & Rowe, 2014 and replies for an overview of this topic; Reader & Laland, 2003). Building a body of studies within a species and using standardized methodologies for behavioural measures may aid in resolving these inconsistencies.

We sought to address these issues by examining the role of a battery of behavioural measures, body mass, and learning in explaining among-individual variation in the propensity to innovate in Trinidadian guppies (*Poecilia reticulata*). We used a trawl escape task to test innovation where individuals had to escape a moving model perch attached to a trawl by swimming the length of a runway into one of two exit holes. Guppies are a social species of fish with well studied ecology, evolution and behaviour (Endler, 1995; Kotrschal et al., 2013; Magurran, 2005), including innovation (Berdal, Rosenqvist, & Wright, 2018; Laland & Reader, 1999b, 1999a; Reader & Laland, 2000). The present study adds to previous work by examining the role of behavioural predictors in explaining individual variation in the propensity to innovate.

We examined the role of several behaviours predicted to be important influences of performance on our task, including activity and exploration in a novel environment, risk-taking, and sociability. Activity and exploration are both thought to promote innovation though by different means. For instance, increased activity may result in further interaction with a novel task and thus increased solving efficiency, though potentially by random chance (Cole, Cram, & Quinn, 2011). In contrast, higher rates of exploration may also result in greater innovation success, but via attraction to novelty (Greenberg, 2003; Reader & Laland, 2003). Novel situations may be dangerous, thus risk-taking propensities likely influence the propensity of individuals willing to seek out and interact with such situations, with greater levels of risk-aversion likely inhibiting the innovation process (Audet, Ducatez, & Lefebvre, 2016; Ducatez, Audet, & Lefebvre, 2014). Because guppies are a social species (Magurran, 2005), social propensities might also promote the innovation process if it leads to individuals to seek out other conspecifics and thus increase exploratory propensities.

Various cognitive processes have also been suggested to play a role in innovation (Bouchard, Goodyer, & Lefebvre, 2007; Brosnan & Hopper, 2014; Reader & Laland, 2003; Taylor, Elliffe, Hunt, & Gray, 2010), though the exact psychological mechanisms likely vary depending on the nature of the task. For example, using an extractive foraging task with a motor feedback system, Cole et al. (2012) found that successful innovators directed more pecks towards the functional parts of the apparatus, suggesting a role for operant conditioning (Shettleworth, 2010). Research in great tits, *Parus major*, supports the idea that learning performance may be positively associated with innovation speed, perhaps by animals learning the affordances or features of the task (Morand-Ferron, Hamblin, Cole, Aplin, & Quinn, 2015), though the generality of such findings has been disputed (Griffin & Guez, 2016) and modelling has suggested that learning will have a smaller role than factors such as task persistence on problem-solving performance (Guez & Griffin 2016). However, we hypothesised that faster learners or individuals that are better able to learn such affordances may be more efficient innovators (Reader & Laland, 2003).

Males and females might also vary in their innovative propensities (Reader & Laland, 2003), though the direction of this may depend on the nature the task. For instance, using domestic guppies and a foraging task, Reader and Laland (1999a) found more female than male innovators. This result was not due to motivational differences in hunger levels, thus they proposed that the difference may be due to greater benefits associated with increased exploratory foraging behaviour in females. Males may be more motivated to seek out mating opportunities with females, which were present in the non-maze area of the tank, thus precluding a need to enter the maze. Such results and conclusions are likely specific to the nature of the task. For instance, comparative primate work has shown the opposite relationship with males exhibiting greater innovation counts than females in mating contexts (Reader & Laland, 2001) and work in guppies suggests that differences between male and female performance on cognitive tasks can vary by task, hypothesized to be a result of sex-specific ecological relevance (Kotrschal, Corral-Lopez, Amcoff, & Kolm, 2015; Kotrschal et al., 2013).

Here, we examined the role of sex, behavioural predictors, body mass, and learning performance in explaining individual variation in the propensity to innovate in Trinidadian guppies. We used initial latency to escape in the trawl test as a measure of innovation and any decrease in escape time as a measure of learning. Guppies provide a useful system for addressing such questions as they have been shown to vary in their innovative (Berdal et al., 2018; Laland & Reader, 1999a), behavioural (Budaev, 1997; Harris, Ramnarine, Smith, & Pettersson, 2010; Jacquin et al., 2016), and cognitive performance (Kotrschal et al., 2015, 2013; Lucon-Xiccato & Bisazza, 2017). Wild populations in Trinidad often encounter variable conditions and can be exposed to novel environments via seasonal flooding (Magurran, 2005). Furthermore, guppies are also successful invaders and can be found in many parts of the world (Lindholm et al., 2005; Magurran, 2005), together, suggesting that they may be well adapted to navigating novel conditions.

We hypothesized that activity, exploration, risk-taking, social propensities, and learning performance would promote innovation speed, predicting positive correlations with the propensity to innovate. We expected that larger bodied fish would be faster innovators if larger fish are faster swimmers given that innovation was measured by the latency to swim into a particular area. Guppies are sexually dimorphic and we expected that females would be faster to innovate and show stronger relationships with the aforementioned predictors than males based on the nature of our task and female ecology. Female guppies have indeterminate growth that is positively correlated with reproductive success (Magurran, 2005) and are generally more risk averse (Harris et al., 2010; Jacquin et al., 2016; Magurran, 2005). Our task involved escape from an aversive stimulus and while escape from such a stimulus should be advantageous for both sexes, females might be expected to be more motivated to flee the stimulus given their higher risk-aversion. We also predicted that females might be faster learners as they would be more responsive to the task stimulus. As our innovation task was the same as that measuring learning, we expected that these same predictors would also promote learning.

2. Materials and Methods

We tested 40 fish, with each individual receiving four behavioural assays (detailed below) followed by the innovation escape test and subsequent retesting over nine additional trials to assess learning. After the 10 escape tests, individuals were weighed before being placed in a 'tested' housing tank. We weighed individuals by lightly dabbing a net containing the fish with a paper towel to remove excess water and placing the individual in a tared beaker of water. All behavioural assays were recorded via webcam and later coded using the event coder software, JWatcher (Blumstein & Daniel, 2007). Behaviour in the escape task was live-coded due to poor video resolution.

2.1 Subjects and Housing

Subjects came from a group of 50 guppies, laboratory-reared descendants (> F_3) of past crosses between fish from the Lower Aripo and Quare rivers in Trinidad, wild populations characterised by high predation pressure (Gotanda, Pack, LeBlond, & Hendry, 2019). During a previous study, fish were crossed and maintained in captive predator-free mesocosms for at least 12 months (see Gotanda, Pack, LeBlond, & Hendry, 2019), and then as part of the mesocosm study they were exposed to the predatory pike cichlid, *Crenicichla sp*. Descendants of these subjects were moved to and raised in our laboratory, under predator-free conditions, and moved to an experimental housing tank (50 x 25 x 30 cm, 25 cm water depth) one week before the experiment began. Of these, we tested 40 individuals (20 males and 20 females), with the other 10 remaining in the housing tank to reduce any isolation stress as subjects were removed from the tank for testing.

We used an additional 24 fish (12 males and 12 females) as ‘shoal fish’ in tests of grouping propensity. These guppies originated from mixed wild Trinidadian populations (‘wild stock’), laboratory-born and reared, and had never interacted with the guppies from the test population before. We placed them into a shoal housing tank (40 x 20 x 25 cm) a week before the experiment began. Shoal fish were visually isolated from subjects to avoid any development of familiarity. All tanks contained gravel, plastic plants, terra cotta shelters, and a sponge filter. Tanks were kept at 25 ± 1 °C with a 12:12 h light:dark cycle with lights on at 07:00. Fish were fed flake food (Tetramin, Tetra, Germany) once a day after testing. The experiment ran for two weeks in June 2014, during which we tested four fish per weekday.

2.2 Experimental Protocol

Shelter emergence, open-field, and shoaling tests took place within a 114 L test tank (92 x 46 x 33 cm, Figure 3.1) separated into three zones: a mid-zone (70 x 46 cm) used as an open-field and two end-zones (11 x 46 cm) separated with transparent plastic sheets, functioning as a shoal compartment and empty control. For the open-field test, removable opaque partitions hid the shoal and empty compartments. The tank had a water depth of 6 cm to limit vertical movement (similar to Dingemanse et al., 2007). A grid (total size of 70 x 45 cm with squares of 5 x 5 cm – corresponding to approximately two body lengths of a wild guppy) drawn onto a white sheet of plastic corrugated board was placed under the tank and used to measure exploration-activity. Tests were conducted in a fixed order for all individuals (Bell, 2013). The shelter emergence, open-field, and shoaling tests were conducted immediately after one another, in that order, and were followed by the escape task. Each individual was given all tests on a single day.

2.2.1 Risk-taking: shelter emergence and open-field location preference tests

We examined the shy-bold axis by exposing individuals to a risky situation as defined by Réale et al. (2007). Here, we use a modified version of the shelter emergence test commonly used to measure risk-taking in fish (Brown, Burgess, & Braithwaite, 2007; Burns, 2008; Harris et al., 2010; Irving & Brown, 2013; Webster, Ward, & Hart, 2009). At testing, individuals were captured with a small net from their group home tank and placed within an opaque white shelter (15 x 11 x 19 cm) with a clear Plexiglas cover over the exit, enabling the individual to observe outside movement. After a two minute acclimation period, we swept a hand net with a model perch lure attached (Storm Wildeye Lures, USA) directly outside the exit four times. Immediately afterwards, the shelter door was lifted remotely by string and we recorded the latency for the fish to emerge from the shelter. After five minutes, if the fish had not exited, we removed the shelter, thus releasing the fish into the central zone, and recorded a ceiling latency of 300 s. We employed the net and lure modification to usual risk-taking protocols to provide cues about a potential risk outside the shelter and to reduce any confound with exploratory behaviour.

We consider this scenario was perceived as risky since we have observed individuals exhibiting anti-predator behaviours (e.g. freezing, shoaling) when exposed to nets, likely as a response from previous capture experience with this stimulus. The perch lure addition was used to increase the ecological relevance of our test and salience of the stimulus as our guppies were from a population with past predation exposure to a visually similar natural guppy predator, the pike cichlid (*Crenicichla alta*) (Magurran, 2005). Once the fish was outside the shelter, the open-field test began. We measured the subjects' open-field preference as the difference in time spent in the outer area (squares alongside the tank walls) minus time in the inner area (all inner squares). This provided an additional measure of risk-taking with positive scores indicating more time spent in the outer area and negative scores indicating more time spent in the inner area. The inner area of the open-field is more exposed than the outer area and is considered to represent greater risk-taking behaviour in studies of, for example, rodents and fish (Ahmad & Richardson, 2013; Lucon-Xiccato, Montalbano, & Bertolucci, 2019; Warren & Callaghan, 1975; Williams & Russell, 1972).

2.2.2 Activity and exploration in the open-field

We also used the open-field test to assess activity and exploratory behaviours in a novel environment (Réale et al., 2007), in line with previous work in fish (Budaev, 1997; Burns, 2008; Dingemanse et al., 2007; Jones & Godin, 2010; Martins et al., 2012). During the open-field test as described above, we also measured exploration as the proportion of unique squares an individual entered ("area covered") and activity as the total number of lines crossed and the total time spent swimming. We observed fish for 10 minutes during the open-field test. Fish were then allowed to swim in the open-field for 2 minutes before beginning the shoaling preference test.

2.2.3 Shoaling propensity: shoaling preference test

Grouping propensity was examined by assaying an individual's propensity to shoal (Réale et al., 2007). During the two minutes following the open-field test, we placed a mixed sex shoal (three males; three females) into one of the empty compartment zones (chosen at random) behind the opaque partitions. We began the shoaling test by gently lifting the opaque barriers on either side of the central-zone, first raising the opaque barrier hiding the empty and then the shoal compartment (Chapman, Ward, & Krause, 2008; Cote, Fogarty, & Sih, 2012; Kydd & Brown, 2009). We then recorded the time spent within two body lengths (~5 cm) (Magurran, Seghers, Shaw, & Carvalho, 1994) of either compartment over 10 minutes.

2.2.4 Innovation and learning

We examined the propensity to innovate in a modified version of the trawl task (Figure 3.2) used in other studies (Bisazza, Pignatti, & Vallortigara, 1997; Brown & Laland, 2002; Lindeyer & Reader, 2010; Reader, Kendal, & Laland, 2003). To complete the task, individuals had to escape an oncoming trawl net by swimming the length of a runway and through one of two exit holes (10 x 8 cm), which led into a compartment with plant cover and gravel that the trawl did not enter. We used a moving net paired with a model perch lure (Storm Wildeye, USA). A black plastic screen fitted to the runway behind the net prevented the fish from swimming behind the trawl.

At test, the fish was given two minutes to acclimate in a holding container at the end of the tank away from the exit holes. An opaque partition separated the holding container from the trawl. After acclimation, we removed the opaque partition and holding container and advanced the trawl at approximately 18 cm per five seconds such that it reached the exits within 90 seconds (Brown & Laland, 2002). We used visual markers on the side of the tank to standardize movement rate. The trawl advanced until the fish escaped via one of the two exits or remained in the runway when the net reached the end of the exits. Fish that did not swim through an exit were given ceiling latencies of 90 seconds and gently moved into the sheltered area. We repeated the procedure for a total of 10 trials with a two minute rest period in between trials. Following the rest period, individuals were netted and returned to the starting holding container. For each trial, we noted the latency to swim through an exit and which exit the fish entered, if any.

2.3 Statistical analyses

2.3.1 Sex differences

We examined if there were sex differences in all behaviours and body mass by fitting separate models with the variable of interest as the response and sex as a predictor. In the case of residual heterogeneity, we either corrected it by log transforming the response when possible or by using heteroscedasticity-consistent standard errors (following Cleasby & Nakagawa, 2011) with the "sandwich" R package (Zeileis, 2004). In the open-field test, time spent swimming and the number of lines crossed were highly correlated ($r = 0.74$, $p < 0.001$), thus we reduced them into a single variable (loadings: 0.93 for both; 86% of the variance explained), hereafter referred to as “activity”, using a Principal Components Analysis (varimax rotation, Kaiser-Guttman criterion >1 Kaiser, 1958, 1960) with the “psych” R package (Revelle, 2017). Activity, shelter emergence latency, and mass were fit as linear models using a natural log transformation for the latter two. The open-field preference was analysed using robust standard errors as a log transformation was not possible given the presence of negative values in this measure. We analysed area covered with a generalized linear model (binomial family) as proportions given the distribution and nature of the data. Initially we planned to measure shoaling propensity as the proportion of time spent shoaling out of the total time spent within 5 cm of both compartments. Subjects spent 79% of the total time within 5 cm of either of the two compartments with the shoal compartment compared to the empty compartment (intercept estimate ± S.E.: 1.35 ± 0.35, $t_{38} = 3.88$, $P < 0.001$). However, this proportional measure of shoaling was strongly correlated with time spent shoaling (Pearson $r = 0.97$, $t_{37} = 22.41$, $P < 0.001$), thus we used time shoaling (poisson family) as our measure of shoaling propensity given its greater ease in interpretation. In the case of non-significant sex differences, we removed sex from the model to estimate average behaviour across sexes (Engqvist, 2005).

2.3.2 Predictors of the propensity to innovate and learn

We used the latency to first escape as our measure of innovation. Thirty-three out of forty individuals solved the task during the first trial and there was insufficient variation in the number of trials until first solution to analyse this as a response variable. We thus calculated initial latency to escape by summing latencies from the initial successful trial and the preceding non-successful trials, henceforth “innovation latency”.

To analyse innovation latency and subsequent learning across trials, we modelled the natural log of escape latency as our response variable, using linear mixed-effect models (LMM). Trial was fit as a fixed effect, standardized to one standard deviation, and centered on one to allow inference of our other predictors to the initial solving event. Learning was assessed as the slope estimate of trial as it measured the subsequent change in latency to escape across the remaining trials after the initial solving event. Thus, individuals which did not solve on the first trial had fewer learning trials and therefore shorter learning lines. Analysing innovation and learning together in the same model provided greater accuracy as it allowed us to account for the bivariate nature of these data as well as test the correlation between the propensity to innovate and learning performance.

We fit individual as a random intercept to account for repeated measures and examine individual differences in the propensity to innovate. Trial was fit as a random slope to examine individual differences in learning. We further analysed the relationship between innovation and learning by fitting a bivariate correlation between the individual random intercept and random slope (Thompson, Evans, Parsons, & Morand-Ferron, 2018; Wilson et al., 2010). Date was also fit as a random intercept to account for variation among test days.

To assess which predictors influenced the latency to escape, we fit our behavioural measures (activity, area explored, open-field location preference, shelter emergence latency, shoaling propensity), and body mass as continuous covariates, and sex as a categorical variable. We also included sex by predictor interactions to examine any sex specific effects. Similarly, we fit these same predictors as interactions with trial to examine their influence on learning (Morand-Ferron et al., 2015) in an additional model which did not contain the aforementioned sex by predictor interactions due to a limited sample size. To examine sex-specific predictor influences on learning performance, we ran the above analyses but split the data by sex when there was evidence of learning (e.g. a significant negative effect of trial). Female was the sex baseline and we refit models with males as the baseline to examine male specific slopes when there were significant sex differences.

We also checked whether individuals preferred their initial escape route (left or right-hand exit) by modelling the probability of subsequent escape routes as the same or different as their initial choice using a generalized linear mixed-effect model (GLMM) with a binomial distribution. Potential side biases were assessed by examining the probability of choosing the right-hand exit for each trial. For the binomial route preference and side bias analyses, we fit sex and trial as fixed effects as well as a sex by trial interaction to examine sex differences, change over trials, and potential sex specific effects.

We tested the significance of random effects using likelihood ratio tests (LRTs) between a model with and without the random effect of interest. Random effects that were not critical to the data structure (e.g. date) and were non-significant or resulted in boundary (singular) fits were removed as they were estimated at approximately zero variance.

Likewise, we reduced the interactions from our models with LRTs and a liberal significance threshold ($P \leq 0.1$) as we wished to conserve potential sex specific effects. In cases where interactions were retained via LRTs but had non-significant estimates, we removed them to facilitate coefficient interpretation. All other selection procedures used the standard alpha threshold of 0.05. We did not remove additional predictors as these were a priori hypotheses and we wanted to reduce extraneous stepwise selection procedures as much as possible (Whittingham, Stephens, Bradbury, & Freckleton, 2006). For mixed models, we tested whether coefficients were significantly different from zero using the corresponding *t*/*z* statistics (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) with the "lmerTest" R package (Kuznetsova, Brockhoff, & Christensen, 2017).

All model assumptions were checked following Zuur et al.'s (2009) recommendations and we used the "DHARMa" R package to assess the GLMMs (Hartig, 2019). When overdispersion was present in the GLM(M)s, we corrected for it by either fitting a quasi family model for non-mixed models (Zuur et al., 2009) or an observation level random effect for mixed models (Gelman & Hill, 2007; Harrison, 2014). All continuous predictors were standardized (mean centered and standardized to one standard deviation) which aided model computation and meaningful interpretation (Gelman & Hill, 2007; Schielzeth, 2010). Thus, continuous coefficients should be interpreted as affecting the response by the coefficient value for 1 standard deviation increase of the predictor. Standard R^2 were calculated for linear models and marginal (variance explained by fixed effects) and conditional R^2 (variance explained by fixed and random effects) for mixed models (Johnson, 2014; Nakagawa & Schielzeth, 2013) using the delta method for the observation level variance (Nakagawa, Johnson, & Schielzeth, 2017) with the "MuMIn" R package (Barton, 2016). All data were analysed using R Statistical Software (R Core Team, 2017).

One individual was immobile for all trials of the escape test and was removed from all escape analyses. Additionally, some individuals were missing data from some of the behavioural predictor tests due to recording malfunctions (*n* = 7) and were subsequently removed to create a standardized dataset for the behavioural and body mass predictors of innovation and learning analyses (*n* = 32). However, the individuals missing some of the behavioural predictor data were included when analysing sex differences in activity, exploration, risk-taking, shoaling propensity, and body mass when data were available. We also included these individuals (*n* = 39) when examining the significance of the random effects for individual and trial, as well as the analyses for route preference, side bias, and the probability of escape as we did not include the behavioural and mass predictors in the latter analyses.

2.3.3 Residual heterogeneity

For the latency to escape analyses, there was some evidence of residual heterogeneity that was unable to be resolved via transformations, potentially due to the presence of several ceiling values in our data from trials where some individuals did not solve the task. We were unable to correct for this issue in our linear mixed model as heteroscedasticity-consistent standard errors are not available for mixed models (Cleasby & Nakagawa, 2011) and generalized least squares (GLS) weighting (Pinheiro & Bates, 2000; Zuur et al., 2009) is only implemented in the R package “nlme” which does not allow more complex random effect structures such as those in our model. However, we assessed the severity of the heterogeneity on our main results by comparing our results to that of a simplified model that accounted for the heterogeneity. Using the same fixed effect structure, we simplified our random effects to only contain individual as a random intercept and used GLS weighting to model the heterogeneity as a function proportional to the response (Cleasby & Nakagawa, 2011; Zuur et al., 2009) with the R package “nlme” (Pinheiro & Bates, 2000). We tested whether the model containing the heterogeneity correction provided a better fit using AIC (delta criterion ≥ 2) to compare models with and without the GLS weights (Burnham & Anderson, 2008; Zuur et al., 2009) but with the simplified random effect structure. Fixed effect selection followed that described above.

Data and source code for analyses will be permanently archived on Zenodo.

2.4 Ethical note

All procedures were approved by the McGill University Animal Care Committee under protocol number 2012-7133, and conform to ASAB and Canadian Council on Animal Care guidelines. We used a mild stressor in this study which did not result in any observable long-term effects or mortality and has previously been used in other fish studies (Brown & Laland, 2002; Lindeyer & Reader, 2010; Reader et al., 2003). At the end of the study, all fish were returned to breeding populations at McGill University.

3. Results

3.1 Sex differences in activity, exploration, risk-taking, shoaling propensity, and body mass

Males and females differed on many of our measures (Table 3.1). Compared to females, males spent more time in the outer area of the open-field ($P = 0.007$, Table 3.1), explored more of the open-field ($P = 0.016$, Table 3.1), were more active ($P < 0.001$, Table 3.1), faster to exit the shelter ($P = 0.006$, Table 3.1), and lighter in body mass ($P < 0.001$, Table 3.1). However, there was no significant difference between males and females in the time spent shoaling ($P = 0.82$, Table 3.1). On average fish shoaled for 416 s of the 600 second test.

3.2 Did individuals successfully escape and learn the task?

All fish successfully escaped at least once over the 10 trials, with 85% (33/39) of subjects completing the task on the first trial. There was significant among individual variation in the initial latency to escape (individual random intercept: LRT: $X_{2,1} = 43.24$, $P < 0.001$, Figures 3.3-3.4) and males were initially faster to escape than females (sex estimate: $P < 0.001$, Figure 3.3, Table 3.2). Although 74% of fish initially took the right-hand exit, this was not significantly different from the chance 50% expectation (intercept estimate ± S.E.: 1.06 ± 0.59, $z = 1.79$, $P = 0.07$, $R^2_m < 0.001$, $R^2_c = 0.7$). There was no significant difference in the preference for the right versus left-hand exit between the sexes (sex estimate ± S.E.: 0.9 ± 1.16, $z = 0.78$, $P = 0.44$), however, individuals significantly varied in their preference for the right-hand exit (individual random intercept: $X_{2,1} = 61.52$, $P < 0.001$).

Individuals varied in the latency to escape over trials, though this result did not reach statistical significance (individual random slope: LRT: $X_{2,1}$ = 3.65, P = 0.06, Figure 3.4). Furthermore, the intercept-slope correlation did not improve the model fit (individual intercept-slope correlation random effect: LRT: $X_{2,1}$ = 2.17, P = 0.14), indicating initial escape latency was not significantly correlated with the change in escape latency over time (our measure of learning). There was evidence that females but not males learned the task. Females decreased their latency to escape over trials (trial estimate: $P < 0.001$, Figure 3.4, Table 3.2), which was significantly different from males (trial x sex interaction estimate: P = 0.008, Figure 3.4, Table 3.2). There was no evidence that male escape latency changed over trials (male trial estimate: ± S.E.: 0.02 ± 0.14, t = 0.13, P = 0.9). After their first escape, individuals subsequently preferred their initial escape route choice (94% probability of choosing the initial escape route, intercept estimate ± S.E.: 2.73 ± 0.54, z = 5.07, $P < 0.001$, R_m^2 = 0.001, R_c^2 = 0.19) and this preference did not significantly vary across trials (trial estimate ± S.E.: -0.21 ± 0.34, z = -0.61, P = 0.54), by sex (sex estimate ± S.E.: -0.57 ± 0.7, z = -0.81, P = 0.42), nor was there a significant sex by trial interaction (sex x trial interaction estimate: LRT: $X_{2,1}$ = 0.01, P = 0.91). Individuals significantly varied in their subsequent preference for their initial escape route (individual random intercept: $X_{2,1}$ = 16.27, $P < 0.001$). There was no evidence that the probability of choosing the right-hand exit changed across trials (trial estimate ± S.E.: 0.02 ± 0.31, z = 0.08, P = 0.94), or a varied by sex across trials (sex x trial interaction estimate: LRT: $X_{2,1}$ = 0.05, P = 0.82).

3.3 Predictors of initial escape and learning to escape over trials

We found no evidence that sex had interactive effects with our predictors (all $P > 0.1$, Table 3.2). None of our behavioural predictors or body mass appeared to influence escape latency (all other $P > 0.1$, Table 3.2). Similarly, neither body mass nor the behavioural predictors had significant impacts on change over trials in escape latency when analysing both sexes together (all trial by predictor interactions: $P > 0.1$, Table 3.2) or females alone (Table S3.1).

3.4 Residual heterogeneity

The significant results from the GLS model (Table S3.2) were the same as the mixed effect model (Table 3.2), except for two differences: in the GLS model, females that explored more of the open-field were slower to escape (area covered estimate: $P = 0.023$) though the sex by area covered interaction only approached statistical significance ($P = 0.07$, Table S3.2), while for the mixed model, the sex interaction effect did not approach significance ($P > 0.1$) and the area covered did not have a significant effect on escape latency ($P = 0.085$, Table 3.2). The GLS model improved the model fit compared to a model with the simplified random effect structure without the GLS correction (delta AIC = 19.43). We interpreted the mixed effect model given the qualitatively similar results and the fact the mixed model allowed us to model a more complex random effect structure to examine our questions of interest.

4. Discussion

All individuals successfully escaped from the aversive stimulus and into the refuge area, with most doing so within the first trial. Males were initially faster to escape but only females improved their escape efficiency over the repeated trials. We found no evidence that the speed of initial escape, our measure of the propensity to innovate, correlated with learning performance. Both sexes showed a strong preference towards their initial escape route on later trials, suggesting they either learned their escape route or there were consistent individual differences in preference for one exit. Surprisingly, neither the behavioural predictors (activity, exploration, shelter emergence, open-field preference, shoaling propensity) nor body mass influenced either the propensity to innovate or learning performance. In contrast to our initial hypotheses, we found that individual variation in the propensity to innovate in this population of guppies was not well explained by commonly hypothesized predictors, joining an increasing body of work that the role of such predictors may be inconsistent (Griffin & Guez, 2014). However, examination of other predictors, such as a broader range of psychological mechanisms (Griffin, 2016), is needed.

4.1 Sex differences in the propensity to innovate

Females were initially slower to escape compared to males, and although individuals varied in their propensity to innovate, this difference was not explained by any of the behavioural predictors or by body mass, suggesting sex differences in the propensity to innovate in our task. This result contrasts with our prediction that females would be more motivated to escape and thus be faster innovators, and with previous work in domestic guppies, which found more female innovators than males when tested in foraging maze tasks (Laland & Reader, 1999a). Laland & Reader (1999a) hypothesized that this sex difference was due to evolved differences in the costs and benefits of exploratory foraging behaviour. While both their and our tasks involved navigating novel structures, their task was in a foraging context, while ours was an aversive escape context. It is unknown whether performance and sex differences are generalizable across a variety of task contexts and types (Griffin, 2016; Reader & Laland, 2003). Furthermore, while the influences of captivity and domestication are not well understood, studies have shown that these factors can influence innovation (Benson-Amram, Weldele, & Holekamp, 2013; Brubaker, Dasgupta, Bhattacharjee, Bhadra, & Udell, 2017; Lehner, Burkart, & van Schaik, 2010; Morand-Ferron, Cole, Rawles, & Quinn, 2011). Another possibility may be that females and males differ in risk-aversion and thus in response to the trawl. For instance, compared to males, we found that females were slower to emerge from the shelter, were less active, and explored less of the open-field, suggesting an aversion to risky and novel situations (Réale et al., 2007) and in line with previous work on sex differences in guppy behaviour (Harris et al., 2010; Jacquin et al., 2016; Magurran, 2005). However, males spent less time in the inner area of the open field than did females. Preference for the more exposed inner area is considered to represent risk taking (Lucon-Xiccato, Montalbano, & Bertolucci, 2019; Warren & Callaghan, 1975), and thus on this measure females appeared to show less aversion to risk than males. We might have expected sex specific interactions with our measures of risk-taking behaviours if they were involved in task performance, however we found no evidence for this. Females may have differed from males in their initial response to the trawl, such as spending more time freezing or inspecting the trawl and model predator (Magurran & Nowak, 1991), common responses to predators (Magurran, 2005). Indeed, freezing or inspection might decrease after learning to escape and about the potential threat, thus explaining the improvement in escape behaviour over time in females, though we were unable to reliably measure this due to poor video resolution.

4.2 Sex differences in learning to escape

Females improved their escape efficiency over trials, consistent with them learning the task, while males did not. There was no effect of body mass or the behavioural predictors on learning performance when examining both sexes or females alone, suggesting that the observed sex difference in learning was not the result of sex differences in body mass or the predictors we measured. Griffin and Guez (2016) have noted that differences in opportunities to interact with the apparatus may explain differences in learning performance. However, in our study individuals were placed directly in the apparatus and thus did not vary in their opportunities to learn. Furthermore, our results were qualitatively the same when we removed the six individuals which solved the task after the first trial and thus had an additional learning opportunity before initial escape. Thus we interpret these sex differences as encompassing differences in learning speed. Individuals also displayed a strong subsequent bias (94% probability) towards their initial escape route, despite both routes being equally efficient. This finding might suggest a role for spatial learning, though it could also represent a consistent individual side bias, or an interaction between the two. Within the tank, there were no landmarks or visually distinct differences between the two routes, which might indicate that females used an egocentric spatial learning mechanism (Shettleworth, 2010). The trawl approach would have provided a strong directional stimulus for such learning, though the use of other cues such as landmarks outside the tank cannot be excluded.

Several studies have found sex differences in learning (Carazo, Noble, Chandrasoma, & Whiting, 2014; Fuss & Witte, 2019; Huebner, Fichtel, & Kappeler, 2018; Kriengwatana, Spierings, & ten Cate, 2016), including in guppies (Lucon-Xiccato & Bisazza, 2014, 2016, 2017; Lucon-Xiccato, Gatto, & Bisazza, 2019; Petrazzini, Bisazza, Agrillo, & Lucon-Xiccato, 2017; Reader & Laland, 2000), though the direction of the difference can be dependent on the type of learning (e.g. reversal versus spatial learning) (Lucon-Xiccato & Bisazza, 2014, 2017) and the nature of the task (e.g. Gatto, Lucon-Xiccato, Savaşçı, Dadda, & Bisazza, 2016), hypothesized to be due to differential ecological relevance of the tasks for males and females. While our measures of risk-taking did not appear to influence the latency to escape, these measures of risk-taking behaviour were in an open-field context which may not generalize well to that of the escape apparatus. Illustrating this, studies using extractive foraging tasks in birds often find that task directed persistence (measured within the innovation task itself) plays an important role in the solving process, though results are more varied for other measures of motivation such as body condition (Griffin & Guez, 2014). Thus, future work might examine task-specific measures of individual response to the stimulus in order to test the influence of task based motivation.

While males did not appear to improve their escape speed over trials and were faster to initially solve the task than females, this result may not necessarily be indicative of ability differences between the sexes. As well as the explanations noted above, males and female may differ in their ‘cognitive styles’ (Sih & Giudice, 2012), for example potentially trading off speed and accuracy differently or showing performance differences on different task types. Lucon-Xiccato and Bisazza (2017) found that while wild-derived male guppies were slower to solve a simple detour task than females, they were also the only ones to show improvement in solving efficiency over five trials. Work in Carib grackles, *Quiscalus lugubris,* also supports the idea of performance trade-offs as grackles which were faster to solve novel foraging tasks were slower to learn a colour discrimination (Ducatez et al., 2014). These differences may be task dependent, even within species. For example, Lucon-Xiccato and Bisazza (2017) also found that while wild-derived male and female guppies varied in the proportion of correct choices made in a more complex spatial detour route task, they did not vary in their solving speed. Furthermore, male and female guppies did not vary in their accuracy when learning a discrimination task but varied in how quickly they made a decision (Lucon-Xiccato & Bisazza, 2016). Examining multiple measures of performance, such as stimulus interactions, learning speed, and accuracy, may yield more general insights into the differences between male and female innovation and learning propensities.

4.3 Predictors of the propensity to innovate

We found no evidence that our behavioural and body mass predictors impacted innovation. There is varying evidence in the literature for the hypothesized predictors of the propensity to innovate (Griffin & Guez, 2014; Overington, Cauchard, Côté, & Lefebvre, 2011; though see Ducatez et al., 2014). One possible explanation for our finding is that our behavioural measures (shelter emergence, behaviour in the open field, and shoaling) might exhibit low repeatability. The repeatability of these behaviours was not assessed in the tested population, thus our measures might reflect labile behavioural propensities. However, we used tests previously shown to capture repeatable behavioural differences in guppies (Brown & Irving, 2014; Burns, 2008; Harris et al., 2010; Jacquin et al., 2016), though repeatability can vary by population (Thompson et al., 2018) and here we deliberately exposed fish to a potential stressor shortly before we began our tests. The second possibility is that these predictors do not play a strong role in the innovative process. Indeed, Tebbich (2016) suggests that the role of different predictors varies depending on both the type of innovation (e.g. exploratory versus extractive foraging) and the stage of the innovative process. The nature of our test may not have required or involved the processes these predictors measure, or at least to as significant a degree as we previously hypothesized. The lack of significant predictors of learning is also in line with a recent meta-analysis finding little evidence on average for correlations between personality and cognitive measures (Dougherty & Guillette, 2018). Dougherty and Guillette (2018) argue that the significant variation among studies suggests that there are effects of personality but the direction of these effects varies by numerous factors. Indeed, this field is relatively young and more studies are needed, particularly with robust sample sizes, as well as accounting for potential moderating variables such as life history. While we found no significant relationship between individual propensities to innovate and learning slopes, we note that our sample may have been underpowered given that the intercept-slope correlation model resulted in a boundary fit with an estimated perfect correlation, often associated with underpowered random effect structures. Thus, greater sample sizes are needed to better assess this relationship to account for the high data costs of such models.

Our study shows that sex differences contribute significantly to among-individual variation for both innovation and learning. However, the relationship between innovation and learning and the role of non-cognitive factors remains to be further explored. While a body of work has contributed to our understanding of the role of various predictors, replication of studies may help tease apart factors contributing to among-study variation in findings, such as developmental environmental effects (Quinn, Cole, Reed, & Morand-Ferron, 2016). Furthermore, examining whether the propensity to innovate varies depending on task context and type may illuminate how this affects discrepancies in the predictors of innovation. Thus conclusions must remain tentative until future work can resolve these differences.

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7. Figures

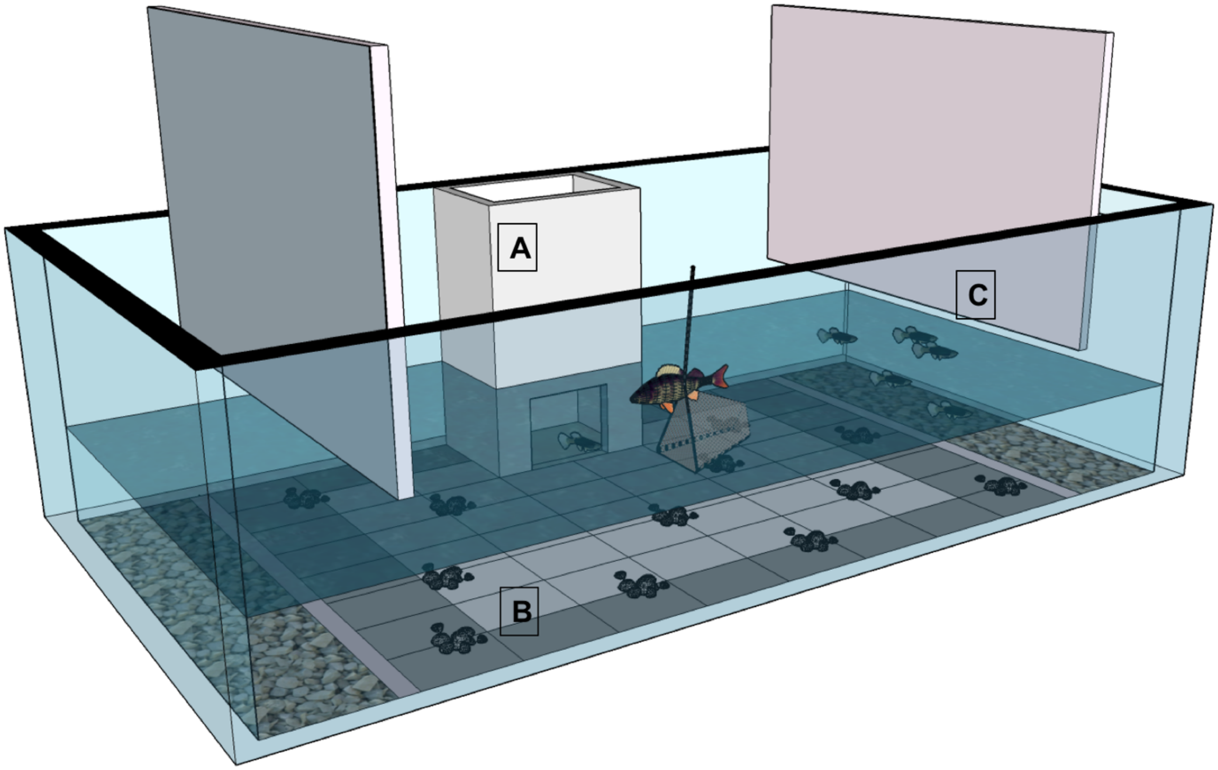

Figure 3.1. The modified open-field apparatus for measuring individual risk-taking, activity, exploration, and social behaviours. The apparatus was divided into three zones, a mid zone (open-field area) and two side zones. In the center, a shelter [A] held the individual at start. The predator and attached net served to increase perceived risk. The open-field [B] was further divided into an inner (here coloured light gray for exposition) and outer (dark grey) area, as well as having individual squares to note the area explored and general activity levels. The two side zones (shoal location and control) were used to examine social propensities, one of which contained a shoal [C], with both zones hidden behind opaque white partitions before testing.

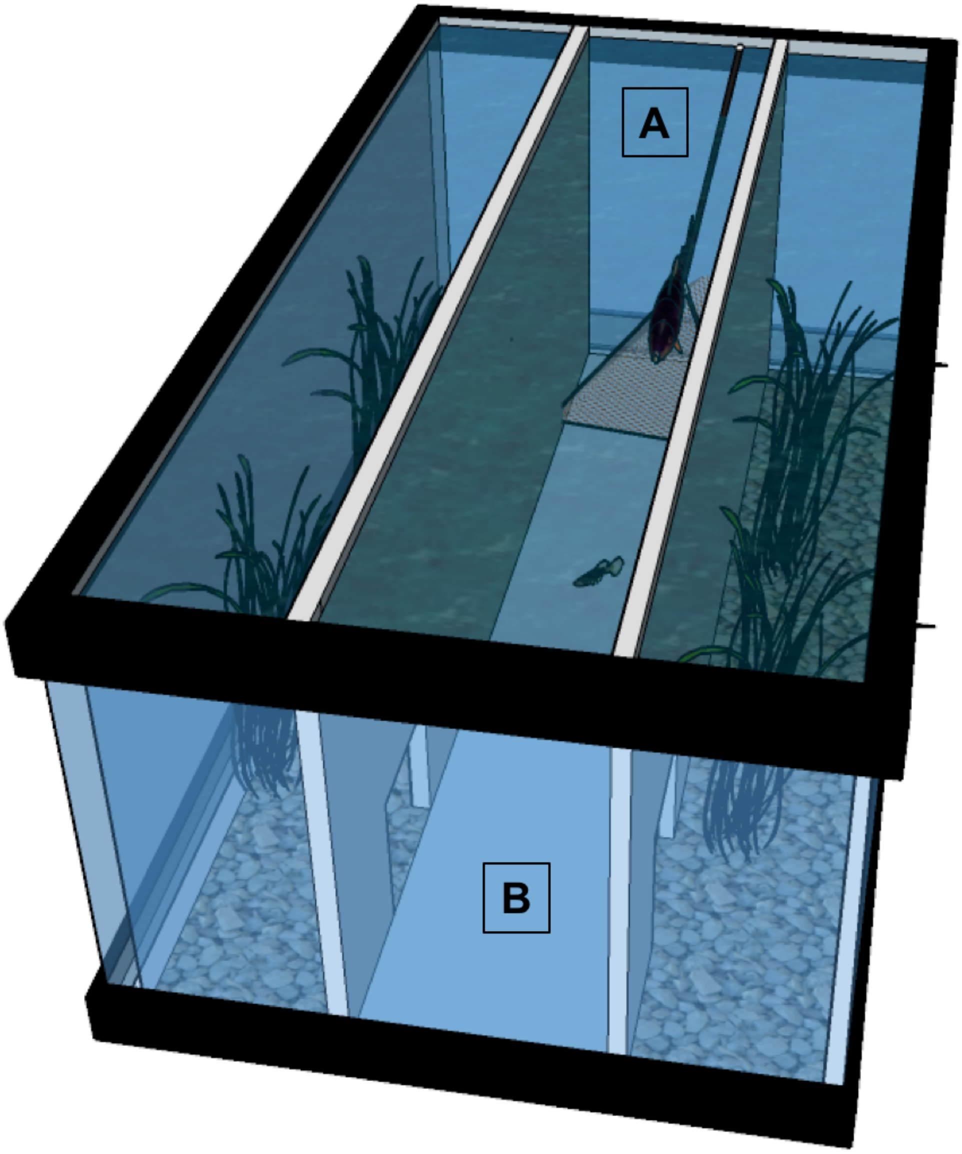

Figure 3.2. The modified trawl apparatus used to test individual propensities to innovate and learn. Individuals started at one end of the runway [A] in front of a perch model attached to a net which advanced ~20 cm every five seconds over 90 seconds. To solve the task, individuals had to swim the length of the runway and escape via one of two exit holes [B] into zones with plant shelters. After completing the task, individuals were retested nine more times for a total of 10 trials with a two minute rest period in between trials. Individuals were unable to swim behind the net as the net handle was fitted to a mesh grid (not pictured) the width and height of the runway.

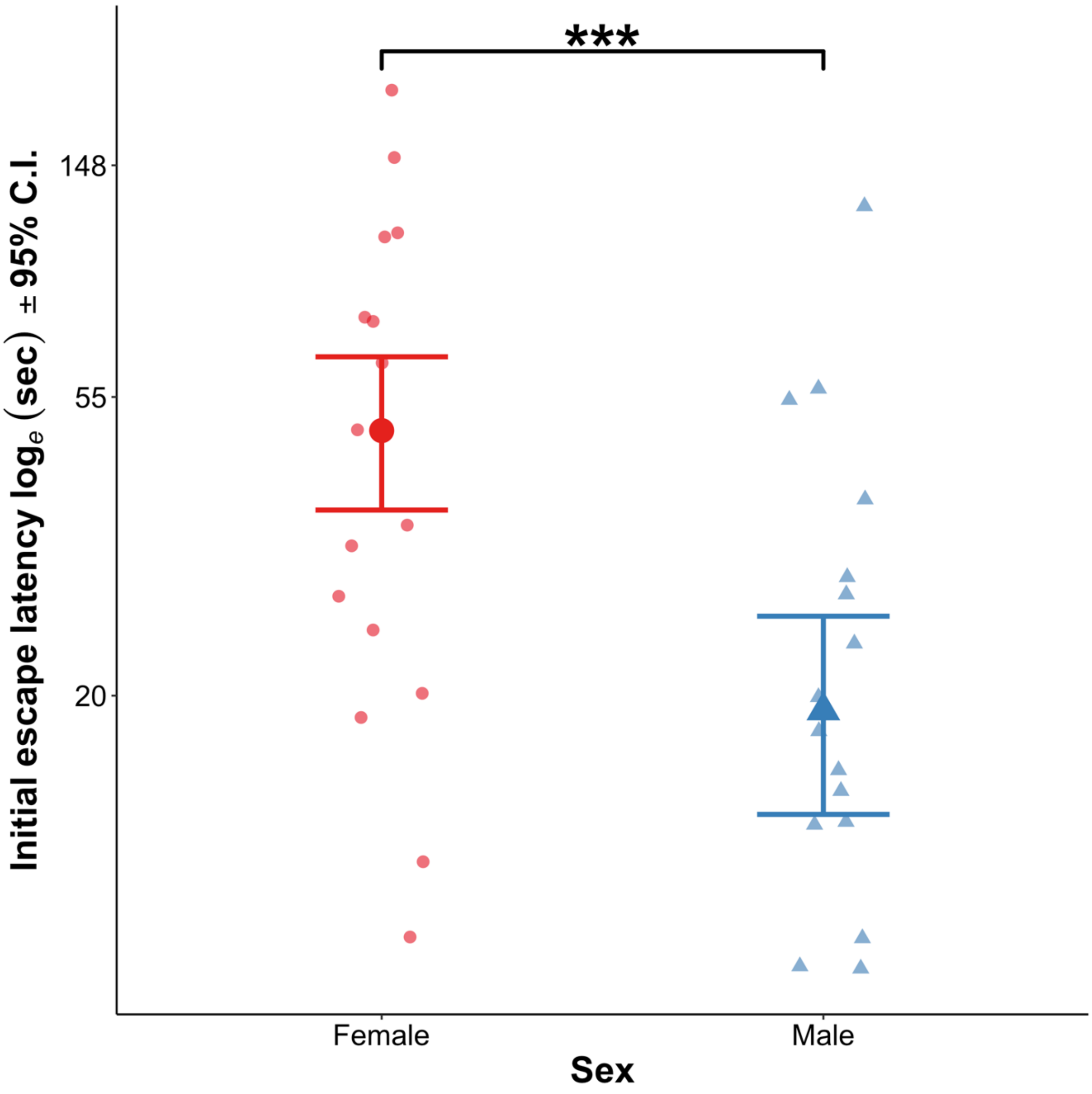

Figure 3.3. The initial latency to escape (natural log transformed) for male and female guppies from a reduced linear mixed effect model containing all predictors. Large points are model estimates ± 95% confidence intervals, smaller transparent points are raw data values (females: red circles; males: blue triangles). *** indicates $P < 0.001$. Marginal $R_m^2 = 0.12$ (variance explained by fixed effects), conditional $R_c^2 = 0.36$ (variance explained by fixed and random effects). Note the logarithmic scale on the y-axis.

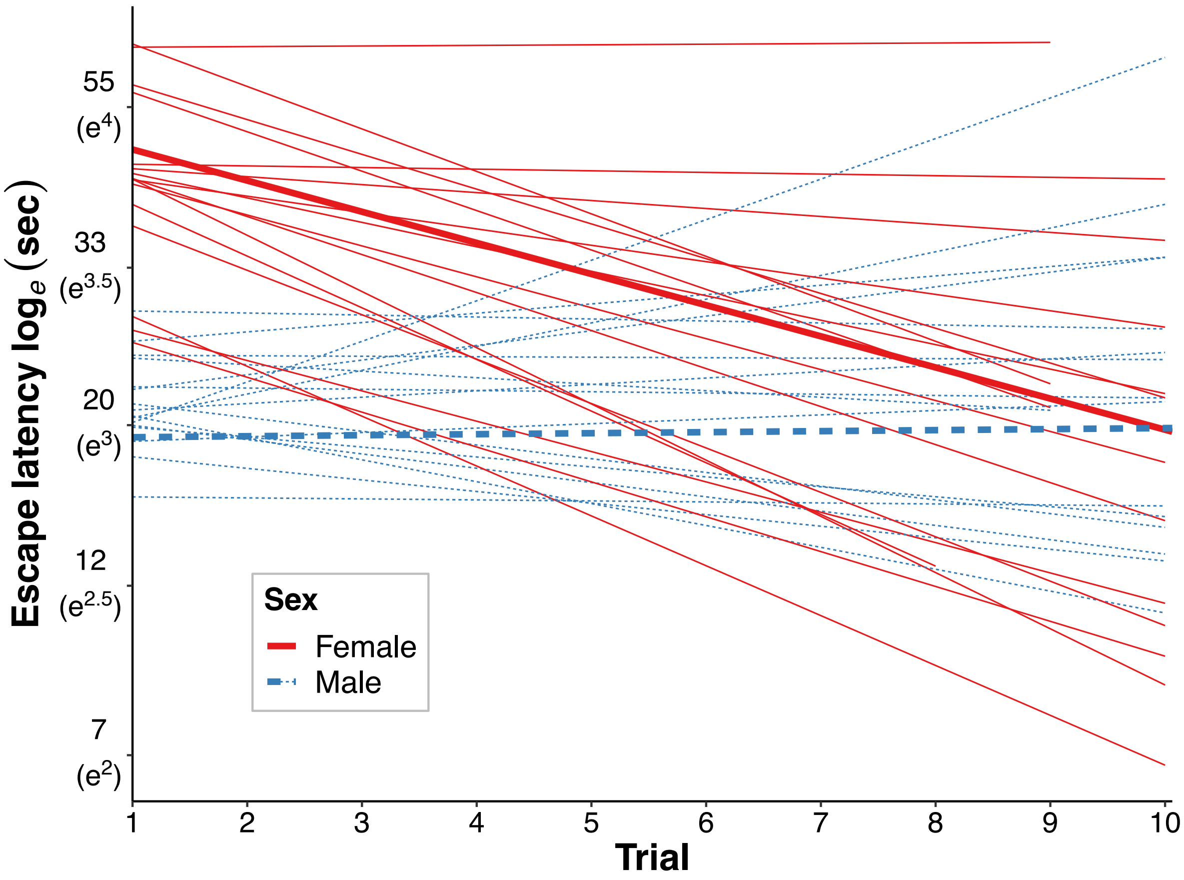

Figure 3.4. Escape latency over trials for males (blue dashed lines) and females (red solid lines) from a reduced linear mixed effect model containing all predictors. Males and females significantly differed in their latency slope across trials: female latencies to solve the task decreased whereas male latencies remained fairly consistent. Thick lines represent model (trial) estimates for each sex and thin lines are the individual predicted values. Marginal R_m^2= 0.12 (variance explained by fixed effects), conditional R_c^2= 0.36 (variance explained by fixed and random effects). Note the logarithmic scale on the y-axis.

8. Tables

Table 3.1. Sex differences in the behavioural predictors examined and body mass. Shelter emergence was measured in a first test, activity, area covered and open-field preference in a second test, and time shoaling in a third test, with the three tests run immediately after one another. The reference group for sex is female. Shelter emergence latency and mass were natural log transformed to remove heterogeneity in the residuals. The open-field preference was unable to be transformed given the data ranged from negative to positive values. Thus, we applied heteroscedastic-consistent standard errors to correct for residual heterogeneity (Cleasby & Nakagawa, 2011). Area covered was modelled as proportional data with a binomial family and time shoaling was analysed using a quasipoisson model.

Response	Estimate name	Estimate	S. E.	t	df	P	Adjusted R^2
Activity	Intercept	-0.68	0.17	-3.95	37	<0.001	0.45
	Sex: Male	1.35	0.24	5.65		<0.001	
Area covered	Intercept	-0.53	0.2	-2.66	30	0.012	-
	Sex: Male	0.71	0.28	2.56		0.016	
Open-field Preference	Intercept	164.6	100.31	1.64	30	0.11	0.19
	Sex: Male	305.23	105.49	2.89		0.007	
Shelter emergence latency	Intercept	4.98	0.34	14.63	37	< 0.001	0.16
	Sex: Male	-1.39	0.48	-2.91		0.006	
Time shoaling	Intercept	6.05	0.12	49.33	37	< 0.001	-
	Sex: Male	-0.04	0.17	-0.23		0.82	
Body mass	Intercept	-1.39	0.08	-17.51	37	<0.001	0.44
	Sex: Male	-0.62	0.11	-5.61		<0.001	

Table 3.2. Standardized (by one standard deviation and mean centered) estimates ± S.E. of the behavioural and body mass predictors of natural log escape latency from a reduced linear mixed effect model containing all predictors, R_m^2= 0.12, R_c^2= 0.36, N = 32. Note that this final reduced model was the same as that obtained from analysing the predictors of learning as none of the predictors were significant (all trial by predictor interactions $P > 0.1$).

Predictor	Estimate	S. E.	t	P
Intercept	3.88	0.14	27.61	< 0.001
Body mass	0.04	0.11	0.32	0.75
Activity	-0.16	0.14	-1.18	0.25
Area covered	0.14	0.08	1.8	0.085
Open-field preference	0.16	0.09	1.73	0.097
Time shoaling	0.05	0.08	0.64	0.53
Shelter emergence latency	-0.14	0.11	-1.26	0.22
Trial	-0.52	0.14	-3.77	< 0.001
Sex: Male	-0.92	0.24	-3.89	< 0.001
Sex: Male x Trial	0.54	0.19	2.78	0.008

9. Appendix 1: Supplementary material

Table S3.1. Standardized (by one standard deviation and mean centered) estimates ± S.E. of the behavioural and body mass predictors of the natural log escape latency from a reduced linear mixed effect model containing all predictors, females only, *n* = 16. Females were analysed alone since there was evidence for learning in females, but not males.

Predictor	Estimate	S. E.	t	P
Intercept	3.91	0.21	18.77	< 0.001
Body mass	0	0.19	-0.01	0.99
Activity	-0.31	0.26	-1.19	0.27
Area covered	0.31	0.16	1.95	0.086
Open-field preference	0.25	0.15	1.65	0.13
Time shoaling	0.11	0.16	0.68	0.51
Shelter emergence latency	-0.11	0.2	-0.55	0.6
Trial	-0.62	0.13	-4.87	< 0.001
Trial x Open-field preference	0.17	0.09	1.92	0.074

Table S3.2. Standardized (by one standard deviation and mean centered) estimates ± S.E. of behavioural and body mass predictors of the natural log escape latency from a reduced generalized least squares model containing all predictors, *n* = 32. Heterogeneity was modelled as proportionate to the response.

Predictor	Estimate	S. E.	d.f.	t	P
Intercept	3.78	0.17	280	21.88	< 0.001
Body mass	0.002	0.13	23	0.01	0.99
Activity	-0.19	0.16	23	-1.21	0.24
Area covered	0.3	0.12	23	2.43	0.023
Open-field preference	0.13	0.11	23	1.26	0.22
Time shoaling	0.01	0.09	23	0.07	0.94
Shelter emergence latency	-0.12	0.13	23	-0.94	0.36
Trial	-0.52	0.1	280	-5.03	< 0.001
Sex: Male	-0.84	0.28	23	-3.06	0.006
Sex: Male x Trial	0.53	0.14	280	3.68	< 0.001
Sex: Male x Area covered	-0.31	0.16	23	-1.9	0.07

Linking statement to Chapter 4

In Chapter 3, I found that males and females differ in their innovation and learning performance but that learning performance does not appear to correlate with the propensity to innovate. This result may suggest that males and females exhibit a speed versus accuracy trade-off between innovation and learning performance and further supports previous findings of sexual dimorphism in guppy innovation and learning. I also found no effect of the behavioural and physical predictors I measured, in contrast to that of Chapter 2 – possibly indicating that our measure was independent of these influences. A plausible explanation for this discrepancy may be differences in the task type used to measure innovation as Chapter 2 used an exploratory maze task whereas Chapter 3 involved escape from an aversive stimulus. The propensity to innovate is often measured via extractive foraging problem-solving tasks and tailored to species ecology, with comparisons within and across species assuming performance on these tasks is congruent, though this assumption is rarely examined. Indeed, some work suggests that foraging versus technical innovations may not be equivalent. Furthermore, studies examining repeatability of performance in such tasks often compare tasks of a similar task type, which may upwardly bias repeatability estimates. Thus, in Chapter 4, I examined whether the propensity to innovate and its predictors are generalizable across four novel tasks falling into two task types. Given the strong differences between the sexes in Chapter 3, I also further investigated how males and females differ in their repeatability across tasks.

Chapter 4: Is the propensity to innovate repeatable across tasks and sexes in Trinidadian guppies, *Poecilia reticulata*?

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Abstract

In recent years there has been increasing research interest in behavioural innovation, the production of novel behaviour patterns. The propensity to innovate is commonly measured using novel problem-solving tasks, often in an extractive foraging context. While this approach has provided many fruitful insights into the patterns and consequences of individual variation in innovation, it is not well understood whether performance on these tasks can be generalized to other tasks, or to contexts outside of extractive foraging, potentially limiting the generality of these results. Furthermore, most studies have been conducted in birds and mammals. Using a social reward context, we examined the performance of male and female Trinidadian guppies (*Poecilia reticulata*) across two task types (maze-like or detour-like tests, requiring either exploration or inhibitory control to solve, respectively) and four task designs. We compared repeatability and the commonality of performance predictors across the four tasks to assess how performance generalizes across tasks and task types. Performance was significantly but not strongly repeatable across all four tasks, an effect mainly driven by repeatability across most tasks in males, with female repeatabilities typically around zero. Individual behavioural and morphological characteristics did not uniformly predict performance across tasks. A second experiment using highly similar maze tasks revealed that females, but not males, were consistent across tasks. Thus performance on tests used to measure problem-solving and innovation may not generalize well between or even within some test-types. Furthermore, sex differences can reveal strikingly different patterns in repeatability. Our results inform work noting diversity in the predictors of innovation and raise questions on the generalizability of results from problem-solving tests.

Key words: behavioural innovation, problem-solving, personality, repeatability, detour test, maze, exploration, *Poecilia reticulata*.

1. Introduction

Understanding how animals respond to and shape environmental change has become of increasing interest to ecologists both from an applied perspective in mitigating anthropogenic induced environmental changes and from a fundamental perspective in understanding links between plasticity and ecology (Candolin & Wong, 2012; Charmantier et al., 2008; Sih, 2013). Behavioural plasticity is a particularly dynamic process as individuals can modulate their existing behaviour or produce novel behavioural variants in immediate response to environmental conditions without the lag time of development or evolution (Snell-Rood, 2013; West-Eberhard, 2003). This potentially allows individuals to quickly adapt to a variety of conditions. For instance, behavioural innovations, i.e. the production of a novel behaviour patterns (Reader & Laland, 2003a), such as foraging on novel resources (Fisher & Hinde, 1949) or using novel foraging techniques (Morand-Ferron, Lefebvre, Reader, Sol, & Elvin, 2004), might allow animals to expand their foraging niche when resources are scarce.

Within species, studies commonly measure how innovations are produced and who innovates via tests of the propensity to solve novel problem-solving tasks. An individual is presented with a restricted reward that can only be obtained once the individual has ‘solved the problem’, such as removing a lever (Cole, Cram, & Quinn, 2011). While a behavioural innovation might occur within different contexts (e.g. ecological, technical, and social: Kummer & Goodall, 1985), tasks are often designed in a single context, i.e. with a common goal/reward and solving mechanisms, such as extractive foraging tasks requiring motor manipulation (though see Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Keagy, Savard, & Borgia, 2009, 2011 for examples of non-foraging related rewards). In some cases, performance on multiple tasks is measured to examine repeatability (e.g. Cole et al., 2011; Lermite, Peneaux, & Griffin, 2017), that is, whether individual performance is consistent across contexts and tasks, relative to other individuals (Nakagawa & Schielzeth, 2010). The process leading to innovations inherently involves novelty, thus repeatability studies must employ different tasks. Tasks are often adapted to the ecology and characteristics of the species studied (e.g. Keagy et al., 2009), adding additional variance for comparing results from different species, though many avian studies on species with similar ecologies employ common tests, e.g. lid piercing or lid flipping tasks (Lermite et al., 2017; Papp, Vincze, Preiszner, Liker, & Bókony, 2015). This work has provided many important insights into the ecological consequences of intraspecific variation in the propensity to innovate (Cauchard et al., 2013; Cole, Morand-Ferron, Hinks, & Quinn, 2012; Huebner, Fichtel, & Kappeler, 2018) as well as the characteristics of among individual differences (Amici, Widdig, Lehmann, & Majolo, 2019; Griffin & Guez, 2014), across a variety of species and taxa, from insects and reptiles, to birds and mammals (Benson-Amram & Holekamp, 2012; Cole et al., 2011; Huebner et al., 2018; Laland & Reader, 1999a; Leal & Powell, 2011; Mirwan & Kevan, 2014). Indeed, some studies have found links with problem-solving performance and measures of fitness such as competitive ability, reproductive success, survival, and body condition (Cauchard et al., 2013; Cole et al., 2012; Cole & Quinn, 2011; Huebner et al., 2018; Laland & Reader, 1999b), implying that this individual variation can have important consequences, though these relationships can be complex (e.g. Huebner et al., 2018; Quinn, Cole, Reed, & Morand-Ferron, 2016). Yet general conclusions from this work remain limited, with notable differences between studies in how innovation is measured and whether repeatability can be generalized beyond the tasks and task type used (Boogert, Madden, Morand-Ferron, & Thornton, 2018).

Some interspecific work supports the idea of differences between contexts in the propensity to innovate, measured as innovation rate via counts of reported innovations in a taxon. For instance, comparative work in birds and primates found that innovation rates in technical contexts but not other contexts (e.g. non-technical foraging, nesting) were positively correlated with some measures of brain size (Lefebvre & Nicolakakis, 2000; Navarrete, Reader, Street, Whalen, & Laland, 2016; Overington, Morand-Ferron, Boogert, & Lefebvre, 2009). Furthermore, another analysis found that avian foraging innovation rates were positively correlated with both diet and habitat generalism, but technical innovation rates were only positively correlated with diet generalism (Ducatez, Clavel, et al., 2014). Within species, in spotted bower birds (*Ptilonorhynchus maculatus*), problem-solving performance in a mating context was not correlated with performance in a foraging context (Isden, Panayi, Dingle, & Madden, 2013), and in common pheasants, *Phasianus colchicus*, performance within a foraging context only correlated within task type, e.g. lid-flipping tasks, but not across task types, e.g. lid-flipping versus lid removal (van Horik & Madden, 2016). Thus, it is unclear if the propensity to innovate (and its relationship with other variables) is restricted to the context and type of tasks provided or can be generalized further.

In this study, we presented four tests involving novel maze exploration and problem-solving in a social context with a shoal reward, separated into two task types based on the relative importance of proposed solving predictors (here, exploratory propensities and inhibitory control) to male and female Trinidadian guppies, *Poecilia reticulata*. We measured a range of possible predictors (activity-exploration, risk-taking, shoaling motivation, learning performance, inhibitory control, body mass) that might influence propensities to innovate. We compared repeatability between and across all tasks as well as whether the proposed predictors played common roles across all tasks.

Several behavioural and morphological predictors have been hypothesized or found to influence innovation and problem-solving (Amici et al., 2019; Griffin & Guez, 2014; Reader & Laland, 2003a; Rowe & Healy, 2014). For instance, higher exploratory, activity, and risk-taking propensities might increase the chance of encountering and interacting with novelty (Lermite et al., 2017; Overington, Cauchard, Côté, & Lefebvre, 2011; Prasher, Evans, Thompson, & Morand-Ferron, 2019; Sol, Griffin, & Bartomeus, 2012). Additionally, interest in the task and reward likely influences the degree to which an individual engages and persists in attempting a task (Guez & Griffin, 2016; Sol et al., 2012; van Horik & Madden, 2016). Individuals might also solve a task through chance, potentially due to higher rates of activity during engagement with the task (Cole et al., 2011; Lermite et al., 2017; Sol et al., 2012). Thus, we assessed individual activity-exploration as measures of encountering and interacting with novelty, risk-taking as a willingness to interact with novelty in potentially risky situations, and shoaling preferences as motivation to reach the shoal reward. We predicted that fish that solved the tasks rapidly would have higher activity-exploration rates, exhibit greater risk-taking propensities, and have a greater affinity to shoal.

We also measured learning speed and inhibitory control as possible correlates of problem-solving performance. Learning ability has been proposed to correlate positively with problem-solving, though this relationship may be dependent on the type of learning measured (Griffin, Guez, Lermite, & Patience, 2013; Reader & Laland, 2003b). For example, certain individuals may rapidly learn the affordances of a task, such as the functional versus non-functional components of an extractive foraging apparatus, and reduce their time spent manipulating non-functional parts, thus solving the task more quickly (e.g. Cole et al., 2012; Thornton & Samson, 2012). Inhibitory control may be particularly important in detour tasks or tasks involving transparent barriers (Boogert, Anderson, Peters, Searcy, & Nowicki, 2011; Lucon-Xiccato, Gatto, & Bisazza, 2019), though this relationship likely also depends on previous experience with transparency (van Horik, Langley, Whiteside, Laker, Beardsworth, et al., 2018).

Sex, age, and body size or condition have also been proposed to influence individual differences in the propensity to innovate. For instance, the ‘necessity’ hypothesis posits that individuals with greater needs will be more likely to innovate (E. A. Fox, Sitompul, & van Schaik, 1999; Laland & Reader, 1999a), such as those individuals in poorer body condition or lower dominance status (Cole & Quinn, 2011; Laland & Reader, 1999b; but see Bókony et al., 2014; Prasher et al., 2019), or a sex with greater resource needs (Laland & Reader, 1999a; Reader & Laland, 2001). Alternatively, the ‘free time and energy’ hypothesis (Kummer & Goodall, 1985) predicts that individuals in superior body condition, those with higher dominance status or larger or older individuals, might exhibit greater propensities to innovate. Age related differences in neophilia might instead cause younger individuals to seek out novelty at greater rates (Greenberg, 2003). Here, we predicted that smaller fish would exhibit higher propensities to innovate since they are both younger and of lower competitive ability. Female guppies are known to generally shoal more than males (Magurran, Seghers, Carvalho, & Shaw, 1992) and thus may be more motivated to seek out and shoal with the stimulus shoal. If this is the case, we would expect to see a significant sex interaction with shoaling propensities.

Guppies are small, live-bearing tropical freshwater fish and provide a useful system for addressing these questions as a body of work already exists on their behaviour and ecology. Previous work has shown that individuals vary in their innovation propensity and that such differences (within the context of exploring a maze) are repeatable (Laland & Reader, 1999a). Studies have also examined their behavioural propensities (Budaev, 1997; Harris, Ramnarine, Smith, & Pettersson, 2010; Jacquin et al., 2016; Magurran, Seghers, Shaw, & Carvalho, 1995; Smith & Blumstein, 2010; Trompf & Brown, 2014) and cognition (Budaev & Zhuikov, 1998; Kotrschal et al., 2013; Petrazzini, Bisazza, Agrillo, & Lucon-Xiccato, 2017; Reader, Kendal, & Laland, 2003; Trompf & Brown, 2014), thus providing paradigms to build upon. Guppies thus offer a convenient study system that allows the high sample sizes needed for examining individual differences and repeatability (Dingemanse & Dochtermann, 2013).

Using guppies, we measured problem-solving and maze exploration performance to examine whether the propensity to innovate was repeatable between and across the four tasks in both males and females. In brief, we used two task types. Tests 1 and 3 (problem-solving) involved a stimulus shoal reward behind a transparent partition, requiring the individual to inhibit a response to swim directly to the shoal and instead take an indirect route to reach the shoal. Thus, we expected that inhibitory control would play a relatively large role in solving these tasks. For Tests 2 and 4 (maze exploration), individuals had to explore a novel environment and structure, and discover and swim through a gap to find a stimulus shoal reward. Here, we expected that exploratory propensities would play a relatively large role in solving success. If guppy innovation is broadly repeatable independent of the nature of the test (here termed the task general repeatability hypothesis), we predicted similar repeatability estimates of problem-solving across and between all four tests and that similar variables would predict problem solving across these tests. Alternatively, repeatability may be higher within the two task types (the task type specific repeatability hypothesis), may not map onto task types, or we may observe no repeatability at all.

2. Materials and Methods

2.1 Subjects and Housing

We used 183 adult laboratory-reared Trinidadian guppies as our test subjects. In order to increase our sample, we used fish originating from four previously studied populations in Trinidad

(Gotanda et al., 2013; Gotanda & Hendry, 2014; Grether, 2000; Jacquin et al., 2016; O'Steen, Cullum, & Bennett, 2002; Rodd, Hughes, Grether, & Baril, 2002; van Oosterhout et al., 2007) These origin populations were: (1) a low predation regime in the Marianne river, with *Gyrodactylus* parasites in the wild (77 subjects), (2) a low predation regime in the Marianne river, without *Gyro. spp.* parasites (53 subjects), (3) a low predation regime in the Upper Aripo river, without *Gyro. spp.* parasites (39 subjects), and (4) a low predation regime in the Quare river, without *Gyro. spp.* parasites (14 subjects), with parasite levels quantified by Gotanda et al. (2013). Thus the populations originated from three Trinidadian rivers (Aripo, Marianne, and Quare), and have been identified to be genetically distinct populations (Willing et al. 2010). Furthermore, the two Marianne populations are geographically separated by waterfall barriers, with some research indicating low gene flow across these barriers (Crispo, Bentzen, Reznick, Kinnison, & Hendry, 2006). Ninety-five subjects were male and 88 female. Thirty-seven fish were wild-born, and the remainder were born in captivity (F1: 62 fish; F2: 83 fish; F3:1 fish). Quare fish were all captive born and had previously been bred without predator exposure in a mesocosm study (Gotanda, Pack, LeBlond, & Hendry, 2019). Captive-born fish were pooled for analyses to account for the largest difference in our sample of wild versus captive-born, given we were not interested in or able given our sample size to examine complex population specific generational effects. An additional 20 laboratory-reared females (10 of large body size, 10 of small) were randomly selected from a mixed wild population background ("wild stock") to be used as a shoaling population from which to sample our stimulus shoals throughout the study.

Test subjects were housed in two 114 L tanks (92 x 46 x 33 cm; water height 28 cm), each filled with eight mesh breeding containers (16.5 x 12.1 x 13.3 cm), a filter, and gravel bottom. Each mesh container allowed water flow but inhibited clear visual contact with outside stimuli, thus physically and visually isolating individuals and allowing individuals to be identified without the use of invasive procedures such as elastomer tagging. Individuals serving as a shoal stimulus were housed in a 38 L tank (50 x 25 x 30 cm; water height 25 cm), along with a sponge filter, gravel bottom, and plastic plants.

Tanks were maintained at 25 ± 1 °C with a 12:12 h light:dark cycle with lights on at 0700. Fish were fed flaked food (Tetramin, Tetra, Germany) once daily, after testing. After the experiment all fish were returned to normal group housing conditions in breeding populations at McGill University.

2.2 Experimental Protocol

Each week, starting in May 2016, for 12 weeks, we randomly selected a cohort of 14-16 individuals from a randomly assigned population for testing, starting with later generations. Experimenters were blind to the population origin. Individuals went through a battery of tests over five consecutive days. Tests were conducted in fixed order due to power restrictions for examining the effects of a randomized test order (Bell, 2013). Behavioural measurements of shelter use, in an open field, and shoaling were taken on Day 1, followed by a different innovation test on each subsequent Day, starting with innovation Test 1 and ending with innovation Test 4 on Day 5. Upon the end of testing each day, individuals were returned to their assigned container in one of the two housing tanks. After the last test on day five, individuals were weighed by being placed in a small net, excess water was removed, and released into a tared beaker. We observed and video-recorded all behaviour from above using a Logitech HD webcam (720 p) with the experimenter watching behind an opaque black blind.

2.2.1 Pre-test measurements of shelter use, behaviour in an open field, and shoaling behaviour

Measurements of behavioural predictors were made in a 38 L tank (50 x 25 x 30 cm, water depth 6 cm, Figure 4.1) modelled as a modified open-field apparatus (as used in other fish studies, e.g. Brown & Irving, 2014; Budaev, 1997; Moscicki & Hurd, 2015). The tank bottom had scattered gravel stones and a grid of 5 by 5 cm squares in order to note the location of the fish. The 6 cm water depth restricted vertical movement and encouraged horizontal exploration of the open-field.

A subject was randomly selected from the population tank and placed within an opening inside a plant shelter in the test tank (Figure 4.1). After a 30 s habituation period we timed the time taken to leave the shelter. No fish exited the shelter in the habituation period or the subsequent 30 s. After 7 minutes or when the fish exited the shelter, we slowly removed the shelter via a remote pulley system and allowed the fish to explore the open-field for the next 5.5 minutes (Figure 4.1). Following the open-field exploration period, the individual was then isolated within a transparent cylinder (10 x 15 cm) in the center of the tank while the experimenter added two transparent sealed 9 x 9 x 9 cm containers to the ends of the tank (Figure 4.1). A stimulus shoal of two small and two large females, randomly selected, was placed into one container. The container with the shoal was randomly assigned on the first trial of the day and then alternated for subsequent trials. After a 30 s wait period, we released the individual and allowed it to swim freely for 5 minutes. The individual was then removed before repeating the procedure for the remaining fish. A 10 L tank (30 x 20 x 15 cm) with plants, air-stone, and heater, housed the stimulus shoal from before and between sociability tests, with the stimulus shoal replaced after half the fish for that day had been tested.

We counted the number of grid lines crossed as both a measure of activity in a novel environment and exploratory propensities (Budaev, 1997; Burns, 2008; Dingemanse et al., 2007; Smith & Blumstein, 2010). Risk-taking was quantified with two measures: the latency to exit the shelter (Brown, Burgess, & Braithwaite, 2007; Burns, 2008; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Dingemanse et al., 2007; Harris et al., 2010) and the difference in time spent between the outer and inner areas of the open-field (Figure 4.1; Ahmad & Richardson, 2013; Gervai & Csanyi, 1985; Lucon-Xiccato, Montalbano, & Bertolucci, 2019; Warren & Callaghan, 1975; Williams & Russell, 1972), with positive scores indicating more time in the outer area and negative scores indicating more time in the inner, more exposed and open area. Last, shoaling propensities were measured by the amount of time spent within one body length, approximately 2.5 cm, of the shoal container (Griffiths & Magurran, 1998). All fish spent proportionally more time within 2.5 cm of the shoal container than the other (empty) container out of the total time spent shoaling next to the containers (66%, one-sample t-test: proportion of time spent shoaling estimate ± S.E.: 0.65 ± 0.08, $t_{182} = 8.28$, $P < 0.001$) and the total time spent shoaling was significantly positively correlated with the proportion of time spent shoaling (Pearson $r = 0.95$, $t_{181} = 40.8$, $P < 0.001$), supporting the use of the total time shoaling measure as a measure of shoaling propensity. These behaviours were recorded in the event coder software, JWatcher v1.0 (Blumstein & Daniel, 2007).

2.2.2 Problem-solving and maze exploration tests

We used four different novel tasks to measure the propensity of individual fish to innovate (Figure 4.2). While each apparatus was unique, we designed them to examine our repeatability hypotheses of context general versus context specific repeatability based on proposed predictors of the solving process. Thus, Tests 1 and 3 were designed as "problem-solving" detour tests where individuals were given visual but restricted physical access to a stimulus shoal reward until discovering the test solution. In contrast, in Tests 2 and 4 the stimulus shoal reward was hidden in maze like structures and individuals could discover it via exploration. In all tests, the stimulus shoal was placed inside a transparent perforated container and thus subjects could potentially detect a shoal was present by odour cues, but the tasks were designed so that they could not be solved by following an odour plume to the shoal. The stimulus shoal was given a five minute habituation period before beginning testing and consisted of two large and two small females that were randomly selected and replaced after testing half the fish for each day.

For all innovation tests, individuals were placed within a transparent cylinder in a starting area for a three minute habituation period before being released by raising the cylinder. We recorded the latency to reach within 2.5 cm of the stimulus shoal container as a measure of innovation propensity, with fish that did not reach the shoal receiving a ceiling value of 1200 s (or 900 seconds for Test 4). Fish that did not solve the test within the ceiling value were gently guided to the shoal with a net and all fish were allowed to shoal for 180 s (60 s for Test 4) before being returned to the home container. This was to attempt to equalize experience of the shoal reward between individuals. Individuals were tested in the same order as previous days.

Test 1 involved swimming around a transparent perforated barrier to reach the stimulus shoal. This was an adaptation of the detour/cylinder test used to test inhibitory control in birds, mammals, and fish (Kabadayi, Bobrowicz, & Osvath, 2018; Lucon-Xiccato, Montalbano, et al., 2019; MacLean et al., 2014), with greater time spent swimming back and forth alongside the transparent barrier (within 2 cm) used as a measure of lower inhibitory control. While this measure was confounded with the latency to solve Test 1, it provided an independent measure for predicting performance on the Test 2-4.

In Test 2, the test area was divided into two equal sections by a semi-opaque perforated plastic grid with plastic plants attached. A 10 x 10 cm square in the far side from the release zone was only visible on approach and provided access between the two sections. The stimulus shoal was located on the other side of the plant barrier and could only be seen by the subject when it had swum through the hole in the barrier. Test 2 thus required exploration of the tank to complete the task.

Test 3 was an escape task. Subjects were placed in a transparent plastic container (20 x 20 x 10 cm, water depth: 7 cm) clipped to the side of the tank that contained a hole (7 x 7 cm) partially covered by a plastic plant. Individuals were able to see the stimulus shoal from within the container, but to reach the shoal had to swim away from it and through the hole. Given the small confines of the container, it was difficult to reliably distinguish behaviour swimming in front of the transparent container walls from general swimming behaviour, thus we were unable to repeat our measure of inhibitory control from Test 1. We noted the time subjects swam through the hole. An additional light above the escape apparatus aided in seeing the subject and likely made the container more aversive.

In Test 4, two partitions (20 cm) created a two-zone maze (20 x 30 cm) with the stimulus shoal at the end and a single entrance from the test area. In this test, individuals were unable to see the stimulus shoal reward and thus had to explore the maze in order to discover it. Latency to reach each maze zone was also recorded. Test 4 differed from the previous ones in that individuals were given 900 s to solve the test and 60 s of shoaling time with the stimulus shoal before being retested for a total of three trials. This procedure allowed us to obtain a measure of individual learning over the course of three trials.

2.3 Statistical analyses

We removed 16 individuals which were missing innovation data in three or more tests due to mortality, escaping the apparatus, or equipment malfunctions, leaving 167 individuals for examining repeatability. Forty-eight additional fish were removed due to missing predictor data from equipment malfunctions and experimental procedural error with 135 individuals for analysing the predictors of innovation propensity.

Both linear (LM[M]) and generalized linear (GLM[M]) mixed models were used based on the response variable (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). In cases of non-normally distributed zero-bounded data (such as behavioural latencies or body mass) or heterogeneity in the residuals, we used natural log transformations or generalized least squares to resolve these issues (Cleasby & Nakagawa, 2011; Zuur et al., 2009). When present in the GLM(M)s, we corrected for overdispersion by fitting an observation level random effect (G. A. Fox, Negrete-Yankelevich, & Sosa, 2015). To facilitate model computation and to provide biologically meaningful estimates, all continuous predictors were mean-centered and scaled by one standard deviation (Schielzeth, 2010). We calculated the marginal and conditional R^2 for all mixed models using the "MuMIn" R package (Barton, 2016), following Nakagawa and Schielzeth (2013). The marginal R^2 represents the variance explained by the fixed effects and the conditional R^2 represents the variance explained by both the fixed and random effects.

Interaction significance was evaluated using Likelihood Ratio Tests (LRT) and maximum likelihood estimation (Zuur et al., 2009) with a liberal significance criterion of ≤ 0.1 to avoid removing interactions that approached the 0.05 threshold for statistical significance. All other significance tests followed the typical alpha criterion of ≤ 0.05. Main fixed effects were not removed from the model as we had *a priori* hypothesized their inclusion and excessive use of stepwise selection procedures has been criticised (reviewed in Whittingham, Stephens, Bradbury, & Freckleton, 2006). Model estimate significance was evaluated with *t* (LM[M]s) or Wald tests (GLM[M]s; Zuur et al., 2009) using the 'lmerTest' R package for mixed models (Kuznetsova, Brockhoff, & Christensen, 2017).

We tested for the significance of the random effects using LRTs (Pinheiro & Bates, 2000) with restricted maximum likelihood estimation (Zuur et al., 2009) and removed non-significant or singular random effects that were not crucial to our questions of interest (G. A. Fox et al., 2015). In order to compare models with similar maximum likelihood estimations when testing the importance of the individual random effect to the model fit, we used an AIC ≥ 2 (Burnham &

Anderson, 2008) as a selection criteria. In a few cases, random effects of interest or crucial to the experimental design, such as individual, were non-significant or resulted in boundary fits. However, we forced these into the model as their removal would result in biased model inferences and problems such as pseudoreplication (Hurlbert, 1984).

Model assumptions were checked using residual plots, using the 'DHARMa' R package (Hartig, 2019) for GLM(M)s. Model checks were assessed with reference to Zuur et al.'s (2009) recommendations. All analyses used R Statistical Software (R Core Team, 2017).

2.3.1 Repeatability

The repeatability of shoaling latency was analysed using mixed models as this approach allowed us to examine both the 'raw' unadjusted repeatability (Unadj. R) as well as the adjusted repeatability (Adj. R) which accounted for potential influences from our experimental design (Nakagawa & Schielzeth, 2010). Unadjusted repeatability was calculated following Nakagawa and Schielzeth (2010) with an intercept only model and individual as a random effect. As we were interested in repeatability without sex, generational or population effects, to calculate the adjusted repeatability we incorporated factors that could influence among-individual variance and our repeatability estimates, such as demographic factors as well as factors related to experimental design (Nakagawa & Schielzeth, 2010; Wilson, 2018). Thus, sex, population, generation (wild versus captive born), and innovation test were fit as fixed effect factors and housing tank, test batch (i.e. week), and individual as random effects. Ninety-five percent confidence intervals for the repeatability estimates were calculated via bootstrap sampling (1,000 iterations). All repeatability tests were performed with R package "rptR" (Stoffel, Nakagawa, & Schielzeth, 2017).

To evaluate our repeatability hypotheses, we calculated the unadjusted and adjusted repeatabilities for all pairwise combinations of tests. The robustness of the mixed-models was checked by examining Pearson correlation coefficients for all pairwise innovation test comparisons. We also calculated repeatability across all four innovation tests (All Tests) for the task general repeatability hypothesis. Sex specific repeatability was examined by repeating the above analyses but splitting the data by each sex and removing sex as a factor in the adjusted repeatability analysis. Sex differences in repeatability were calculated by taking the mean of a distribution of the difference between the male and female bootstrapped repeatability estimate distributions. We examined the significance of the sex differences by checking whether the 95% confidence of the differences overlapped with zero.

2.3.2 Predictors of problem-solving and maze exploration

We examined the role of our proposed predictors (and potential sex by predictor interactions) by fitting them as explanatory variables into full models (containing all the predictors and interactions of interest) for each innovation test. Time swimming at the barrier (our measure of inhibitory control), was only included for Tests 2-4. All models were fit with the same fixed and random effects as in the adjusted repeatability models, except we excluded the individual random effect since there were no repeated measures and the test factor since there was only one test level per model. Sex specific influences were examined by fitting predictor by sex interactions. These models were then reduced by removing non-significant interactions and random effects as above.

2.3.3 Sex differences in behaviour and body size

We also examined sex differences in our behavioural variables and body mass by modeling the variable of interest as the response explained by sex. Mean values for each sex (when there were significant sex differences) were calculated by refitting the model with the baseline sex switched.

Data and code will be permanently archived at Zenodo.

2.4 Ethical Note

All procedures were approved by the McGill University Animal Care Committee under protocol number 2012-7133, and conform to ASAB guidelines and Canadian Council on Animal Care. At the end of the study, all fish were returned to breeding populations at McGill University.

3. Results

3.1 Did fish successfully complete the tests?

Fish were largely successful in completing the tests, though this varied by test (proportion of solvers; Test 1: 167/167 [100%], Test 2: 151/167 [90%], Test 3: 108/167 [65%], Test 4: 151/167 [90%]). On completing the test fish typically interacted and grouped with the shoal. Shoaling latency varied widely by test (means ± 1 S.D.: Test 1: 120 ± 150 s, Test 2: 357 ± 366 s, Test 3: 520 ± 402 s, Test 4: 312 ± 265 s). There was no evidence that individuals improved their efficiency in solving the maze during the repeated testing of Test 4 (trial estimate ± S.E.: $< -0.01 \pm < 0.01$, $P = 0.99$; trial by sex interaction estimate ± S.E.: 0.03 ± 0.08, $P = 0.97$), thus we did not further analyze this variable as a measure of individual learning ability.

3.2 Is problem-solving and maze exploration repeatable (across both sexes)?

We found low repeatability in the latency to reach the shoal across all four tests, although the adjusted repeatability was statistically significant (Unadj. R: <0.01, $P = 0.5$; Adj. R: 0.09, $P = 0.006$, Table 4.1). Pairwise examination of the four tests revealed evidence for repeatability between Tests 1 and 2 (Unadj. R: 0, $P = 0.5$; Adj. R: 0.14, $P = 0.035$) and Tests 2 and 4 (Unadj. R: 0.23, $P = 0.001$; Adj. R: 0.21, $P = 0.003$), with all other pairwise test comparisons not repeatable (Figure 4.3, Table 4.1).

3.3 Sex specific repeatability and sex differences in the repeatability of shoaling latency

Repeatability of shoaling latency differed between males and females, though the magnitude of these differences was dependent on the test comparison and whether additional factors were accounted for (Figure 4.3, Table 4.1). Shoaling latency was not significantly repeatable across all four tests for males or for females when examining unadjusted repeatability (all $P > 0.05$, Table 4.1). However, shoaling latency was significantly repeatable in males, though not in females, after adjusting for additional factors (All Tests: males Adj. R = 0.19, $P < 0.001$, females Adj. R = 0, $P = 1$; Table 4.1). When comparing the two sexes, males had significantly higher repeatability estimates over all 4 tests than females for the adjusted repeatability only (Adj. R. difference: 0.18, 95% C.I.s did not overlap with 0; Table 4.1), suggesting that females drove the lower repeatability estimates seen when combining both sexes.

We then examined repeatability estimates for the four tests pairwise for each sex separately (Figure 4.3, Table 4.1). In males, the unadjusted shoaling latency was only repeatable between Tests 2 and 4 (Unadj. R = 0.29, *P* = 0.004) and approached significance in Tests 1 and 2 (Unadj. R = 0.14, *P* = 0.1). However, after adjusting for additional factors, Tests 1 and 2 (Adj. R = 0.3, *P* = 0.004), Tests 1 and 4 (Adj. R = 0.22, *P* = 0.023), and Tests 2 and 4 (Adj. R = 0.24, *P* = 0.012) were significantly repeatable. The repeatability of Tests 2 and 3 also approached statistical significance (Adj. R = 0.17, *P* = 0.06) while Tests 1 and 3 or 3 and 4 repeatabilities were not significant (all *P* > 0.1). In contrast, female performance only approached significance between Tests 2 and 4, for both the unadjusted and adjusted repeatability estimates (Figure 4.3, Table 4.1). All other test comparison repeatability estimates were non-significant for females (Table 4.1). Together, these results indicate that the repeatability estimates from the sexes-combined analysis were primarily driven by male repeatability.

When examining sex differences in pairwise test comparisons of repeatability, male and female repeatability only significantly differed for Tests 1 and 2 (Adj. R. difference: 0.25, 95% C.I.s did not overlap with 0; Table 4.1) and Tests 1 and 4 (Adj. R. difference: 0.23, 95% C.I.s did not overlap with 0; Table 4.1) with no sex differences present in the unadjusted repeatability estimates (95% C.I.s overlapped with 0; Table 4.1).

The Pearson correlations revealed qualitatively similar patterns and estimates to the unadjusted repeatability estimates from the mixed-models, except for a positive correlation between Tests 1 and 2 for the both sexes analysis as compared to a non-significant repeatability estimate from the mixed-models (Figures S4.1-4.2).

3.4 Is shoaling latency explained by common predictors?

The predictors of shoaling latency varied among the four tests, showing a general lack of consistency, though some predictors were consistently non-significant regardless of the model (Figure 4.4, Table S4.1). Time spent swimming in front of the transparent barrier on Test 1 did not influence solving latency in Tests 2, 3, or 4 (all $P > 0.1$, Figure 4.4, Table S4.1). Fish that crossed more lines were slower to reach the shoal reward in Test 3 (Test 3: lines crossed: $P = 0.002$, Figure 4.4, Table S4.1). Total time shoaling only influenced the latency to reach the shoal in Test 2 in a sex specific manner, with males that spent more time shoaling being faster to reach the shoal reward (Test 2: sex by total time shoaling interaction: $P = 0.035$, Figure 4.4, Table S4.1). There was no relationship with total time spent shoaling and latency to reach the shoal reward in females or in other tests (total time shoaling: all $P > 0.1$, Figure 4.4, Table S4.1). In regards to the open-field location preference, females which spent more time in the outer area of the open-field were faster to reach the shoal reward in Test 3 ($P = 0.049$, Figure 4.4, Table S4.1). In contrast, there was no significant relationship in males between the open-field location preference and the latency to reach the shoal in Test 3. In Test 4, fish which spent more time in the outer area of the open-field were faster to reach the shoal reward, regardless of sex (Test 4: open-field location preference: $P = 0.034$, Figure 4.4, Table S4.1). There were no other significant predictors of the latency to reach the shoal reward. All other predictors and sex by predictor interactions had non-significant effects (all $P > 0.1$, Figure 4.4, Table S4.1).

3.5 Sex differences in behaviour and body size

We found several differences in behaviour and physical characteristics between males and females. Specifically, males spent less time than females in the outer area of the open-field test (sex estimate: $P = 0.036$, Table 4.2), though both sexes preferred the outer over central area of the open-field compared to chance (female estimate: intercept: $P < 0.001$, Table 4.2; male estimate ± S.E.: 98.52 ± 16.44, $t_{162} = 5.99$, $P < 0.001$). Compared to females, males also emerged from the shelter faster (sex estimate: $P < 0.001$, Table 4.2), spent more time shoaling (sex estimate: $P < 0.001$, Table 4.2), and were smaller in mass (sex estimate: $P < 0.001$, Table 4.2).

However, males and females did not significantly differ in the number of lines crossed, the time in front of the barrier during Test 1, or in the latency to reach the shoal (all $P > 0.1$, Table 4.2).

Study 2: Is solving latency repeatable between highly similar test contexts?

The results above suggested that the latency to reach the shoal was not broadly repeatable across and between the four tests, though the extent of this varied between males and females and the tests compared. The lack of broad repeatability was further supported by a lack of consistency in the predictor relationships with the latency to reach the shoal. Lower repeatability estimates may have resulted from the use of dissimilar task designs. Furthermore, the behavioural predictors may not have been repeatable, which may explain a lack of consistent relationships with latency to reach the shoal. We thus evaluated these possibilities by repeated testing of an additional small set of individuals ($n = 30$) on two very similar mazes and a battery of behavioural tests given twice over two weeks. The supplementary material describes fully the methods and results. Briefly, we found that the latency to solve was not repeatable between the two mazes when examining both sexes together (Both sexes: UnAdj. R: 0.06; Adj. R: 0.08, all $P > 0.1$, Table S4.2). However, when split by sex, females, but not males, exhibited repeatable latencies to reach the shoal reward (females: UnAdj. R: 0.56 [95% C.I.: 0.13–0.81], $P = 0.012$, Adj. R: 0.60 [95% C.I.: 0.2–0.85], $P = 0.005$; males: UnAdj. R = 0 [95% C.I.: 0–0.47], $P = 1$, Adj. R = 0 [95% C.I.: 0–0.53], $P = 1$). Pearson correlation tests split by sex revealed qualitatively similar results to the unadjusted repeatability estimates: a significant correlation in shoaling latency across tests in females but not males (female r: 0.6, $P = 0.019$; male r: -0.17, $P = 0.55$). We note some caution in interpretation given the small sample size (Dingemanse & Dochtermann, 2013). Lines crossed, shelter emergence latency, and shoaling measures were all repeatable (all R > 0.4, all $P < 0.05$, Table S4.2), indicating that these measures appeared to capture consistent among individual differences and were relatively high repeatability estimates. The sexes did not significantly differ on solving latency or other behavioural measures (Tables S4.3, S4.4).

4. Discussion

Repeatability estimates in solving latency over innovation tests differed between males and females. In males, adjusted repeatability estimates ranged from 0.2-0.3 for four test pairs, with three pairs reaching statistical significance (Tests 1 and 2, 1 and 4, 2 and 4) and a fourth approaching significance (Tests 2 and 3). Thus males showed repeatability both within and between the two test types of maze exploration and problem-solving, but escape Test 3 appeared to be an outlier. In females, the highest adjusted repeatability was 0.16 (Tests 2 and 4: maze exploration) and no pairwise test repeatability reached statistical significance. Repeatability over all four tests mirrored these pairwise results: a significant repeatability of 0.2 for males, a zero repeatability for females, and significantly higher repeatability for males than females. However, females, but not males, exhibited repeatable latency to the shoal reward in the two maze exploration tests of the second study. Together, these results suggest that males and females exhibit different degrees of repeatability in their problem-solving and maze exploration behaviour, and that the specific test design can impact repeatability.

Our moderate repeatability estimates were lower than those found in the animal personality literature (average adj. R: 0.37: Bell, Hankison, & Laskowski, 2009), but were similar to those found in meta-analysis for contextual repeatability, i.e. performance on different tasks assumed to have similar cognitive underpinnings, including measures of innovation propensity (average adj. R: 0.2: Cauchoix et al., 2018). There were few significant predictors of shoaling latency and these predictors appeared to be test specific with little to no evidence of sex-specific results, supporting the diverse repeatability estimates. Our findings highlight that the repeatability of problem-solving and maze exploration can depend on numerous factors, including test design and selection, and emphasizes the importance of evaluating the generality of repeatability when interpreting results and designing studies. These results also indicate that predictors of problem-solving and maze exploration may be test dependent, further supporting the need to consider this in future work, even when such behaviour is repeatable.

4.1 Repeatability in males

Males exhibited repeatable behaviour in most of the pairwise comparisons in Study 1, but with no repeatability found when comparing performance with Test 3 and in Study 2. While Tests 1 and 3 were designed as problem-solving detour tasks requiring inhibitory control to solve, Test 3 appeared to be more difficult given the higher latency to complete the task compared to the other tests. In Test 1, fish had to swim around a barrier to reach the shoal whereas in Test 3, fish had to swim through a small partially covered hole which may have been more difficult or aversive due to its size. While these tasks were grouped into a problem-solving inhibitory control type, task performance may be moderated by additional factors such as the difficulty or averseness of the solution or the specific motor behaviours required to solve the task. For instance, Bokony et al. (2014) found that house sparrow (*Passer domesticus*) performance across four different extractive foraging tasks was only positively correlated on two out of the six possible task comparisons. They proposed that these differences may have been influenced by the difficulty of the tasks (Bókony et al., 2014). In a similar vein, van Horik and Madden (2016) found that performance in common pheasants was only positively correlated across similar task variants, e.g. flip tasks, but not with the dissimilar petri-dish lid removal task, though all three tasks were within an extractive foraging context and problem-solving task type. Here, the authors proposed that such differences were due to the different motor actions required to solve the task (van Horik & Madden, 2016). In our study, given that all tasks required similar motor behaviour, i.e. swimming around and navigating structures, task difficulty seems the most likely explanation for the lower repeatability estimates involving Test 3.

However, in contrast to Study 1, Study 2 found low repeatability in males between two very similar and relatively simple maze exploration tasks. Study 2 differed from the first study in several factors, including the increased length of time between testing and the mixed but unknown population composition. Indeed, research in guppies has shown that populations can vary widely in their behaviour and we were unable to account for this variation in our model in Study 2. Perhaps the conditions of Study 2 impacted males differently from females, such as the increased isolation stress. Future studies will be needed to examine which factors moderate repeatability between tasks (e.g. task difficulty, solving mechanisms, population origin, sex, etc.) and if they have interactive effects.

4.2 Repeatability in females

Female problem-solving and maze exploration behaviour was not found to be repeatable in Study 1. However, female performance in the two maze exploration tasks of Study 2 was repeatable, indicating females can display consistent behaviour. These results support previous findings in guppies which showed that female maze exploration behaviour was repeatable across three different maze configurations (Laland & Reader, 1999a). Notably, in Study 1, the highest female repeatability was observed in the two maze exploration tasks, which may tentatively support the task type specific repeatability hypothesis. Under this hypothesis, we also expected that a higher repeatability within a task type would be a product of the two tests having similar solving predictors, e.g. activity-exploratory and social propensities. However, neither of these predictors influenced maze exploration behaviour consistently between the two tests. Thus, while there was higher repeatability for females in maze exploration tasks, it is unclear whether this result is due to similar, but unmeasured solving predictors, or whether it is specific to the task type, or even to the specific test designs. Further replication of similar task types and comparisons would be needed to confirm why the higher repeatability in this task type was observed and whether it was specific to this combination of tasks.

4.3 Sex differences in repeatability

Our finding that problem-solving and maze exploration repeatability varies between the sexes, with more general and higher repeatability in males, raises interesting questions about when and why sexes might differ in this way. Notably, we did not observe significant differences in shoaling latency between males and females, just differences in repeatability. Perhaps females, with higher and potentially more variable feeding demands due to variation in reproductive state, and evidence for more risk-averse behaviour than males (i.e. slower shelter emergence and more time spent at the periphery of the open field) (Harris et al., 2010), monitor and adjust behaviour according to the potential costs and benefits of innovation more than do male guppies

(Greenberg, 2003; Lee, 2003). In contrast, males might be more consistent with their propensity to innovate if the potential payoff, such as increased mating opportunities, outweighs the potential costs and is stable (Kummer & Goodall, 1985; Reader & Laland, 2001). Thus, the costs and benefits of plasticity may benefit females more than males in this domain.

A meta-analysis on the repeatability of personality traits found that males had higher repeatability estimates than females, but only when mate preference tests were included. (Bell et al., 2009). When these behaviours were excluded, females exhibited higher repeatability than males. Though Bell et al. (2009) note mate preference data were limited to male preferences for females, potentially sex differences in motivation for our tests may have played a role in the sex differences in repeatability we observed as the stimulus shoal was all female. Perhaps, in what is a mating context for males but not females, males performed to the maximum of their ability, resulting in more consistent performance across tasks compared to females. Future work might examine sex differences in repeatability when comparing foraging and mating tasks.

4.4 Predictors of innovation propensity

We found no evidence for the task general or task type specific hypotheses for all predictors, and instead, results supported test specific influences. For example, we found test specific effects in risk-taking, activity-exploration, and a sex by shoaling interaction. These results emphasize the importance of examining whether such relationships are task general or test specific (Prasher et al., 2019).

The general lack of consistent predictors of the propensity to innovate suggests that our measure was independent of the motivational and behavioural predictors we measured and was partially representative of individual propensity to solve these tests. The non-significant effects of the hypothesized predictors also matches with the inconsistencies found in the extractive foraging literature (Griffin & Guez, 2014), suggesting similar issues in determining general predictors of innovation in non-foraging contexts. Still, individuals may have learned the nature of the tasks (i.e. finding the shoal reward) across the tests and thus increased their proficiency to reach the shoal, but we were unable to evaluate this possibility due to the different test designs used. In addition, while our measure focused on solving speed, other measures such as the number of errors made (Cole et al., 2012; Thornton & Samson, 2012), might exhibit different relationships. Another possibility is that the behavioural predictors measured may be highly plastic and thus poorly representative of an individual's propensities. However, the second study, which measured repeatability of similar behaviours, found they were generally highly repeatable, though we did not examine the repeatability of inhibitory control. Indeed, a recent study in guppies found that inhibition of foraging behaviour towards a restricted food stimulus was not repeatable across two trials (Lucon-Xiccato, Montalbano, et al., 2019), thus the repeatability of our measure of inhibitory control will need to be evaluated before strong conclusions can be made about its influence on the propensity to innovate.

Within species, studies examining a wider or different variety of test contexts and task types (e.g. not limited to extractive foraging contexts or problem-solving tasks) find notably lower or non-significant repeatability estimates (Isden et al., 2013; Keagy et al., 2009, 2011; Preiszner et al., 2017; Sol et al., 2012; van Horik, Langley, Whiteside, Laker, & Madden, 2018), suggesting that not all innovative behaviour is repeatable. These results contrast with some of the avian literature on extractive foraging contexts and tasks. For example, problem-solving task performance is repeatable in several studies of avian species (Audet, Ducatez, & Lefebvre, 2016; some tasks: Bókony et al., 2014; Cole et al., 2011; Ducatez, Audet, & Lefebvre, 2014; Papp et al., 2015; Lermite et al., 2017; Preiszner et al., 2017; Indian mynas only: Griffin & Diquelou, 2015; but see Prasher et al., 2019; van Horik & Madden, 2016; and Griffin et al., 2013) often with persistence and motor diversity as predictors of success (Griffin & Guez, 2014, 2016). Furthermore, when including non-avian taxa, several studies using similar contexts and task types find a lack of repeatability (Madame Berthe's mouse lemurs, *Microcebus berthae*, grey mouse lemurs, *Microcebus murinus*, eastern grey squirrels, *Sciurus carolinensis*, and Eurasian red squirrels, *Sciurus vulgaris*: Cauchoix et al., 2018; rock pool prawns, *Palaemon spp*: Duffield, Wilson, & Thornton, 2015; meerkats, *Suricata suricatta*: Thornton & Samson, 2012). These findings tentatively support the idea that some measures of the propensity to innovate may be context or task type specific, though taxonomy may also play a role as well. However, further studies are needed to determine which factors (e.g. test contexts, task types, species, and populations) account for variation in repeatability estimates.

4.5 Conclusion

Overall, we found that propensities to innovate in guppies were repeatable for some tests, but this result was largely conditional on the choice of test comparison and the sex examined. Our study provides novel insights into how the task context can influence the propensity to innovate and raises important questions regarding the generality of measures of innovative and problem-solving behaviour as it is commonly measured in the literature. While our results show initial support for both the task general repeatability hypothesis (in males) and the task type specific repeatability hypothesis (females), further work is needed to confirm the generality of these findings and to understand what influences individual variation in performance. Furthermore, our findings highlight the importance of decomposing repeatability estimates when there may be strong moderating factors of individual variation, such as sex, which can have differential conclusions on repeatability. Together, our results demonstrate that among individual variation in the propensity to innovate can be influenced by a variety of factors and disentangling the role these play may help shed light on discrepancies in the literature for what predicts among-individual variation in innovation propensity.

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7. Figures

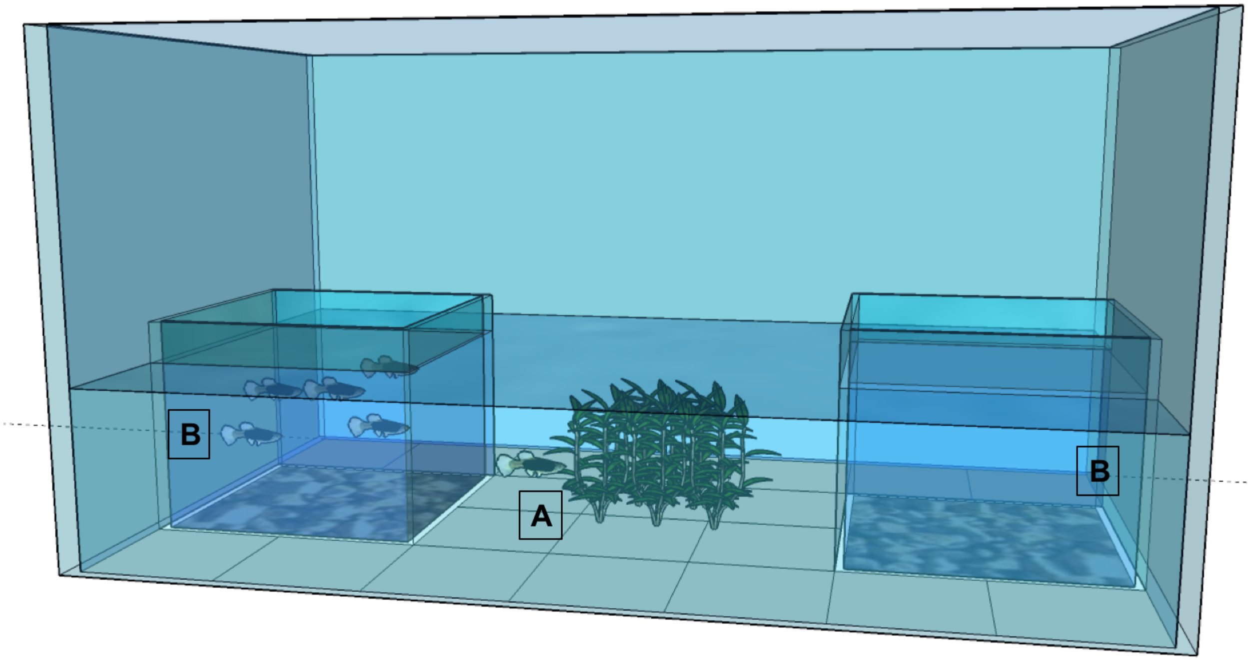

Figure 4.1. Tank apparatus for testing shelter use, behaviour in an open-field, and shoaling. Lines for measuring location and activity-exploration were drawn on the tank bottom. A: Starting position within the plant shelter, later removed upon fish exit. The open-field test followed the removal of the plant shelter. B: Shoal holding containers for testing shoaling preference which were added to the tank after the open-field test.

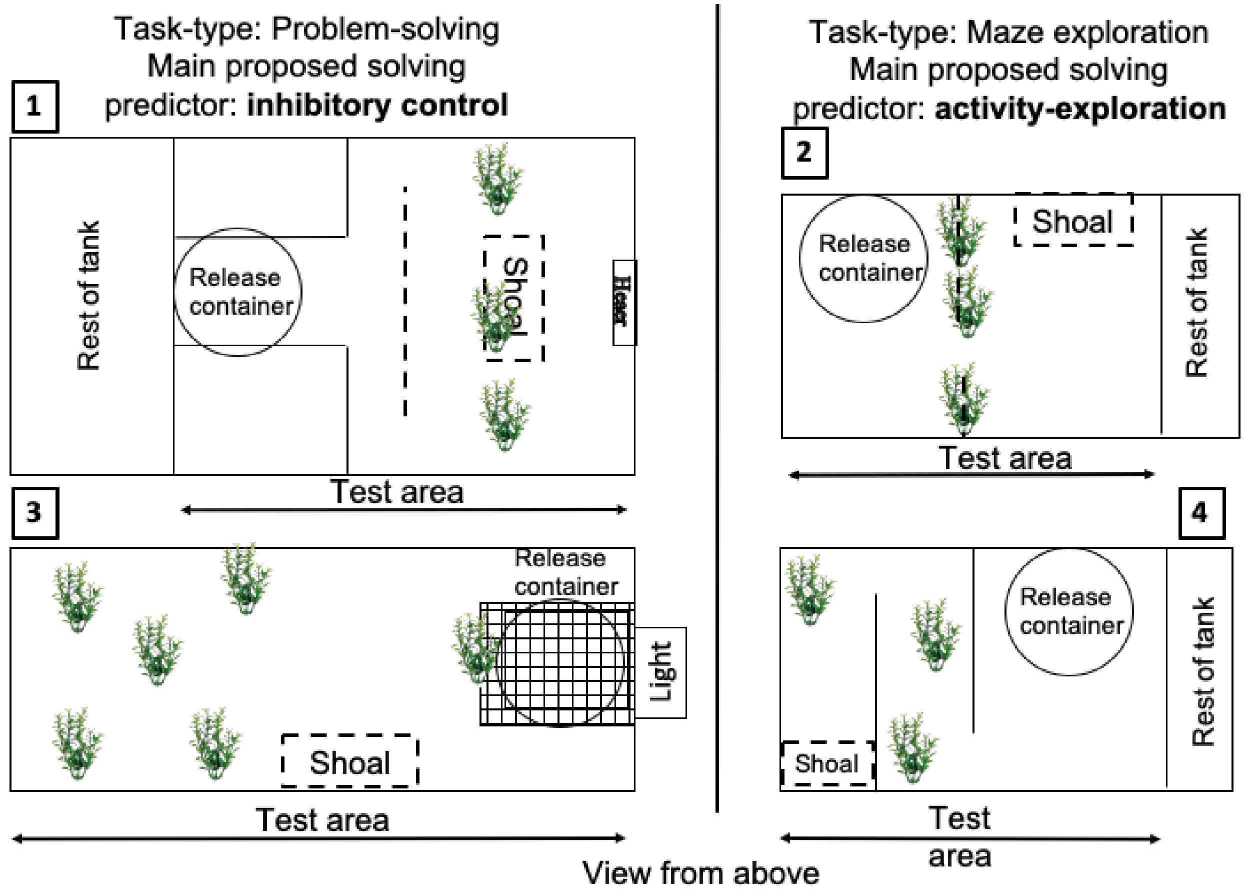

Figure 4.2. The four apparatuses used to test the latency to reach the shoal, numbered in order of test sequence and split into two contexts based on the proposed main solving predictors. Solid lines indicate white opaque partitions. Perforated lines indicate transparent partitions with holes (2 x 2 mm) to allow some water flow. All tanks were 76 L: 76 x 30 x 30 cm, except for Test 3, 114 L: 92 x 46 x 33 cm. Water depth was 10 cm for Test 1, 28 cm for Tests 2 and 4, and 25 cm for Test 3. In Tests 1, 2 and 4, a white opaque partition separated the test area from the rest of the tank to decrease tank size. In Test 1, the starting recess was 15 by 10 cm. In Tests 1, 2 and 4, the test area was 50 by 30 cm. Sand covered the bottom of all tanks and gravel was scattered on top of the mesh bottom of the container in test 3. Plastic plants provided shelter. Subjects could only see the shoal from the release container in tasks 1 and 3. Images not to scale.

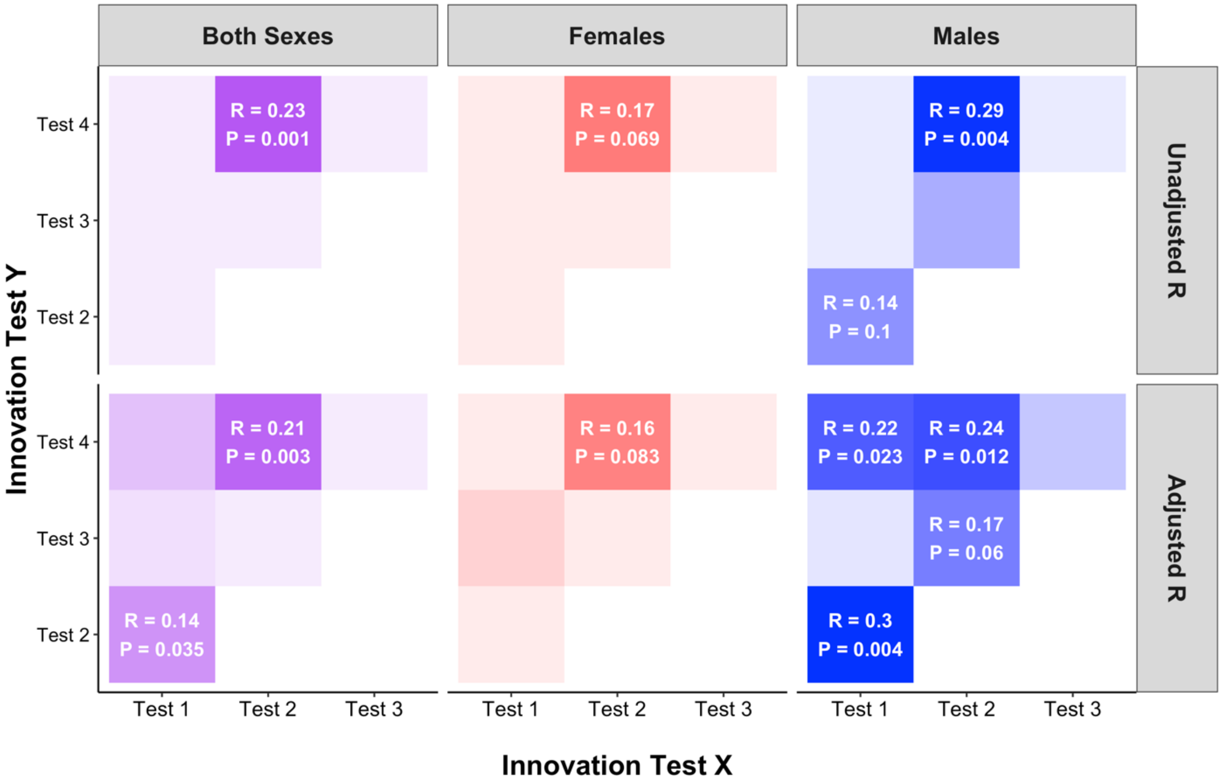

Figure 4.3. Matrix of unadjusted (top row) and adjusted (bottom row) repeatability (R) estimates of the latency to reach the shoal coloured by both sexes (purple), females (red), and males (blue) for all pairwise test comparisons. Shade gradient corresponds to the size of the R estimate with darker shades having larger estimates. Correlations of test to itself (e.g. Test 2 to Test 2) and repeated correlations are left blank. R estimates and P-values are indicated for repeatability estimates with $P \leq 0.1$ only.

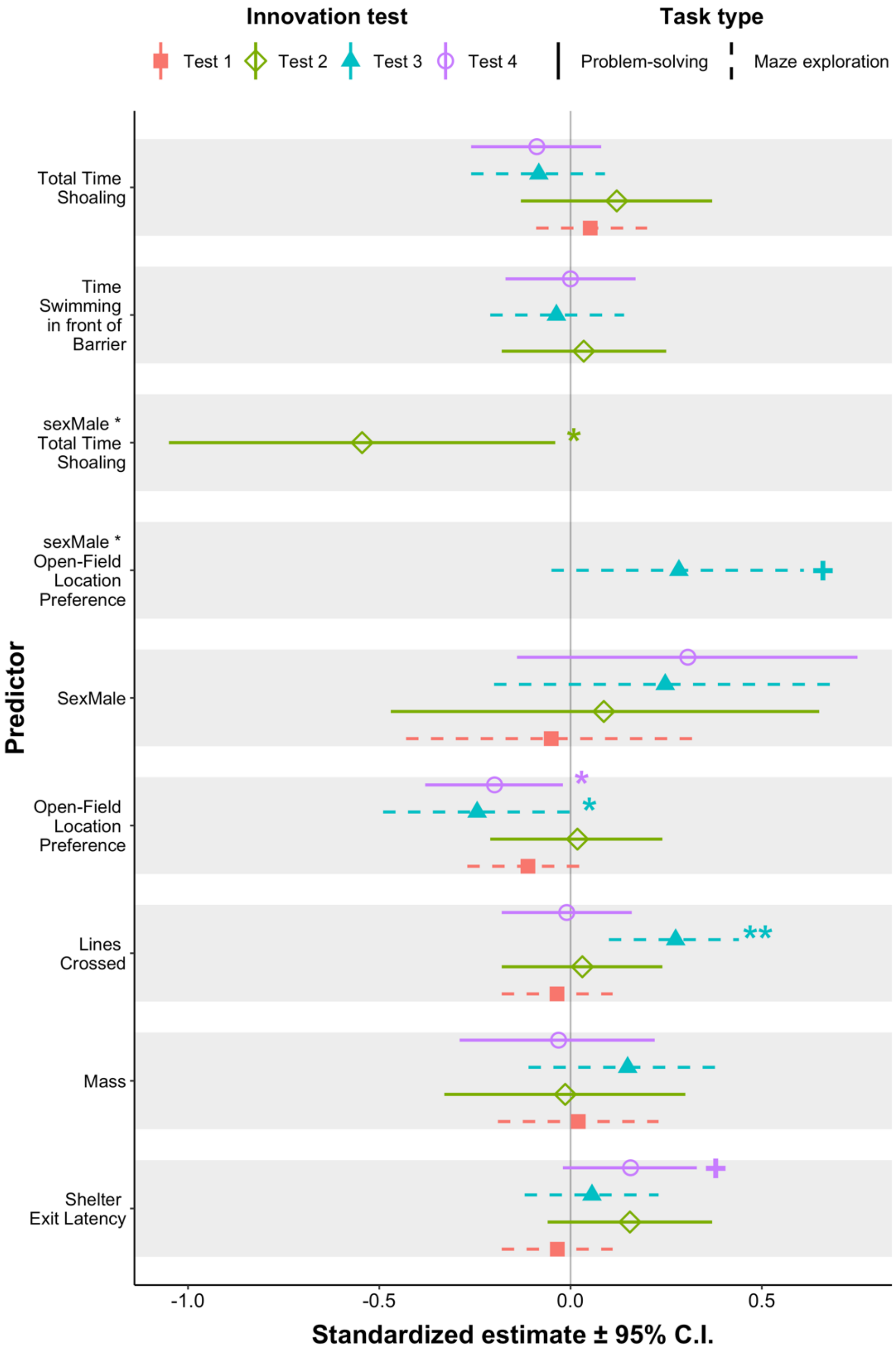

Figure 4.4. Predictors of the latency to reach the shoal for each innovation test. Coloured lines and points represent 95% confidence intervals around the associated estimate. Solid lines indicate the ‘problem solving’ task type, dashed lines the ‘maze exploration’ task type. Squares: Test 1; diamonds: Test 2; triangles: Test 3; circles: Test 4. Interaction estimates are only shown for $P \leq 0.1$. For brevity, estimates for the intercept, innovation test, population, and generation are not shown. Symbols for significance are as follow: +: $P \leq 0.1$; *: $P \leq 0.05$; **: $P \leq 0.01$; ***: $P \leq 0.001$

8. Tables

Table 4.1. The repeatability of the latency to reach the shoal for all pairwise test comparisons for both sexes (*n* = 167), males (*n* = 88), females (*n* = 79), and compared between the two sexes. Adjusted repeatability models accounted for the effects of the housing container and test batch as random effects, and sex (for the 'both sexes' models), population, generation (wild versus captive born), and innovation test as fixed effects. P-values were obtained via likelihood ratio tests and confidence intervals were computed via 1,000 bootstrap iterations. Marginal R^2 (R_m^2)is the variance explained by the fixed effects and conditional R^2 (R_c^2) is the variance explained by the fixed and random effects.

Test comparison	Sex group	R	95% C.I.	P-value	R_m^2	R_c^2
All Tests (Tests 1-4)	*Unadjusted Repeatability*					
	Both sexes	<0.01	0–0.06	0.5	0	<0.01
	Males	0.06	<0.01–0.16	0.087	0	0.06
	Females	0	0–0.09	1	0	<0.01
	Sex Diff.	0.05	-0.05–0.15	-	-	-
	Adjusted Repeatability					
	Both sexes	0.09	0.02–0.16	0.006	0.26	0.32
	Males	0.19	0.08–0.31	<0.001	0.25	0.5
	Females	0	0–0.1	1	0.27	0.28
	Sex Diff.	0.18	0.06-0.3	-	-	-
Tests 1 and 2	*Unadjusted Repeatability*					
	Both sexes	0	0–0.15	0.5	0	0
	Males	0.14	<0.01–0.33	0.1	0	0.14
	Females	0	0–0.21	1	0	0
	Sex Diff.	0.1	-0.14–0.33		-	-
	Adjusted Repeatability					
	Both sexes	0.14	0.01–0.3	0.035	0.22	0.34
	Males	0.3	0.11–0.49	0.004	0.17	0.44
	Females	0	0–0.24	1	0.28	0.28
	Sex Diff.	0.25	0.01–0.49	-	-	-
Tests 1 and 3 Task Type: Problem-solving	*Unadjusted Repeatability*					
	Both sexes	0	0–0.16	1	0	0
	Males	0	0–0.21	1	0	0
	Females	0	0–0.22	1	0	0
	Sex Diff.	<-0.01	-0.18–0.17		-	-
	Adjusted Repeatability					
	Both sexes	0.02	0–0.19	0.41	0.43	0.45
	Males	0.01	0–0.24	0.45	0.43	0.44
	Females	0.04	0–0.3	0.38	0.43	0.46
	Sex Diff.	-0.03	-0.24–0.19	-	-	-
Tests 1 and 4	*Unadjusted Repeatability*					
	Both sexes	0	0–0.15	1	0	0

Tests 1 and 4	Males	0	0–0.21	1	0	0
	Females	0	0–0.22	1	0	0
	Sex Diff.	<-0.01	-0.18–0.18	-	-	-
	Adjusted Repeatability					
	Both sexes	0.07	0–0.22	0.17	0.27	0.32
	Males	0.22	0.03–0.43	0.023	0.29	0.49
	Females	0	0–0.19	0.5	0.26	0.26
	Sex Diff.	0.23	0.01–0.44	-	-	-

Test comparison	Sex group	R	95% C.I.	P-value	R_m^2	R_c^2
Tests 2 and 3	*Unadjusted Repeatability*					
	Both sexes	0	<0.01–0.16	1	0	0
	Males	0.1	<0.01–0.29	0.19	0	0.1
	Females	0	<0.01–0.2	1	0	0
	Sex Diff.	0.07	-0.16–0.29	-	-	-
	Adjusted Repeatability					
	Both sexes	0	<0.01–0.17	1	0.1	0.14
	Males	0.17	0–0.39	0.06	0.12	0.29
	Females	0	0–0.18	0.5	0.12	0.2
	Sex Diff.	0.16	-0.06–0.39	-	-	-
Tests 2 and 4 Task Type: Maze exploration	*Unadjusted Repeatability*					
	Both sexes	0.23	0.07–0.37	0.001	0	0.23
	Males	0.29	0.09–0.47	0.004	0	0.29
	Females	0.17	0–0.37	0.069	0	0.17
	Sex Diff.	0.11	-0.16–0.38	-	-	-
	Adjusted Repeatability					
	Both sexes	0.21	0.07–0.37	0.003	0.04	0.25
	Males	0.24	0.04–0.44	0.012	0.06	0.32
	Females	0.16	<0.01–0.39	0.083	0.04	0.19
	Sex Diff.	0.06	-0.23–0.36	-	-	-
Tests 3 and 4	*Unadjusted Repeatability*					
	Both sexes	0	0–0.15	1	0	0
	Males	0	0–0.21	1	0	0
	Females	0	0–0.21	1	0	0
	Sex Diff.	<-0.01	-0.18–0.18	-	-	-
	Adjusted Repeatability					
	Both sexes	0	<0.01–<0.01	1	0.08	0.1
	Males	0.06	0–0.29	0.28	0.08	0.22
	Females	0	<0.01–<0.01	0.5	0.09	0.13
	Sex Diff.	0.09	-0.07–0.24	-	-	-

Table 4.2. Sex comparisons of behaviour in the open-field, inhibitory control (from Test 1), and body mass. The reference group for sex is female. Shelter emergence latency and the time spent in front of the barrier were ln (1+x) transformed, which helped to reduce heterogeneity in the residuals. We used generalized least squares to analyse the number of lines crossed, body mass, and time shoaling to account for residual heterogeneity that was not resolved via log transformations.

Response	Predictor	Estimate	S. E.	t	df	P	Adjusted R^2
Lines crossed	Intercept	107.72	6.8	15.84	162	< 0.001	-
	Sex: Male	10.65	8.59	1.24		0.22	
Time in front of barrier	Intercept	2.19	0.2	11.06	181	< 0.001	< 0.01
	Sex: Male	-0.36	0.28	-1.3		0.19	
Open-field preference	Intercept	147.33	16.24	9.07	162	< 0.001	0.02
	Sex: Male	-48.80	23.11	-2.11		0.036	
Shelter emergence latency	Intercept	5.71	0.04	128.27	181	< 0.001	0.08
	Sex: Male	-0.26	0.06	-4.17		< 0.001	
Time shoaling	Intercept	222.91	10.79	20.65	181	< 0.001	-
	Sex: Male	50.06	12.46	4.02		< 0.001	
Body mass	Intercept	0.37	0.03	12.55	158	<0.001	-
	Sex: Male	-0.26	0.03	-8.76		<0.001	

9. Appendix 1: Supplemental material and Study 2

9. 1 Methods

We tested 30 adult fish (15 males, 15 females) across a battery of four behavioural tests, measuring similar hypothesized predictors under the same conditions as the main study. Activity-exploration (open-field) and shoaling preferences were measured consecutively on day one and risk-taking (shelter use) and maze exploration consecutively on day two, with tests repeated one week later and each test running for 10 minutes. We used fish from the "wild stock" population.

We modified the design of three behavioural tests from the main study (shelter use, shoaling preference, open-field). We detail here differences between the tests compared to those in the main study. In particular, we divided the open-field and shelter use into separate tests. The modified open-field test was a 38 L tank (50 x 25 x 30 cm, water depth 6 cm, Figure 4.1), but without the shelter or the shoal containers. The tank bottom had scattered gravel stones and a grid of 5 by 5 cm squares in order to note the location of the fish. The 6 cm water depth restricted vertical movement and encouraged horizontal exploration of the open-field. In the modified open-field test, individuals were placed into a transparent cylinder and released after a 30 second habituation period, after which we measured time spent in the inner (squares >1 square from the center) and outer areas (squares that touched the edges of the tank) of the open-field.

The modified shelter use test took place in a separate 38 L tank (50 x 25 x 30 cm, Figure S4.3) with a gravel slope gradually increasing from the bottom (length wise) up to 20 cm, similar to that used in other fish risk-taking assays Nakayama et al. (2012). This test was designed to simulate a potentially more natural experience where the shelter was not physically removed, thereby removing possible additional stress to the subject. Several plastic plants were placed as shelter at the deepest part of the tank. As before, fish began the trial placed within the sheltered area. We measured the shelter emergence latency, the total time spent within the shelter (including return trips), and the proportion of the remaining time spent outside the shelter after initial exit as measures of risk-taking.

We also modified the shoaling test to compare preference for a small (2 fish) versus a large shoal (5 fish) as shoaling propensities in Study 1 were highly skewed to the maximum possible time (median of 93% time spent shoaling), potentially comprising the use of this variable as a predictor. Following the open-field test, individuals were returned to the center of the tank within the transparent holding cylinder for a 30 second habituation period before releasing for observing shoaling behaviour. We measured time spent shoaling overall as well as the relative preference of fish for the large shoal (time spent with the large shoal – time spent with the small shoal).

We examined shoaling latency via exploration of a novel maze (Figure S4.4A) in which individuals had to swim between and then around several partitions to find a shoal reward for the first test. For the second week/test, we slightly modified the test by reversing the arrangement of the partitions such that individuals had to swim around and then between the partitions (Figure S4.4B). This design allowed a high degree of similarity between tests while allowing a slight novelty modification. We measured the latency to reach the shoal reward as before.

Due to video recording malfunction, we were unable to code the location in the open-field preference and thus excluded this measure from the analyses.

We analysed the data as in Study 1 and looked at the unadjusted and adjusted repeatability for our measure of the propensity to innovate (latency to reach the shoal) as well as our behavioural predictors, adjusting for the fixed effects of test and sex. Sex specific repeatability for the latency to reach the shoal was examined using linear mixed-models as in Study 1 and Pearson correlation tests (comparable to unadjusted repeatability estimates) due to the small sample size when splitting the dataset by sex. We also analysed the predictors solving latency and included sex by predictor interactions.

9.2 Results

9.2.1 Repeatability of behaviour in the open-field, shelter emergence, and shoaling tests

Repeatability estimates for the total time in shelter, and the proportion of time outside shelter after initial exit were non-significant (all $P > 0.1$, Table S4.2). However, we found significant unadjusted and adjusted repeatability estimates for lines crossed (Unadj. R: 0.42, $P = 0.01$; Adj. R: 0.42, $P = 0.01$, Table S4.2), time shoaling (Unadj. R: 0.46, $P = 0.005$; Adj. R: 0.45, $P = 0.006$, Table S4.2), large shoal preference (Unadj. R: 0.75, $P < 0.001$; Adj. R: 0.82, $P < 0.001$, Table S4.2), and shelter emergence latency (Unadj. R: 0.49, $P = 0.003$; Adj. R: 0.45, $P = 0.006$, Table S4.2), indicating these measures represent consistent individual differences and relatively high R values.

9.2.2 Predictors of shoaling latency

Fish that spent more time shoaling were faster to reach the shoal in the maze tests (time shoaling estimate: $P = 0.051$, Table S4.3), though this result was non-significant. No other predictors or sex by predictor interactions had a significant effect on the latency to reach the shoal (all $P > 0.1$, Table S4.3).

9.2.3 Sex differences in behaviour and mass

There were no significant differences in behaviour between the sexes (all $P > 0.1$, Table S4.4). Males were significantly smaller in mass than females (sex estimate: $P < 0.001$, Table S4.4).

9.3 Supplementary Figures

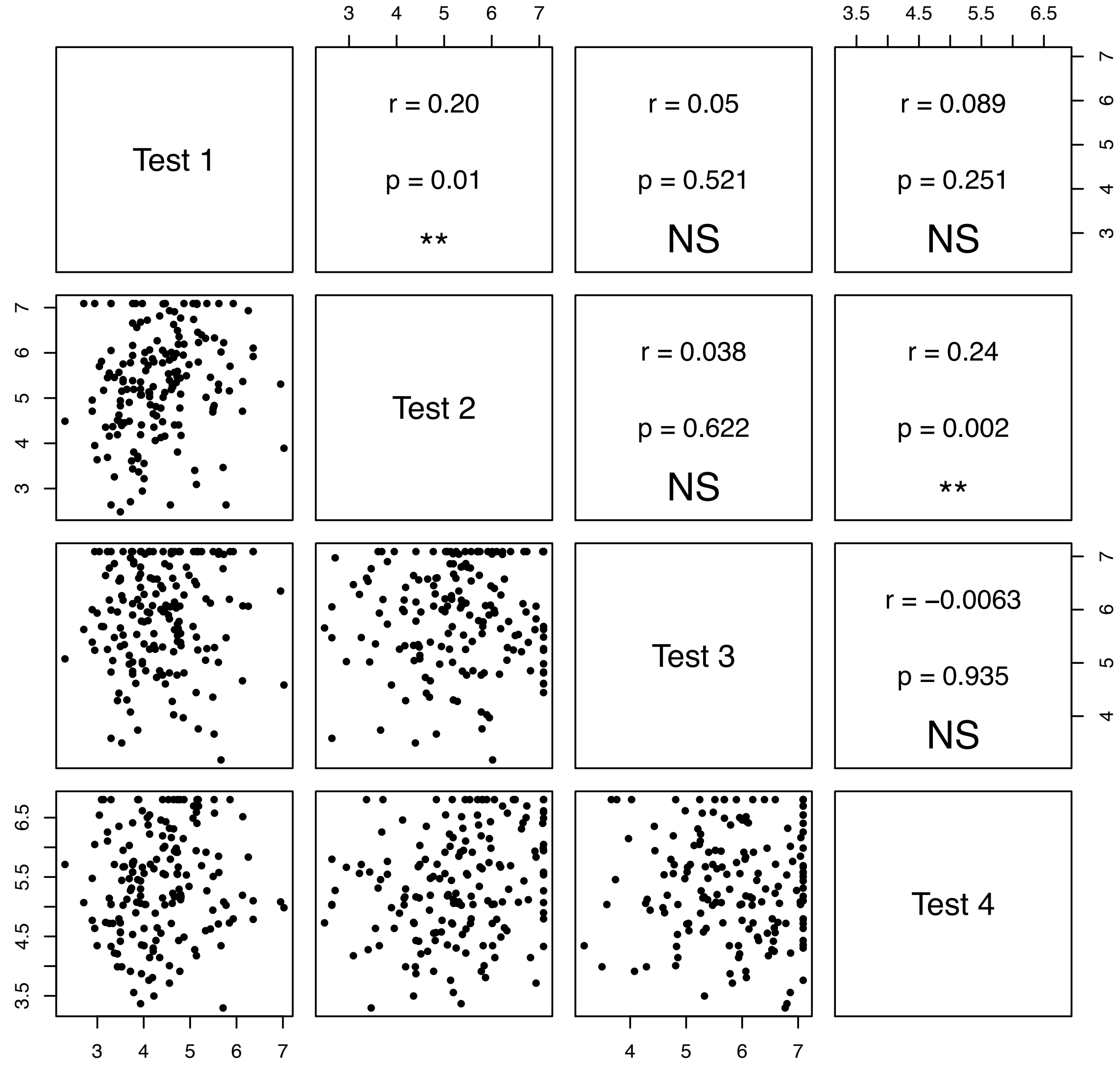

Figure S4.1. Pearson *r* correlation matrix of the log latency to reach the shoal in all pairwise test comparisons when analysing both sexes together. Symbols for significance are as follow: +: P ≤ 0.1; *: P ≤ 0.05; **: P ≤ 0.01; ***: P ≤ 0.001, NS = non-significant.

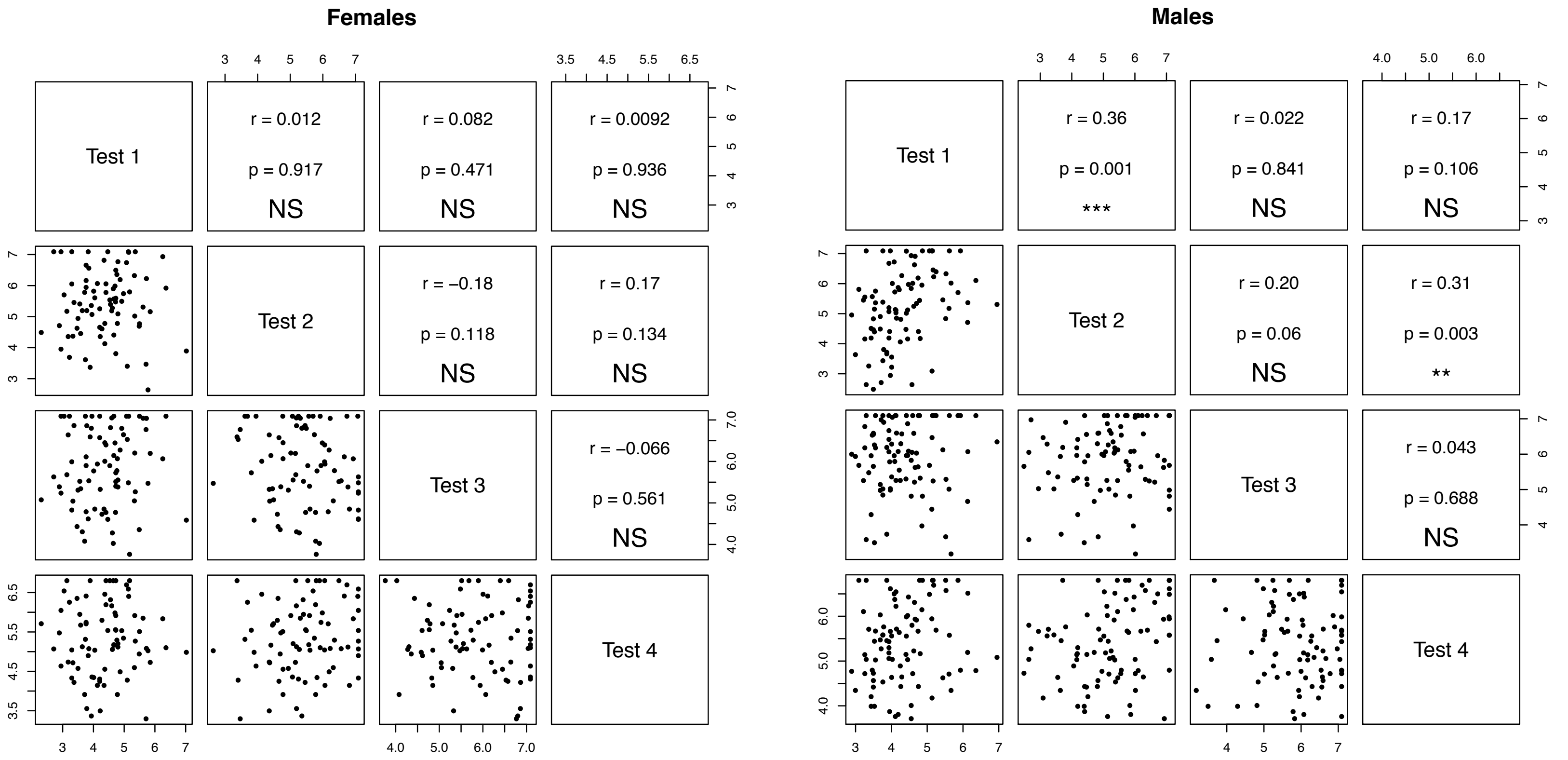

Figure S4.2. Pearson *r* correlation matrix of the log latency to reach the shoal in all pairwise test comparisons when analysing females and males separately. Symbols for significance are as follow: +: P ≤ 0.1; *: P ≤ 0.05; **: P ≤ 0.01; ***: P ≤ 0.001, NS = non-significant

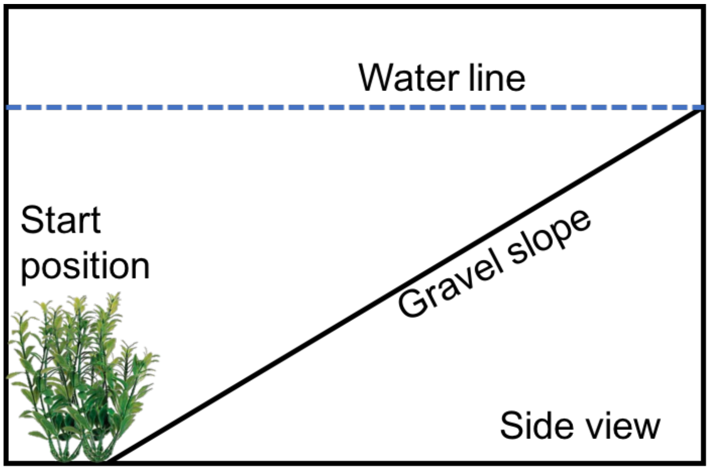

Figure S4.3. Shelter apparatus for testing risk-taking behaviour in Study 2. Plastic plants indicate the sheltered area. Image not to scale.

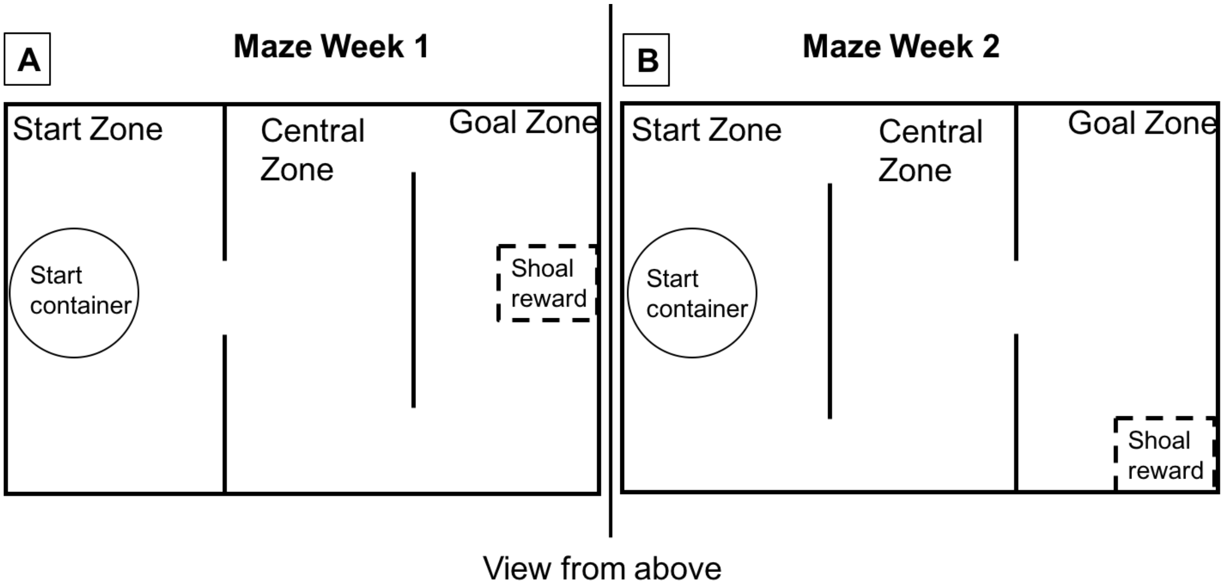

Figure S4.4. Maze apparatus configurations (A: week 1; B: week 2) used for testing innovation in Study 2. Thick opaque lines indicate opaque white partitions. Dotted lines indicate transparent perforated partitions. Thin lines indicate transparent partitions. Image not to scale.

9.4 Supplementary Tables

Table S4.1. Standardized (by one standard deviation and mean centered) estimates ± S.E. of the behavioural predictors and body mass on the natural log latency to reach the shoal from reduced linear mixed models containing all predictors for study 1. Intercept, innovation test, population, and generation estimates are not shown for brevity. Reference group for sex is female.

Test	Variable	Estimate	Std. Error	Lower 95% C.I.	Upper 95% C.I.	df	t value	P-value
Test 1	Lines crossed	-0.04	0.07	-0.18	0.11	121	-0.49	0.63
Test 2	Lines crossed	0.03	0.11	-0.18	0.24	121	0.29	0.77
Test 3	Lines crossed	0.27	0.09	0.1	0.44	122	3.17	0.002
Test 4	Lines crossed	-0.01	0.09	-0.18	0.16	121	-0.12	0.91
Test 1	Body mass	0.02	0.11	-0.19	0.23	123	0.18	0.85
Test 2	Body mass	-0.01	0.16	-0.33	0.3	122	-0.09	0.93
Test 3	Body mass	0.15	0.13	-0.11	0.41	122	1.13	0.26
Test 4	Body mass	-0.03	0.13	-0.29	0.22	122	-0.24	0.81
Test 1	Open-Field location preference	-0.11	0.08	-0.27	0.04	123	-1.41	0.16
Test 2	Open-Field location preference	0.02	0.11	-0.21	0.24	121	0.16	0.88
Test 3	Open-Field location preference	-0.24	0.12	-0.49	0	122	-1.99	0.049
Test 4	Open-Field location preference	-0.2	0.09	-0.38	-0.02	122	-2.14	0.034
Test 1	Sex: Male	-0.05	0.19	-0.43	0.32	124	-0.26	0.79
Test 2	Sex: Male	0.09	0.29	-0.47	0.65	122	0.3	0.76
Test 3	Sex: Male	0.25	0.23	-0.2	0.7	122	1.08	0.28
Test 4	Sex: Male	0.31	0.23	-0.14	0.75	123	1.35	0.18

Test 3	Sex: Male x Open-Field location preference	0.28	0.17	-0.05	0.61	122	1.69	0.094

Test	Variable	Estimate	Std. Error	Lower 95% C.I.	Upper 95% C.I.	df	t value	P-value
Test 2	Sex: Male x Total time shoaling	-0.54	0.26	-1.05	-0.04	120	-2.13	0.035
Test 1	Shelter exit latency	-0.03	0.08	-0.18	0.11	116	-0.46	0.65
Test 2	Shelter exit latency	0.16	0.11	-0.06	0.37	121	1.42	0.16
Test 3	Shelter exit latency	0.06	0.09	-0.12	0.23	122	0.62	0.54
Test 4	Shelter exit latency	0.16	0.09	-0.02	0.33	122	1.76	0.081
Test 2	Time swimming in front of barrier	0.03	0.11	-0.18	0.25	120	0.32	0.75
Test 3	Time swimming in front of barrier	-0.04	0.09	-0.21	0.14	122	-0.42	0.68
Test 4	Time swimming in front of barrier	0	0.09	-0.17	0.17	122	0	1
Test 1	Total time shoaling	0.05	0.07	-0.09	0.2	122	0.69	0.49
Test 2	Total time shoaling	0.12	0.13	-0.13	0.37	121	0.95	0.34
Test 3	Total time shoaling	-0.08	0.09	-0.26	0.09	122	-0.92	0.36
Test 4	Total time shoaling	-0.09	0.09	-0.26	0.08	122	-1	0.32

Table S4.2. The unadjusted and adjusted repeatability estimates of the behavioural measures when analysing both sexes together for Study 2. Adjusted repeatability models controlled for the effects of sex and week. P-values were obtained via likelihood ratio tests and confidence intervals were computed via 1000 bootstrap iterations. Marginal R^2 is the variance explained by the fixed effects and conditional R^2 is the variance explained by the fixed and random effects. Solving latency and the shelter emergence latency were natural log transformed and the proportion of time outside the shelter was modelled as a proportional count with a binomial distribution – all other behaviours followed Gaussian distributions.

	Behaviour						
	Solving latency	Lines crossed	Time shoaling	Large shoal preference	Shelter emergence latency	Total time in shelter	Proportion of time outside shelter
Unadjusted Repeatability							
R	0.06	0.42	0.46	0.75	0.49	0.02	<0.01
95% C.I.	0-0.41	0.07-0.68	0.13-0.7	0.52-0.87	0.19-0.71	0-0.36	0.0-0.07
P-value	0.42	0.01	0.005	<0.001	0.003	0.48	0.5
Marginal R^2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Conditional R^2	0.06	0.42	0.46	0.75	0.49	0.02	0.22
Adjusted Repeatability							
R	0.08	0.42	0.45	0.82	0.45	0.03	<0.01
95% C.I.	0-0.47	0.12-0.68	0.12-0.73	0.67-0.91	0.15-0.71	0-0.43	0-0.07
P-value	0.36	0.01	0.006	<0.001	0.006	0.48	0.5
Marginal R^2	0.04	0.01	0.03	0.07	0.07	0.03	< 0.01
Conditional R^2	0.12	0.42	0.46	0.83	0.49	0.06	0.22

Table S4.3. Standardized (by one standard deviation and mean centered) estimates ± S.E. of the behavioural predictors and body mass on the natural log solving latency from reduced linear mixed models containing all predictors for Study 2. Marginal $R^2 = 0.11$, Conditional $R^2 = 0.11$. Marginal R^2 is the variance explained by the fixed effects and conditional R^2 is the variance explained by the fixed and random effects. Reference group for sex is female, test 2 for innovation test.

Predictor	Estimate	S. E.	t	df	P
Intercept	5.22	0.31	16.84	53	< 0.001
Sex: Male	-0.08	0.25	-0.34	53	0.73
Body mass	0.0	0.12	-0.01	53	0.99
Lines crossed	-0.09	0.09	-1.01	53	0.32
Time shoaling	-0.18	0.09	-2	53	0.051
Shelter emergence latency	-0.01	0.1	-0.14	53	0.89
Innovation Test: 2	-0.24	0.18	-1.35	53	0.18

Table S4.4. Sex differences in behaviour and body mass in Study 2. The reference group for sex is female. Shelter emergence latency was natural log transformed. We used generalised least squares to analyse body mass to account for residual heterogeneity that was not resolved via log transformations. The proportion of time spent outside the shelter was modelled as a proportional count model with a binomial family distribution. Estimates and standard errors for this latter model are presented as odds ratios. All other variables were followed Gaussian distributions. We included a random effect for individual and a fixed effect for week for all variables except mass, which we measured once and thus modelled as a linear model only. Marginal R^2 (R_m^2) is the variance explained by the fixed effects and conditional R^2 (R_c^2) is the variance explained by the fixed and random effects.

Response	Predictor	Estimate	S. E.	t	df	P	R_m^2	R_c^2
Lines crossed	Intercept	264.48	41.26	6.41	49	< 0.001	0.01	0.42
	Sex: Male	-14.57	34.61	-0.42	28	0.68		
Shelter emergence latency	Intercept	3.09	0.54	5.69	49	< 0.001	0.07	0.49
	Sex: Male	-0.81	0.47	-1.72	28	0.096		
Total time in shelter	Intercept	341.16	51.02	6.69	49	< 0.001	0.03	0.06
	Sex: Male	-29.76	31.47	-0.95	28	0.35		
Proportion of time outside shelter	Intercept	0.76	1.16	-1.88	49	0.06	0.01	0.07
	Sex: Male	1.27	1.22	1.25	28	0.21		
Time shoaling	Intercept	209.48	76.27	2.75	49	0.008	0.03	0.46
	Sex: Male	64.88	65.46	0.99	28	0.33		
Large shoal preference	Intercept	284.36	87.99	3.23	49	0.002	0.07	0.83
	Sex: Male	112.82	103.39	1.09	28	0.28		
Body mass	Intercept	0.14	0.01	13.94	28	< 0.001	-	-
	Sex: Male	-0.06	0.01	-4.82	28	< 0.001		

Chapter 5: General Discussion

This thesis examined potential sources and predictors of intraspecific variation in behavioural innovation, measured via maze exploration and problem-solving tasks, in a small tropical freshwater fish, the Trinidadian guppy, *Poecilia reticulata*. I found that population origin (Chapter 2), sex (Chapters 3 and 4), and test type (Chapter 4) had a significant influence on intraspecific variation. I also examined the role of several behavioural, cognitive, and morphological predictors thought to characterize among-individual differences but found inconsistent findings, with some evidence suggesting that their relationship with the propensity to innovate was dependent on several factors, including population origin (Chapter 2), sex (Chapter 3 and 4), and the type of innovation task (Chapter 4). Last, I assessed the repeatability of the propensity to innovate between four different tests, finding that the propensity to innovate in guppies is repeatable, but that this repeatability depends on sex and task type (Chapter 4). Here, I synthesize the findings of my thesis, consider their relationship to the literature and their implications. I also provide suggestions for future work throughout and draw general conclusions from my results.

Measuring the propensity to innovate and assessing repeatability

Is the propensity to innovate repeatable in guppies?

In Chapter 4, I evaluated whether the propensity to innovate generalizes across task types and tasks, and whether these results differed between males and females. I found some support that performance was repeatable across three of the four tasks and two tasks types in males. In contrast, there was some support for repeatability within a task type in females, but only in the second study. The specific nature of these results raises important questions about how to interpret fish performance on the tasks in previous chapters (Chapters 2 and 3). Here, I discuss how these findings impact the interpretation of Chapter 2, which only studied females, and Chapter 3, which examined both females and males.

In Chapter 4, there was support for repeatability in Tests 2 and 4 for males, with tentative support for repeatability in females. Furthermore, females, but not males, displayed repeatable performance on highly similar task types in the second study. Tests 2 and 4 in the first study and the tests in the second study were a maze exploration task type, requiring individuals to navigate a novel structure without initial knowledge of the shoal reward. In contrast, in Tests 1 and 3, individuals were presented with problem-solving type tasks where they had visual knowledge of a shoal reward but had to inhibit direct responses to reach it. This specific comparison tentatively suggests that maze exploratory, but not necessarily goal-directed problem-solving, innovation is repeatable in male and female guppies and matches Laland and Reader's (1999) finding of repeatability in domestic guppies using similar maze exploration tasks, albeit with a food reward. In Chapters 2 and 3, both tests also involved the navigation and exploration of a novel structure, either a maze or a runway leading to different compartments, and without initial knowledge of the reward, e.g. a shoal or sheltered area. Thus, given the similarities in task types, it may be reasonable to assume such performance in Chapters 2 and 3 might follow similar findings of repeatability. However, additional testing involving a variety of maze exploration tasks would be needed to fully assess whether such performance in Chapters 2 and 3 is specific to task type and if it can be generalized beyond the particular task and study. It is unclear how factors such as differences in context details (e.g. the nature of the reward: exploration to find shoal reward versus exploration to escape from an aversive stimulus), population origin, responses to testing conditions, and potential sex specific biases in the former variables might influence performance. Controlling for and examining the influences of these variables may resolve the partial discrepancies in repeatability between studies 1 and 2 of Chapter 4 and help elucidate whether these repeatability estimates are specific to the tests themselves or can be generalized to maze exploration task types.

Is all innovative behaviour the same?

As seen in Chapter 4, repeatability varied, depending on sex and task type, with only partial evidence for the task type specific hypothesis between Tests 2 and 4, and no evidence of repeatability between Tests 1 and 3. This finding was hypothesized to be a result of greater dissimilarity between tests than expected, as partially evidenced by the lack of common predictors. However, these results raise general questions about whether all innovative behaviour is the same and explained by the same predictors. For instance, Tebbich et al. (2016) notes that the commonly used problem-solving paradigm may be limited in scope as tasks are goal-oriented and usually in an extractive foraging context, thus they may not be representative of all aspects of behavioural innovation, such as the propensity to express novel behaviours spontaneously in a non-goal oriented manner. However, many mammalian and avian studies focus on problem-solving type tasks and it is poorly understood how performance on these problem-solving tasks is indicative to that on more exploratory type tasks.

In Chapter 4, female repeatability was restricted to a maze exploration task type, which might be considered non-goal oriented as there was no visible reward, yet we did not find a common influence of activity-exploratory behaviours on task performance. This result potentially suggests that more exploratory innovation in females may differ from goal-directed problem-solving and that our hypothesized predictors of innovation do not have task type specific influences. However, our measure of activity-exploration in the open-field may have been affected by other behaviours also captured by this test (as discussed below), thus independent measures of activity and exploration as well as potential behavioural contributors such as neophilia, would be needed to fully evaluate the relationship between exploration and the propensity to innovate. While we suggested that navigating novel structures was in a socially motivated context and an exploratory innovation task type, it could be argued that such tasks involved some degree of non-goal-directed problem-solving as well. In our study, individuals were physically socially isolated in-between test days to serve as a degree of social motivation as guppies prefer to shoal with conspecifics, perhaps particularly in stressful conditions such as being moved to a new tank. Thus, navigating the novel structures might be seen as solving the problem of finding shoal mates. However, there was no evidence of a general effect of shoaling preference on performance in these two tasks, suggesting overall performance was not based on motivation to find a shoal. To formally examine non-goal directed exploratory innovation, future work might provide novel structures to guppies within their home tank after controlling for potential motivational confounds (e.g. Laland & Reader, 1999) and risk levels or to free ranging individuals within rivers, though field observations suggested a high degree of neophobia towards entering a free floating maze in the river (P.Q.S. personal observation), similar to field work in orangutans showing high rates of neophobia and low exploratory propensities towards novel objects (Forss, Schuppli, Haiden, Zweifel, & van Schaik, 2015).

While I distinguished non-goal directed exploratory innovation as a different type of innovation compared to the problem-solving paradigm, it remains an important consideration whether and how this behaviour is distinct from exploration. For instance, given that fish were unable to see the shoal from their starting position in the Chapter 2 task and the exploration tasks in Chapter 4, it could be argued that the exploratory innovation behaviour would be better described as simply ‘exploration’. That is, exploration could be methodologically inseparable from innovation in these tests. However, in Chapter 4 (tests 2 and 4), while the individuals could not see the shoal at the beginning of the trial, perforations in the partitions did allow the exchange of water, which might carry olfactory cues as to the presence of the shoal. Indeed, previous work suggests guppies can detect and prefer water containing the scent of conspecifics compared to water controls (Shohet and Watt 2003, Sato, Ozawa, & Karino, 2014). Thus, this criticism is potentially most applicable to Chapter 2’s maze as groups were unable to see or smell the presence of the shoal at the beginning of the trial and thus may have found the shoal by chance during exploration. However, if these two behaviours are the same, we might have expected to find strong and highly significant effects of exploration-activity on the propensity to innovate in Chapters 2 and 4, though as discussed below, the role of this behavioural predictor was variable and often non-existent. Still, another possibility is that the measure of exploration in the open-field test represents a different dimension of exploration than exploratory innovation, thus perhaps a more accurate measure of exploration as a predictor of innovation would be exploration within the innovation task itself, though this measure would suffer from within-test correlation biases. Notably however, conclusions on distinguishing these two non-goal directed exploratory innovation and exploration remain limited until further analyses can determine the causes of such swimming behaviour in these test contexts. One possibility may be to place individuals in novel mazes with and without the presence of a shoal, manipulating both visual and olfactory cues, to determine how this might influence behaviour in such mazes.

Still other categories might further differentiate innovative behaviour (Reader, Morand-Ferron, & Flynn, 2016), which may influence its repeatability. For instance, animal innovation is not limited to problem-solving and exploratory tasks but also encompasses foraging or ‘consumer’ innovation, i.e. the ingestion of novel food items, which does not always correlate with other measures of innovation (Sol, Griffin, & Bartomeus, 2012) or share the same relationships with neural substrates (Overington, Morand-Ferron, Boogert, & Lefebvre, 2009). Furthermore, innovations can result from a broad range of sources and processes (Reader et al., 2016), including modifications of previously exhibited behaviours as well as entirely novel behaviours, though teasing apart such distinctions is likely difficult (Reader & Laland, 2003b). van Schaik et al. (2016) also discuss at least six factors which might elicit innovation, including (III) accidental or chance innovations as well as those previously mentioned by Reader and Laland (2003b) and within this thesis. Notably, following the contexts proposed by van Schaik et al. (2016), problem-solving innovation could be further broken down into (IV) recognition of a clearly defined problem and reward, such as that in commonly deployed in goal-directed tasks, or could be (V) exploratory and driven by a need to solve a general problem of resource needs, such as finding shelter or food, among other categories such as a (II) failure of a pre-existing routine. The nature of the task such as foraging versus social tasks (Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013; Cole, Cram, & Quinn, 2011) or solitary versus group or cooperative innovation (Griffin, Lermite, Perea, & Guez, 2013; Morand-Ferron & Quinn, 2011; Seed, Clayton, & Emery, 2008) as well as the reward, may also influence performance, though variation attributed to alternative task rewards may simply reflect motivational differences due to differences in reward salience. Thus, innovative behaviour might be composed of a broad range of categories.

Clearly, there are many ways to categorize innovation and some evidence, including my findings from Chapter 4, to indicate that some of these categories may not necessarily be positively correlated among themselves or have the same relationships with other variables. Which categories to examine will likely depend on the question of interest and how measures in these categories relate to each other and to measures of fitness. Notably, the extractive foraging problem-solving paradigm has yielded numerous fruitful insights into innovative behaviour and examining how this paradigm relates to other contexts or categories of innovation may provide greater insight into why individuals vary and how such behaviour has evolved.

While examining a range of different categories is daunting, it can be logistically feasible (e.g. van Horik, Langley, Whiteside, Laker, & Madden, 2018), though some species will likely be better candidates due to their proclivity to rearing large numbers in captivity or field paradigms allowing automated large scale testing. Alternatively, lower sample sizes might be supplemented by greater numbers of trials or test variants, thus increasing the resolution around performance estimates. When the question of interest is of a general propensity to innovate, regardless of these categories, Lermite et al. (2017) provide an efficient way of examining this by using randomized but counter-balanced task assignments to individuals, though in this particular instance, tasks were all in a foraging context and problem-solving task type. This design might be easily modified to include tasks across a variety of contexts, task types, or other categories to obtain a context general measure of the propensity to innovate, though it may be useful to examine pairwise repeatability estimates between tests, as in Chapter 4, to ensure a lack of task specific biases.

Sources of intraspecific variation

The role of genetics and plasticity in shaping the propensity to innovate

In Chapter 2, I found that one population of guppies (Upper Aripo) was faster to navigate a maze and reach the shoal reward as compared to a second population from the same river (Lower Aripo). I hypothesized that these differences were due to population variation in predation driven competition and density, following the ‘necessity drives innovation’ hypothesis. This chapter raises questions about which ecological factors drive intraspecific variation and the relative influence of genetics versus plasticity. If the differences found between environments, such as between populations in Chapter 2, are due to necessity, this could correspond to genetic differences in innovative propensities but also to plastic differences if individuals from poorer environmental conditions are more motivated. Furthermore, environmental conditions and their impact might fluctuate from year to year (Quinn, Cole, Reed, & Morand-Ferron, 2016), thus assessing the repeatability of performance across significant time scales, such as between seasons, is needed to clarify the stability and context of these population differences.

While we were unable to evaluate the genetic and plastic basis of the population difference found in Chapter 2, work in guppies suggests that several population differences in behaviour can have both genetic and developmental influences (Jacquin et al., 2016; O’Steen, Cullum, & Bennett, 2002; Song, Boenke, & Rodd, 2011), thus follow up studies such as common garden and developmental experiments in varying rearing densities may help elucidate the roles of both genetics and environmental conditions in a competition context. Experiments manipulating densities and/or body condition would also help to shed light on the plasticity of the propensity to innovate as well as well as confirm the hypothesized causal role of necessity.

In Chapters 3 and 4, I used wild-derived laboratory populations of guppies, which also included wild caught F0 fish in Chapter 4. However, some research indicates that behaviour in the laboratory, including the propensity to innovate, may not always represent behaviour in the wild (Fisher, James, Rodriguez-Munoz, & Tregenza, 2015; Morand-Ferron, Cole, Rawles, & Quinn, 2011). The correspondence between the two conditions likely depends on several factors (Huntingford, 2004), including: whether the laboratory populations are domesticated strains (Benhaïm, Bégout, Lucas, & Chatain, 2013; Huntingford, 2004), the role of experience and genetics in producing the behaviour (Roth, LaDage, & Pravosudov, 2010; von Bayern, Heathcote, Rutz, & Kacelnik, 2009), the plasticity of the behaviour of interest, the nature and extent of selection (if any) in the laboratory, and the costs of maintaining a behaviour across laboratory generations (e.g. O'Steen et al., 2002). Thus, as our understanding of the influence of these factors on the propensity to innovate is limited, our results would need to be validated with field studies to confirm ecological relevance. Indeed, several authors have advocated the importance of studying behaviour in the wild (Morand-Ferron, Cole, & Quinn, 2015; Pritchard, Hurly, Tello-Ramos, & Healy, 2016) and in some species, such as passerine birds, radio-frequency identification (RFID) tagging technology coupled with automated foraging tasks can allow rapid assays of individual behaviour in a natural setting with large sample sizes (Cole, Morand-Ferron, Hinks, & Quinn, 2012; Croston et al., 2016). However, such technology is limited by size and weight constraints of the focal species and visual markers such as elastomer tagging for fish are not always reliable identifiers in field conditions for visual tracking. Furthermore, observations in Trinidad indicated that individuals were unwilling to enter a free-floating maze in the river, potentially suggesting that neophobia may inhibit measurements of innovation for some designs (Reader & Laland, 2003a), though some work indicates that individuals are willing to approach free floating feeders (Reader, Kendal, & Laland, 2003) which may present foraging task alternatives. Work in larger fish species, such as Atlantic cod (*Gadus* *morhua*), that can be identified with RFID or other tagging methods and are willing to approach and learn to feed from novel foraging apparatuses (Millot et al., 2014; Millot, Nilsson, Fosseidengen, Bégout, & Kristiansen, 2012) may provide additional opportunities for examining innovative fish behaviour in the wild.

Characterizing intraspecific variation

Are there general predictors of the propensity to innovate in guppies?

In Chapters 2-4 of this thesis, I measured several behavioural, physical, and cognitive predictors hypothesized to contribute to among-individual differences in the innovation process (Figure 5.1), though not all predictors were able to be measured for each chapter. Furthermore, our measures of cognitive processes such as learning (in the context of learning to navigate a maze) and inhibitory control appeared to be limited in the sense that we could not assess performance in some contexts. These difficulties restricted our ability to examine the relationship of these measures with the propensity to innovate as seen in Chapters 2 and 4 with the measures of learning. In general, the behavioural and physical predictors did not reliably predict individual propensities to innovate across the tasks as can be seen by the lack of consistent relationships for some predictors (Figure 5.1). These data tentatively suggest that these predictors may have task specific relationships with the propensity to innovate when such relationships are present. Furthermore, the lack of general as well as highly correlated predictors may indicate that our measure of innovation was not simply an artefact of behavioural propensities, such as exploratory propensities. However, several factors, including population origin, differences between tests in the task type, and the validity of the behavioural predictors may have influenced consistency in results, thus conclusions remain limited until these factors can be investigated.

Recently, Griffin and Guez (2016) proposed a key role for motor flexibility in the propensity to innovate. Motor flexibility is an index of motor diversity, adapted from the Shannon-Wiener species diversity index, that quantifies the number of different motor techniques used and frequencies in which each one occurs (Griffin & Diquelou, 2015). Griffin and Guez (2016)'s review notes the stark contrast of the consistent role of motor flexibility in predicting problem-solving performance compared to the mixed findings with cognitive measures. They also suggest that the influence of motor flexibility on the propensity to innovate is general across different contexts and presumably different task types, though this argument is largely within the framework of the avian literature which has focused on extractive foraging contexts and problem-solving task types. It is relatively unknown whether such behavioural variability also plays a role in non-foraging contexts and task types requiring exploratory behaviour to solve. In this thesis, the propensity to innovate was measured in a social context by the latency to reach a shoal reward by navigating a novel structure in both maze exploration and problem-solving task types, utilizing swimming motor behaviour. All tasks used did not require motor manipulation to solve, and it is unclear whether and how different swimming behaviours might be distinguished and measured independently of exploratory propensities. One possibility may be to use a multi-access maze structure requiring fish to swim through different maze configurations involving swimming around, under, and above to reach the reward (e.g. Laland & Reader, 1999), assuming such differences reflect distinct motor behaviours and after controlling for exploratory propensities. Alternatively, developing or modifying extractive foraging tasks from the avian literature for fish species more capable or known for motor manipulation, such as tool using wrasse (Dunn, 2015), may provide opportunities for examining the generality of these predictions to fish. Comparisons with mammalian species as well as species with less flexible motor manipulation capabilities, may help distinguish whether these results are specific to birds, due to their morphological capabilities, or represent a general role of motor flexibility.

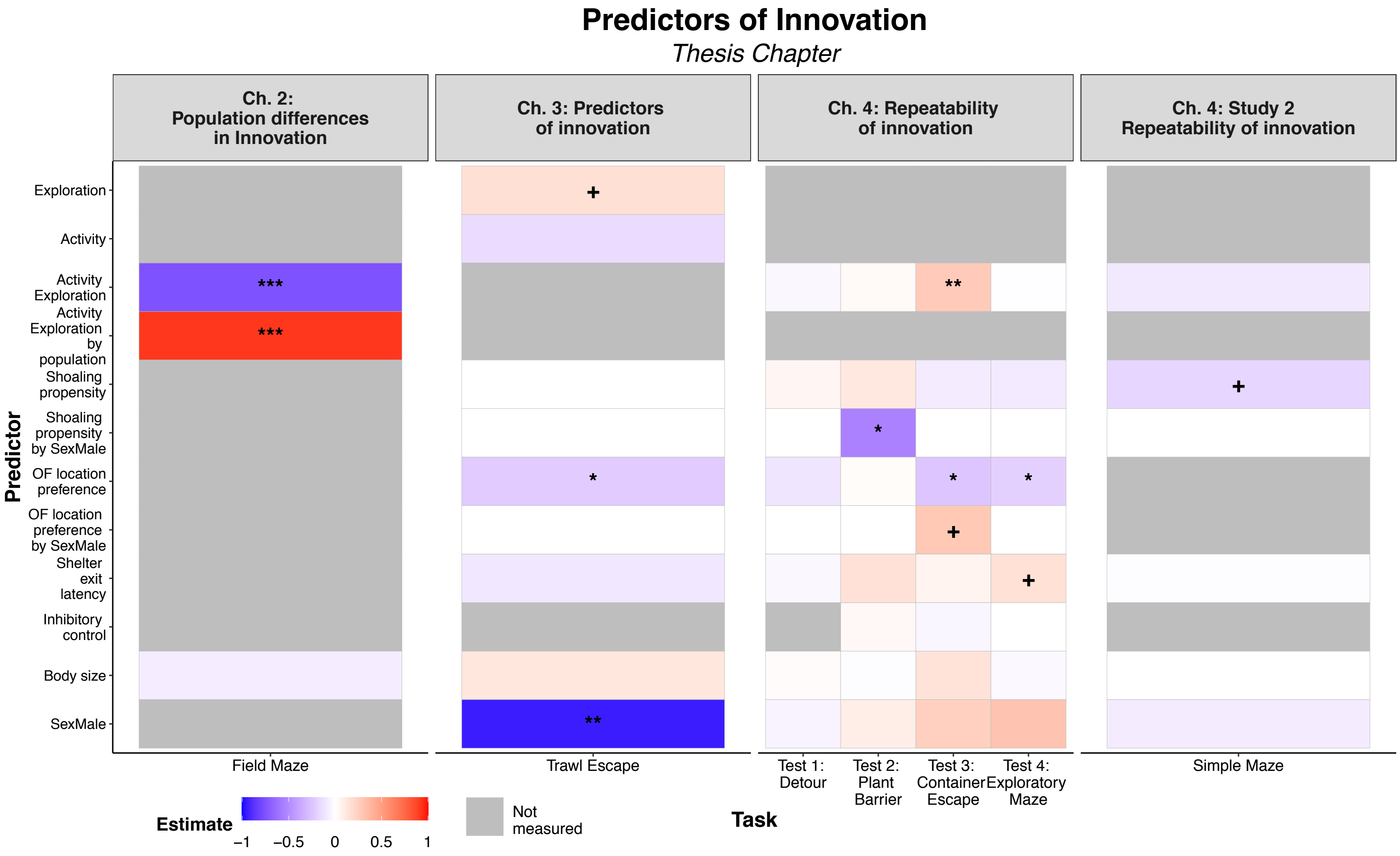

Figure 5.1 General relationships across chapters of the predictors of the latency to reach the reward for all tasks in this thesis. Estimated effect size and direction is given by colour gradient with blue indicating a negative influence on the latency to complete the task, red indicating a positive influence on the latency to complete the task, and white indicating no influence on the latency to complete the task. Grey indicates predictors not measured for that task. OF = open-field. Symbols for significance are as follows: +: P ≤ 0.1; *: P ≤ 0.05; **: P ≤ 0.01, ***: P ≤ 0.001.

Population influences on the predictors of the propensity to innovate

As seen in Chapter 2, populations can differ in which predictors influence the propensity to innovate, which has also been documented in other studies (e.g. Papp, Vincze, Preiszner, Liker, & Bókony, 2015; Prasher, Evans, Thompson, & Morand-Ferron, 2019). All studies in this thesis varied in their population origin and the second study in Chapter 4 contained an unknown mixed-population composition. Furthermore, while we accounted for variance attributed to population differences in Chapter 4's first study, we were unable to test for interactions between populations and predictors in addition to our main questions due to a limited sample size and the degree to which testing for these interactions would have overfit the model. Thus, future work might address possible population by predictor interactions by obtaining appropriate population specific sample sizes to examine the prevalence of such population differences in predictors. Alternatively, individuals from a single population could be examined across a variety of tasks to see whether predictor performance is general (e.g. Bókony et al., 2014; Ducatez, Audet, & Lefebvre, 2014).

Greater rates of the propensity to innovate in captive versus wild populations (e.g. Benson-Amram, Weldele, & Holekamp, 2013; Lehner, Burkart, & van Schaik, 2010) suggests that captive settings may induce higher performance in innovation tasks. This potential bias may also influence the relationships with predictors as individuals are 'forced' to interact with tasks in that they are put within close proximities of such tasks. Thus, innovative behaviour in captivity may have relatively weaker or different relationships with the hypothesized predictors than in the wild if captive settings are poor reflections of the wild (but see Benson-Amram et al., 2013). Indeed, one study found that individual performance on problem-solving tasks in captivity did not correspond to performance in the wild (Morand-Ferron et al., 2011), though such comparisons are generally lacking and would be valuable.

The validity of the measures of the behavioural predictors of innovation

While we chose tests and measures that have been frequently used in the fish and guppy literature for testing our behavioural predictors, it is possible that our measures were not relevant to guppy ecology in the context of our innovation tests or may have not been representative of the behaviours we were interested in measuring, though some of these behavioural measures have been linked to survival and fitness outcomes in fish, including guppies (Smith & Blumstein, 2010; Wilson, Brownscombe, Sullivan, Jain-Schlaepfer, & Cooke, 2015; Wilson, Godin, & Ward, 2010). For instance, we measured activity and exploration in an open-field context without any structures, objects, or plants. However, our tests often contained these components, thus if the open-field test provided a more limited measure of activity-exploration, it might explain the lack of general influence of activity-exploration on the propensity to innovate. The behavioural measures we used are often assumed to be reflective of behaviour across contexts and situations when studies find evidence of significant repeatability (i.e. 'personality') (Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih, Bell, Johnson, & Ziemba, 2004) yet this assumption is rarely assessed as many studies perform repeated testing with the exact same test, thereby measuring the reliability, but not necessarily validity, of the measure's relevance to a purported behaviour (Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013). In some of our innovation tests, we found that fish that spent more time in the outer area of the open-field (more risk averse) were faster to reach the shoal, but no evidence of a significant effect in the shelter exit latency (another commonly used metric of risk aversion in fish) (Figure 5.1). The lack of consistency in our measures of risk-taking suggest that they may be limited in context, measure different aspects of risk-taking behaviour, or may even be measuring different behavioural propensities. Our measures may also have been confounded by simultaneously measuring other behaviours, e.g. the 'jingle fallacy', whereby a single trait label captures different traits measured with different tests (Block, 1995; Carter et al., 2013; Gosling, 2001). In Chapters 2 and 4, we did not separate our measures of activity and exploratory behaviour in the open-field test and Chapter 3 found that exploration versus activity-exploration behaviours exhibited different, albeit non-significant relationships with the propensity to innovate. If activity and exploration have opposing relationships with the propensity to innovate, such a difference could result in a zero-sum relationship with innovation. Furthermore, the open-field test is also thought to measure stress related behaviour to some degree, though we sought to decrease this possibility by allowing individuals to enter freely or habituate to it in most cases. Thus, work is needed to determine the generality for which our measures reflect these behaviours across a variety of test contexts, including in the field, and how different measures of the same behaviour relate to each other, such as in Perals et al. (2017). Future studies might attempt to examine some of these behaviours in home environments (though it can be difficult to obtain individual measures with species housed in groups such as guppies), e.g. measuring activity in a home tank, to reduce additional influences of stressors, though such measures would have to be validated and compared to measures of activity in novel environments as well.

Cognitive predictors of the propensity to innovate

In general, measures of cognitive processes such as learning (Chapter 3) and inhibitory control (Chapter 4) did not appear to exhibit general relationships with the propensity to innovate, contrary to our expectations. Our results join the mixed evidence in the literature, with studies finding both positive (Boogert, Reader, Hoppitt, & Laland, 2008; Morand-Ferron, Hamblin, Cole, Aplin, & Quinn, 2015; Overington, Cauchard, Côté, & Lefebvre, 2011), negative (Ducatez et al., 2014; Griffin & Guez, 2016; Griffin, Guez, Lermite, & Patience, 2013), and non-existent relationships (Bókony et al., 2014; Huebner, Fichtel, & Kappeler, 2018) between innovation and different types of learning, as well as both positive (Chow, Lea, de Ibarra, & Robert, 2019; Thornton & Samson, 2012) and non-existent relationships with inhibitory control (Amici, Caicoya, Majolo, & Widdig, 2020; Johnson-Ulrich, Johnson-Ulrich, & Holekamp, 2018). The mixed nature of these findings match Griffin and Guez's (2016) predictions regarding the reliability of the relationship between cognitive measures and the propensity to innovate, where they suggest that this relationship is driven by environmental factors and is correlational, but not causal, when present. This idea may partially explain our mixed findings with cognitive measures as we used fish from different populations, including wild caught fish, and guppy populations have been well documented to differ in several environmental variables as well as exhibit significant differences in behaviour (Endler, 1995), including across generations (e.g. Jacquin et al., 2016). However, other factors, such as differences due to test design as seen in Chapter 4, would need to be ruled out before such conclusions are well supported.

Throughout my thesis, I examined the correlation between various cognitive measures and the propensity to innovate, hypothesizing that these measures influence performance; however, experimental manipulations, such as pharmacological injections, would be needed to confirm a causal role of such mechanisms (e.g. Roth & Krochmal, 2016). In cases where the relationship between the propensity to innovate and cognitive processes are the focus, future work might examine such cognitive measures and mechanisms in more detail, such as through batteries of different cognitive tests (e.g. Keagy, Savard, & Borgia, 2011; van Horik et al., 2018). However, as noted by some authors (Boogert, Madden, Morand-Ferron, & Thornton, 2018; Griffin, 2016), more work is also needed to determine the repeatability of such cognitive measures, e.g. learning slopes or task performance, as studies often employ a single measure of a particular cognitive trait and recent meta-analytic findings suggest that repeatability can be relatively low for these measures (mean adjusted R: 0.2-0.28: Cauchoix et al., 2018) as compared, for example, to the personality literature (mean adjusted R: 0.37) (Bell, Hankison, & Laskowski, 2009).

Sex differences in the propensity to innovate

In Chapters 3 and 4, I found mixed evidence for sex differences in the propensity to innovate, varying by study. As previously discussed, these studies varied in several factors which could have influenced the nature of these differences. However, another possibility is that males and females had pre-existing biases towards the design of the task, as might be seen when comparing the sex difference in Chapter 3 with the general direction of the (non-significant) sex bias across tasks in Chapter 4's first study (Figure 5.1). For instance, using artificially selected lines for larger and smaller brain size (relative to body size), Kotrschal et al. (2013) found that larger brained females outperformed smaller brained females on a numerical cognition task with a food reward, but there was no difference in performance between the two brain size lines on the same task in males. The authors hypothesized one reason for the lack of a difference in males may have been due to sex specific biases in task motivation and response to the design. A follow up study examined this possibility, finding that larger brained males were faster to learn the route to a female reward in a mate searching task than smaller brained males (Kotrschal, Corral-Lopez, Amcoff, & Kolm, 2015), supporting the idea that male and female task performance may be depend on the behaviour measured and test design. A meta-analysis examining guppy sex differences in three different reversal learning tests (colour, numerical, and spatial), found that overall, females performed better than males, but this difference appeared to be mainly driven by the colour task (Petrazzini, Bisazza, Agrillo, & Lucon-Xiccato, 2017). Furthermore, within test comparisons found no sex differences except in the colour task (Petrazzini et al., 2017), suggesting that these differences can be dependent on the task and behavioural context. Thus, differences in how males and females responded to the nature of the tasks and stimulus may explain the variation between male and female performance, both in sex differences in the latency to solve the task and in repeatability. Varying similar tasks with social versus foraging rewards might help elucidate how the nature of the reward can contribute to task performance.

Implications

Understanding the sources and characteristics of among-individual variation in the propensity to innovate has important implications for studying behavioural plasticity and responses to environmental change, as well as the roots of behavioural traditions. For instance, the propensity to innovate might be considered a mechanism of plasticity that generates novel behaviours. While some studies have indicated that the propensity to innovate can be negatively correlated with some measures of learning (e.g. reversal learning) (Ducatez et al., 2014; Griffin, Guez, et al., 2013), its relationship to other measures of behavioural plasticity is not well studied. If the propensity to innovate is part of a suite of traits in response to dealing with environmental change (Griffin, 2016), we might also expect it to positively correlate with other measures of functionally similar plasticity, though this relationship likely depends on how different measures of plasticity also contribute to responses to environmental changes. This research also has applied value as behavioural plasticity, including the propensity to innovate, is thought to be an important component of understanding how individuals respond to urbanization and anthropogenic habitat changes (Wong & Candolin, 2015), though the importance of these behaviours may depend on the stage of invasion and levels of colonization and gene flow (Griffin, Netto, & Peneaux, 2017).

Behavioural traditions are considered to be behaviours that are enduring within a group, shared among group members, and which are maintained in part by social influences (Fragaszy & Perry, 2003), such as some population specific foraging techniques (Krützen et al., 2005) or mating site selection (Warner, 1988). Behavioural innovations provide the initial starting material for such traditions in animals, and thus understanding how these behaviours are introduced to populations can provide key insights into how such traditions start, though notably, not all innovations may become stable traditions (Thornton & Malapert, 2009). Behavioural traditions can have significant influences on species and population ecology and may be important considerations in conservation and management plans (Brakes et al., 2019). For instance, choosing to conserve individuals with knowledge of key migratory routes that are socially learned or predator avoidance (Griffin, 2004) may be a significant consideration in some species (Brakes et al., 2019). Knowledge of which individuals innovate, why they innovate, and how these innovations spread to members of a population may also be a central aspect of managing urban populations. For example, social learning is thought to be an important component of the development of brown bear (*Ursus arctos*) foraging preferences, such as the exploitation of novel urban food resources (Hopkins III, 2013; Mazur & Seher, 2008). A study comparing the effects of rearing location in urban versus wild settings on cub foraging preferences found that out of 46 cubs that were reared in urban environments and conditioned to exploit urban foraging resources, 22 died before their second year, with 16 of these deaths attributed to association with their urban environments (Mazur & Seher, 2008). If such innovative urban feeding behaviour is driven by necessity, supplemental feeding programs or habitat restoration may provide ways to reduce the likelihood of nuisance innovations. Alternatively, if these innovations are driven by high exploratory propensities, selective culling or translocation to rural areas may help halt the spread of such problematic behaviours. Thus studying the sources and characteristics of among-individual variation in the propensity to innovate can provide both ecological and applied benefits. While this thesis does not directly examine such links, the studies presented here add to our understanding of individual variation in innovative behaviour and thus contribute important fundamental knowledge needed for examining such questions.

General conclusions

This thesis aimed to understand how ecological factors influence intraspecific variation in the propensity to innovate, describing the role of various physical, behavioural, and cognitive predictors in influencing the innovation process, and examining the generality of performance on different tasks. Several key findings for the study of innovative behaviour in animals emerge from my results. First, population origin represents an important contributor to intraspecific variation in the propensity to innovate and its predictors, though the roles of genetics and development in shaping these differences are not well understood. Second, there were no general predictors of the propensity to innovate across studies, but this conclusion is confounded with population and task differences between studies. Future work should first be conducted within a single population and across robust tasks to eliminate these confounds. While the behavioural predictors used in these tests need to be validated across different tasks, contexts, and measures, independent behavioural measures (e.g. activity and exploration measured separately) or measures specific to the task context (e.g. exploration in a novel maze) may provide clearer insights into general patterns of predictors. Third, sex differences can represent an important source of variation in performance on some innovation tasks and should be explicitly accounted for in analyses, though these differences are likely most prominent or present within species with a high degree of sexual dimorphism. Fourth, while there is some evidence for a general propensity to innovate, my findings indicate that the nature of the task design and context can strongly influence results, in conjunction with sex specific biases, thus understanding these influences will be crucial to generalizing the results of studies. Future analyses examining the repeatability of innovation should also consider splitting the data by factors known to influence among individual differences as I found that such factors can have a differential influence on the results. While fish are relatively understudied when examining innovative behaviour, they can provide a useful reference point to the avian and mammalian literature. Studying a variety of innovative behaviours in different taxa will be crucial in understanding the evolution and ecology of intraspecific variation and establishing the generality of findings.

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